

# Growth and Energy Expenditures of Eurasian Perch *Perca fluviatilis* (Linnaeus) in Different Temperatures and of Different Body Sizes

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## Abstract

To calculate the theoretical daily energy requirement of fish, information about the daily growth increment and the amount of digestible energy needed (DEN) to obtain one unit of biomass gain is required. The thermal unit growth coefficient (TGC) can be used for estimation of the daily growth increment. TGC is thought to be less affected by body size of the fish and temperature than the specific growth rate (SGR). However, there are some indications that the TGC may not be as stable as previous studies have shown. Furthermore, according to the theoretical background, DEN should increase as fish body size increases and with temperature. However, some data indicate that the DEN for percid fish may be unaffected by both these factors. The main objectives of this study was to estimate the effects of temperature and fish body weight on growth (TGC and SGR) and digestible energy need (DEN) of the Eurasian perch *Perca fluviatilis* (Linnaeus). In two separate laboratory experiments, feed intake, growth and energy expenditures were measured at either different temperatures (8.5-27.1°C) or for fish of different body sizes (20-110g). TGC and SGR proved to be affected by temperature and body size of the fish, while DEN was only affected by body size. The advantages with TGC for growth model construction thus seem to be less apparent than earlier believed. Thus, for evaluation of the theoretical daily energy requirement of fish, a growth model including both temperature and body size of fish, and an energy expenditure model including body size of fish is required.

**Keywords:** *Perca Fluviatilis*; Temperature; Body size; Growth rate; TGC; Energy expenditures; DEN

## Introduction

To calculate feed requirements of farm animals, approaches based on energetic principles are frequently used. For livestock, the extent of nutritional knowledge is much more developed compared to that of fish, and there is a long tradition to utilize this knowledge for calculation of the daily feed allowances of the animals [1,2]. The energy requirements of fish has traditionally been estimated by constructing complete energy budgets, balancing energy intake against energy expenditures such as faecal production, nitrogen excretion, metabolism and growth [3-6]. Despite improvements in methodology, this approach is often associated with several potential sources of error [4,5,7,8] and many of the developed energy budgets prove to deliver inaccurate results when tested [9-11].

Due to the problems with the classical bioenergetics approach, a more general method to calculate the theoretical daily energy requirement ( $\text{kJ}\cdot\text{day}^{-1}$ ) of fish was developed by Alanärä et al. [12]. The proposed model was based on two major components; one that estimates the daily growth increment (g) of the fish and one that calculates the amount of digestible energy needed (kJ) to obtain one unit of biomass gain (g) of the fish.

There are several ways to calculate the daily growth increment of fish. The most commonly used estimate of fish growth is the specific growth rate (SGR, [13]). However, as SGR is affected by both temperature [14-17] and body size of the fish [5,18-20] data collection for model construction is very time consuming and labour demanding. To reduce the problem with the effect of body size when expressing growth rate, Iwama & Tautz [21] developed another growth index, the daily growth coefficient (DGC). Instead of using the logarithm of the fish weight for calculating growth rate as SGR does, DGC uses a power function ( $W^{1/3}$ ). This mathematical adjustment of the growth coefficient provides a better fit to the actual growth pattern of the fish [20,21], and in accordance, DGC have been found to be more stable over a range of

body weights [22].

As a final developmental stage, temperature was added to the DGC equation, resulting in the formation of the thermal unit growth coefficient (TGC, [21]). Due to the mathematical structure of the TGC coefficient and with the inclusion of temperature in the calculation of growth rate, TGC is thought to be less affected by body size of the fish [22-24] and temperature [24-26] than SGR. In addition, the TGC coefficient has been shown to predict growth over time quite accurately [21,27]. However, there are some indications that the TGC may not be as stable as previous studies have shown [28,29]. Whether the TGC of Eurasian perch (from here on referred to as perch) is affected by temperature and fish body size has not earlier been thoroughly studied.

Data on digestible energy need (DEN) of the fish can be obtained by measuring the digestible energy intake of fish divided by the obtained growth. The advantage with the DEN model is that since the values for the different energy expenditures need not be quantified, estimates of the energy requirements can be made when the fish are being raised under normal culture conditions. As standard metabolic rate of fish increases with increasing temperature [5,30,31] so does the energy expenditures of the fish, and hence the DEN values. Moreover, as fish increases in size, a shift in fish body composition occurs, with increased deposition of fat in larger fish [4,5]. The energy value of fat is much higher compared to that of protein [3] and deposition of fat also leads to less deposition of water in the body compared to when proteins are

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deposited [5]. As a consequence, DEN should increase as fish body size increases. However, data presented by Bailey and Alanärä [32] indicate that the DEN value of percid fish may be unaffected by both these factors. The temperature and body size dependence of DEN for perch thus needs to be evaluated further.

The main purposes of this study were to estimate the effects of temperature and fish body weight on growth (TGC and SGR) and digestible energy need (DEN) of perch. We predicted that SGR and DEN but not TGC would be affected by temperature and body size of the fish.

## Material and Methods

### Fish and rearing

In autumn 2004, young-of-the-year perch were bought from a fish hatchery (located in Söderköping: 58°48'N; 16°34'E, Sweden) and transported to the university research facility in Umeå, Sweden (63°47'N; 20°17'E). The juveniles were hatched from eggs collected from wild spawners, and the fry were habituated to dry feed before they were delivered to the research facility. At the research facility, the juveniles were placed in square, grey, fibreglass indoor tanks (0.3 m<sup>3</sup>). The water used in the facility was tap water, which was aerated and heated to approximately 17°C in the tanks. The light regime was 12L:12D, with light switched on at 07.00 and off at 19.00. During on-growing, the fish were fed with increasingly larger pellet sizes (Dana Feed, Horsens, Denmark, DAN-EX 1051, 1 mm and 1.8 mm and DAN-EX 1344, 2 and 3 mm) delivered by automatic point source feeders set to deliver feed in excess.

### Experimental setup

Twelve dark green cylindrical plastic tanks (100 L) were used in the experimental setup. Inside each tank was a plastic cone connected to a hole in the tank bottom, creating a space (approximately 55 L) with tilting walls, thus enabling uneaten pellets to tumble down along the walls to the collection hole in the bottom of the tank. For more details regarding the experiment tanks please refer to Strand et al. [33]. An automatic point source feeder was placed above each tank. The feeders (manufactured by Storvik AS, Norway) were set to deliver

formulated feed (DAN-EX 1344, 2 or 3 mm, 13 % fat, 44 % protein, 25% carbohydrates, Dana feed, Horsens, Denmark,) in excess. The daily feed ration was divided into two meals, at 07.00-09.00 and 18.00-19.00. Feed waste and faeces were automatically evacuated from the tanks daily at pre-programmed time intervals. The number of pellets flushed out from each tank was counted daily. The light regime used was 16L:8D, with light (125 lux at surface) switched on at 06.00 and off at 22.00. Flow rates to the tanks were about four litres per minute. All tanks were separated by black plastic sheets.

The experiment regarding effect of temperature was performed during May to July 2005 when the fish were approximately one year. The optimal temperature for growth of perch is reported to be between 23°C [34,35] and 26°C [36], and the temperature preference is considered to be 18 to 27°C [36], although growth can occur as low as 14°C [37] to 11°C [34]. For this reason, the temperature range in the experiment was set to between 8 and 27°C. Five different temperature regimes (average temperatures ± SD) were used in the experiment; 8.5 ± 0.8°C, three tanks; 12.9 ± 0.4°C, three tanks; 18.2 ± 0.4°C, two tanks; 23.1 ± 0.5°C, two tanks; 27.1 ± 2.2°C, two tanks. The temperature of each tank was recorded continuously by temperature loggers. For tanks with high temperatures (18-27°C) the duration of the experiment was three weeks, and the experiment was repeated in three consecutive rounds (experimental round 1a, b and c). Three weeks has previously been demonstrated to be long enough to allow reliable recordings of growth of perch reared at 23°C [38]. However, as growth of the species in low temperatures (< 14°C) is very slow [34,37], a longer period was chosen for low temperatures in this study to provide time enough for measurable growth to occur. In tanks with low temperatures (8 and 13°C) the experiment was thus extended to four weeks and was repeated in two consecutive rounds (experimental round 2a and b). Experimental rounds for both high and low temperatures were run in parallel. By having different duration of the experimental rounds for high and low temperatures, respectively, identical numbers of replicates could be obtained for all temperatures while limiting the experiment to approximately two months. This was desirable in order to reduce season related variations in growth [39,40]. Groups of eight fish were used and initial average live weight (± SD) of the fish was 28.3 g (± 6.9). At the start and end of each experimental round, the feed (DAN-

Experimental round	Dates	Temperature category	Average temperature (°C)	Average W <sub>1</sub> (g) <sup>2</sup>	Average W <sub>2</sub> (g) <sup>3</sup>	Number of fish-group <sup>-1</sup>	Number of replicates	
							SGR, TGC, feed intake (% of BW <sup>1</sup> )	DEN
1a	May 12-June 2	18	18.0	33.0	37.0	8	2	2
		23	22.7	31.3	34.3	8	2	2
		27	26.9	33.6	23.3	8	2	0
1b	June 2- June 23	18	18.4	26.6	35.3	7	2	2
		23	23.1	24.6	33.8	8	2	2
		27	27.3	25.0	21.0	8	2	2
1c	June 23- July 14	18	18.3	31.4	37.2	8	2	2
		23	23.4	30.6	26.5	8	2	2
		27	27.0	33.7	19.4	8	1	0
2a	May 12-June 9	8	8.0	33.7	34.8	8	3	1
		13	12.8	32.3	28.6	8	3	1
2b	June 9-July 7	8	9.1	20.3	35.5	8	3	3
		13	13.0	19.8	31.5	8	3	3
Total numbers of replicates							29	22

<sup>1</sup>BW is the body weight of the fish

<sup>2</sup>W<sub>1</sub> is the initial weight of the fish

<sup>3</sup>W<sub>2</sub> is the final weight of the fish

**Table 1:** Summary of the experimental conditions for the study of effects of temperature on growth (SGR and TGC), feed intake (% of BW<sup>1</sup>) and energy requirement (DEN, kJ DE·g<sup>-1</sup>) of Eurasian perch (*Perca fluviatilis*).

(DAN-EX 1344, 2 mm, 13 % fat, 44 % protein, 25% carbohydrates, Dana feed, Horsens, Denmark,) in the feeders were weighed and the fish were tranquilized with 10 mg•L<sup>-1</sup> AQUACALM (MARINIL, Syndel Laboratories Ltd., Qualicum Beach, British Columbia) and their live weight and total length was recorded. After weighing, the fish were left alone in the experimental tanks for 24 hours to recover from the handling stress before feeding was initiated. For transfer of fish to the highest temperature, the temperature in the 27°C tanks was lowered to approximately 19°C when fish were introduced to the tanks and was then gradually increased to 27°C during the following 24 hours. New fish were used in each experimental round. The experimental data is summarized in Table 1.

After the temperature experiment, all fish (both fish used in the experiment and fish not used in the experiment) were divided into two tanks, one kept at approximately 17°C and one kept at approximately 12°C from July to January. This was done in order to increase the body size span among the fish of identical age in preparation for the body size study. In the end of January, the temperature was increased to 17°C in the previously cold water tank (12°C), and was then maintained at 17°C for three and a half months until the body size experiment was started. This was done in order to reduce the risk of growth compensation occurring for the fish previously held in 12°C when the experiment was started. During this period (July-May), rearing conditions were similar to before the temperature experiment.

The body size study was performed in the same system with the same light, management and feeding regime settings as the temperature study. The temperature in each tank was recorded continuously by temperature loggers and were on average (± SD) 21.1°C (± 0.6). The body size study was performed during May to June 2006 in two consecutive rounds of three weeks each, with fish at an age of approximately two years and between 20 and 110 g. To avoid crowding and to maintain an even rearing density, number of fish in each group was reduced as body

size of the fish increased. In size range 20 to 50 g six fish, in size range 50 to 80 g five fish, and in size range 80 to 110 g four fish were placed in each group. The entire size range (20-110 g) was represented in each experimental round by groups of fish with different average body size. Within each group, standard deviation (SD) of fish body live weight (g) was as most 2.8, but on average 1.6 g. Condition factors of the groups ranged between 0.84 and 1.04 but were in average (± SD) 0.96 (± 0.06). Average condition factors for each size category are displayed in Table 2. The same feed and weighing procedures for feed and fish was used as in the temperature experiment. New fish were used in each experimental round. The experimental data is summarized in Table 2.

### Calculations

The SGR [13] and TGC [21] were used to calculate growth rate. SGR is expressed mathematically as:

$$SGR = (\ln W_2 - \ln W_1) / \Delta t \cdot 100$$

TGC is expressed mathematically as:

$$TGC = (W_2^{1/3} - W_1^{1/3}) / (T \cdot \Delta t) \cdot 1000$$

where  $W_2$  is the group average weight at time t (g),  $W_1$  is the group average initial weight (g), T is the water temperature (°C) and  $\Delta t$  is the duration of the experiment (number of days).

In both experiments, feed intake was calculated as weight of the feed delivered to each tank minus the number of collected pellets from the same tank multiplied by the average weight of one pellet. The feed intake was then expressed as % feed intake of average fish body weight per day and per fish.

The digestible energy need (DEN: kJ DE•g<sup>-1</sup>) [12] describes the amount of digestible energy (kJ) the fish needs to ingest to increase 1 g in wet weight. The DEN is calculated as:

$$DEN = (FI \cdot DE) / (W_2 - W_1)$$

where FI is the average feed intake per fish during the experimental period (g) and DE is the digestible energy content of the feed (kJ•g<sup>-1</sup>). Energy values of macronutrients (23.7, 36.3 and 17.2 kJ•g<sup>-1</sup> for protein, fat and carbohydrates, respectively) were obtained from Brett & Groves (1979) [3] and apparent digestibility coefficients (ADC) used were obtained from industry standards and were 0.87, 0.90 and 0.65 for protein, fat and carbohydrates, respectively (pers. comm. M. Jobling). From this, the following values were obtained and then used to calculate the digestible energy content of the feed: 20.6, 32.7 and 11.2 kJ•g<sup>-1</sup> for protein, fat and carbohydrates, respectively.

Fulton's condition factor (K; [41]) of each group in the body size experiment was calculated as the average condition factor of all individuals in a group. The K is calculated as:

$$K = W_1 / L^3 \cdot 100\ 000$$

where  $L_1$  is the initial length of each fish (mm).

### Statistics

The statistical software used was SPSS 15.0 and Minitab 15.0 for Windows. For the temperature data, one group in temperature category 27°C died during the experiment and was thus excluded from the dataset. The resulting numbers of replicates for growth and feed intake data in 27°C were thus five. Moreover, despite a high feed intake, three of the groups in temperature category 27°C demonstrated negative growth rates. As accurate calculation of DEN from negative growth rates is not possible, energy requirement data for these replicates had to

Experimental round	Size category	Number of individuals	Average $W_1$	Average $W_2$	$K_1$	$K_2$
1	20-50	6	39.9	43.3	0.9	0.9
1	20-50	6	44.8	53.1	0.9	1.0
1	20-50	6	20.7	23.3	0.9	0.9
1	20-50	5	25.2	28.3	0.9	0.9
1	50-80	5	70.4	73.6	1.0	1.0
1	50-80	5	60.9	69.4	1.0	1.1
1	50-80	5	75.4	82.7	1.0	1.0
1	80-110	4	89.6	97.1	1.0	1.0
2	20-50	6	30.8	36.4	0.9	1.0
2	20-50	5	34.3	44.3	0.9	1.0
2	20-50	6	21.5	31.3	0.9	1.1
2	20-50	6	26.0	32.6	0.8	1.0
2	50-80	5	55.5	61.3	1.0	1.0
2	50-80	5	65.2	74.2	1.0	1.0
2	80-110	4	96.1	105.1	1.0	1.1
2	80-110	4	100.9	109.0	1.0	1.0
2	80-110	4	95.1	110.1	1.0	1.0
2	80-110	4	85.1	89.5	1.0	1.0
2	80-110	4	105.4	111.5	1.0	1.0
2	80-110	4	106.4	116.1	1.0	1.1

**Table 2:** Summary of the experimental conditions for the study of effects of fish body size on growth (SGR and TGC), feed intake (% of body weight) and energy requirement (DEN, kJ DE•g<sup>-1</sup>) of Eurasian perch (*Perca fluviatilis*).  $W_1$  and  $W_2$  represents the initial and final weight of the fish and  $K_1$  and  $K_2$  represents the average condition factor at the start and end of the experiment.

from the dataset. This resulted in only two replicates for the DEN data in the 27°C temperature category. Due to low feed intake and the resulting negative growth, two replicates from 8°C and two from 13°C also had to be excluded from the DEN data (Table 1). Feed intake had to be square root ( $X^{1/2}$ ) transformed to fulfil homogeneity assumptions of univariate general linear models (GLM). The observed variations in growth (SGR and TGC) and feed intake were tested statistically using GLM (type III: unbalanced ANOVA), with temperature category (8, 13, 18, 23 and 27°C) as factor and tank number as nested factor. Tukey's test was used as post-hoc test. Despite transformation, DEN data did not fulfil homogeneity assumptions of univariate general linear models (GLM) and was therefore analyzed using robust ANOVA with Tamhane's T2 test as post-hoc test. Experimental round was not used as a covariate in the general temperature analysis due to the parallel experimental rounds of varying time length for low (8-13°C, experimental rounds 2a and b) and high (18-27°C, experimental rounds 1a, b and c) temperatures. The effect of experimental round was evaluated separately for high and low temperatures, respectively. For high temperatures only two replicates were available for temperature category 27°C for the DEN data. As both existing replicates came from experimental round 1b, temperature category 27°C was excluded from experimental round analysis for the DEN data. The DEN data was analyzed using robust ANOVA with experimental round (18 and 23°C: 1a, b and c) as factor. Furthermore, in the low temperatures only one replicate per temperature category existed in experimental round 2a thus no analysis was made regarding the effect of experimental round on DEN at low temperatures. The effect of experimental round on growth (SGR and TGC) and feed intake was evaluated using GLM (type III: unbalanced ANOVA) and with temperature category (high temperatures: 18, 23 and 27°C ; low temperatures: 8 and 13°C) and experimental round (high temperatures: 1a, b and c; low temperatures: 2a and b) as factors. Feed intake was transformed as in the previous analyses. Tank number was not used as a nested factor as it proved to be insignificant in the general analysis (Table 3). Tukey's test was used as post-hoc test.

For the body size data, four replicates (three from the largest size category and one from the middle size category) had to be excluded from the dataset due to technical problems with feeding, resulting in feed restriction of the fish during the experiment. The observed variations

in growth (SGR and TGC), feed intake and energy requirement (DEN) were tested statistically using univariate general linear models (GLM) with experimental round (1 and 2) as factor and average body weight (Ln transformed) as covariate. Condition factor (K) of the fish was also initially used as a covariate in the GLM analysis, but as it turned out to be insignificant for all variables it was excluded from further analysis. The effect of body size on condition factor (K) of the fish was, however, evaluated using linear regression analysis with average weight (Ln transformed) as factor. The effect of body weight on growth (SGR and TGC), feed intake and energy requirement (DEN) was then evaluated using linear models ( $Y = A + B \cdot X$ ) with average body weight (Ln transformed) as X.

## Results

### Temperature data

Growth rate (SGR and TGC) and feed intake (Table 3) and DEN (robust ANOVA,  $F_{4,17}=6.77$ ,  $P=0.002$ ) were significantly affected by temperature. Tank number did not affect the results significantly (Table 3). Growth (SGR and TGC) increased with temperature from 8 to 23°C, and was then reduced at 27°C. However, growth was only significantly higher in 18 and 23°C than in 8, 13 and 27°C, but did not differ between 18 and 23, or between 8, 13 and 27°C, respectively (Tukey post hoc test  $P<0.05$ ) (Figure 1). Feed intake followed a similar pattern but differences were significant between all temperature categories except for between 18 and 27°C (Tukey post hoc test  $P<0.05$ ) (Figure 1). DEN at 27°C was higher compared to all other temperature categories but did not differ between temperature categories 8-23°C (Tamhane's T2 post hoc test, Figure 1).

Moreover, at high temperatures (18-27°C), growth (SGR and TGC), feed intake (Table 3) and energy requirement (DEN) (robust ANOVA,  $F_{2,9}=23.60$ ,  $P<0.001$ ) were significantly affected by experimental round. Growth (TGC; Tukey post-hoc test,  $P=0.002$  but not SGR) and feed intake (Tukey post-hoc test,  $P=0.038$ ) were significantly higher, and energy requirement (DEN) (Tamhane's T2 post hoc test,  $P=0.025$ ) was significantly lower, in experimental round 1c compared to in round 1a. Furthermore, growth (SGR; Tukey post-hoc test,  $P=0.021$ , TGC; Tukey post-hoc test,  $P=0.004$ ) was higher and energy requirement (DEN) (Tamhane's T2 post hoc test,  $P=0.018$ ) was lower in round 1b

		df	SGR		TGC		Feed intake (% of BW <sup>1</sup> )	
			F	P	F	P	F	P
All temperature categories	Temperature category	4, 17	96.98	<0.001	35.57	0.001	102.93	<0.001
	Tank number	7, 17	0.23	0.972	0.37	0.906	0.80	0.601
High temperature categories	Temperature category	2, 8	14.82	0.002	73.86	<0.001	14.65	0.002
	Round	2, 8	5.92	0.026	11.43	0.005	4.59	0.047
	Temperature category* Round	4, 8	0.82	0.547	1.61	0.262	0.641	0.648
Low temperature categories	Temperature category	1, 8	1.84	0.212	0.52	0.492	13.09	0.007
	Round	1, 8	18.06	0.003	15.80	0.004	1.46	0.262
	Temperature category* Round	1, 8	0.26	0.623	1.85	0.211	<0.00	1.000

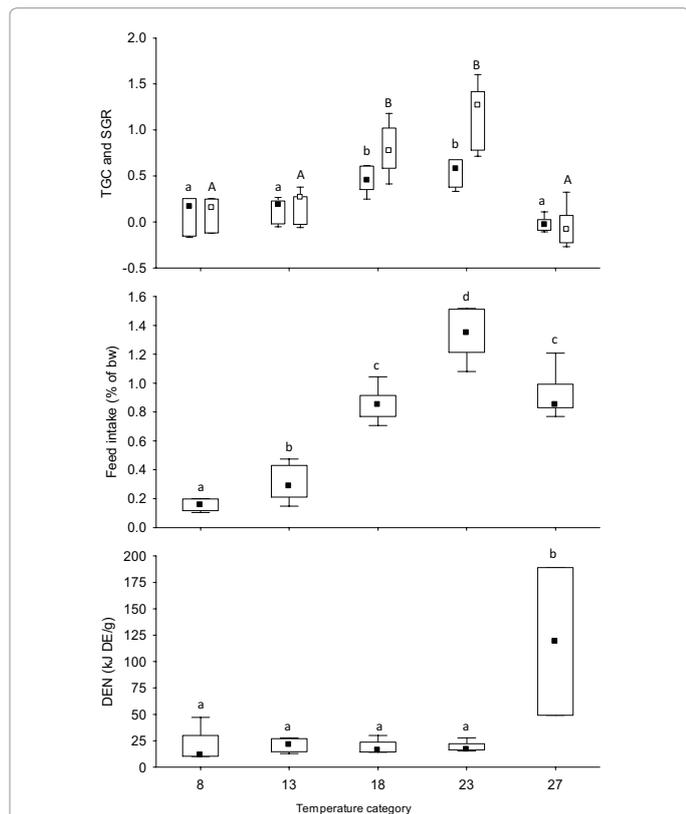
<sup>1</sup>BW is the body weight of the fish

**Table 3:** General linear model analyses (GLM, type III, unbalanced ANOVA) of the effect of temperature category (low=8 and 13°C, high=18, 23 and 27°C) and experimental round (1a, b and c for high temperatures and 2a and b for low temperatures) on growth (SGR and TGC) and feed intake (% of BW<sup>1</sup>) of Eurasian perch (*Perca fluviatilis*) from the temperature study. For the general analysis (only temperature categories), tank number was used as a nested factor. In the table are degrees of freedom (df) and F- and P- values for growth rates (SGR and TGC), feed intake and energy requirements (DEN) demonstrated.

compared to in round 1a. In the low temperatures (8-13°C), growth was also significantly higher (SGR and TGC) in round 2b than in round 2a while feed intake was unaffected by experimental round (Table 3).

### Body size data

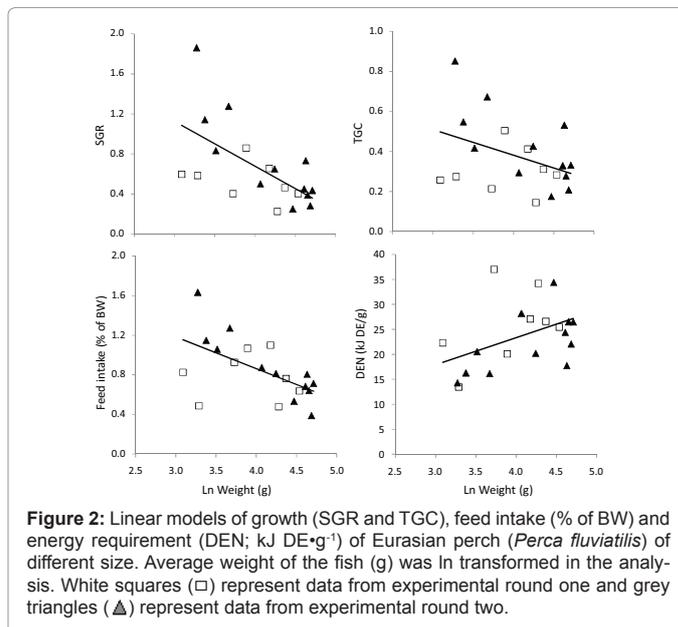
Growth (SGR and TGC), feed intake and energy requirement (DEN) were significantly affected by average body weight of the fish (Table 4). Growth (SGR and TGC) was also affected significantly by experimental round (Table 4), and increased from experimental round one to two.



**Figure 1:** Box-plots of growth rates (SGR and TGC), feed intake (% of BW) and energy requirement (DEN, kJ DE·g<sup>-1</sup>) of Eurasian perch (*Perca fluviatilis*) in different temperature categories (8, 13, 18, 23 and 27°C). Square symbols within boxes represent the median of the sample (white square symbols for SGR and black square symbols for TGC), boxes represent quartiles and the whiskers show non-outlier range. Identical lower and upper case letters indicates no significant differences (P>0.005) between temperature categories. For growth rates (SGR and TGC) and feed intake, number of replicates in temperature categories 8-23°C were six and in category 27°C five. For the energy requirement (DEN) data, numbers of replicates were four in temperature category 8 and 13°C, and six in categories 18 and 23°C.

	GLM			
	N	P (BW <sup>1</sup> )	P (Experimental round)	Model
SGR	20	0.001	0.041	SGR=2.49-0.45·lnW
TGC	20	0.015	0.040	TGC=0.97-0.15·lnW
Feed intake	20	0.005	0.136	FI=2.14-0.32·lnW
DEN	20	0.019	0.079	DEN=1.70+5.41·lnW

**Table 4:** General linear model analyses (GLM, type III, unbalanced ANOVA) and regression analysis of the effect of average body weight (BW) and experimental round (1 and 2) on growth (SGR and TGC), feed intake (% of BW) and energy requirement (DEN, kJ DE·g<sup>-1</sup>) of Eurasian perch (*Perca fluviatilis*) from the body size study. In the table is number of replicates, P- values and the resulting linear models for growth rates, feed intake and energy requirements demonstrated. W represents the weight of the fish.



**Figure 2:** Linear models of growth (SGR and TGC), feed intake (% of BW) and energy requirement (DEN; kJ DE·g<sup>-1</sup>) of Eurasian perch (*Perca fluviatilis*) of different size. Average weight of the fish (g) was ln transformed in the analysis. White squares (□) represent data from experimental round one and grey triangles (▲) represent data from experimental round two.

round two. Neither feed intake nor energy requirement were affected by experimental round. Development of the linear models revealed a decreasing growth rate (SGR and TGC) and feed intake and an increasing energy requirement (DEN) of fish with increasing body size (Figure 2). Furthermore, the condition factor (K) of the fish was significantly increased with increasing size of fish (linear regression analysis, F<sub>1,18</sub> = 35, 51, P<0.001).

### Discussion

Our prediction that TGC of perch is unaffected by temperature and body size was not fulfilled. In this study, TGC of perch was affected by temperature in a similar way as SGR, and thus follow the classical bell-shaped curve of increasing growth rate with increasing temperature to an intermediate temperature, after which the growth rate declines. The effect of reduced TGC for perch at low temperatures is in contrast with data on rainbow trout *Oncorhynchus mykiss* (Walbaum) for which TGC has been found to be unaffected by temperature within a range of temperatures below the optimal for growth [24-26]. There are indications that cold water adapted species may have evolved a compensatory response to the low temperatures of their environment, thereby maintaining a metabolic rate at low temperatures above the expected [3,42]. Thus, if feed is not restricted at low temperatures, cold water adapted species may have a higher growth potential than warm water adapted species due to the higher metabolic rate.

Furthermore, TGC has been reported to be unaffected by body size of fish [22-24]. Even though the size interval used in this study was quite limited, a clear negative relationship was found between body size of the fish and TGC. This is similar to the response of SGR with varying body size of fish [5,22]. The condition factor of the fish was found to increase significantly with increasing body size of the fish. Allometric growth with increasing condition factors with increasing body size is common in fish [43,44]. One assumption for use of the TGC coefficient is that the relationship between weight and length of the fish is constant, i.e. isometric growth occurs, thus TGC should only be used when the condition factor remains stable [28]. This may explain the size dependence of TGC found in this study. The temperature and body size dependence of TGC for perch causes the same problems in

data collection for growth model construction as does SGR. For perch, the TGC thus lose its advantage as a simple coefficient for practical use in aquaculture.

The digestible energy need of perch increased exponentially at temperatures above 23°C. Below 23°C, the relationship between temperature and DEN are in accordance with the data presented by Bailey and Alanärä [32] on percid fish species, i.e. no clear relationship. A positive relationship between temperature and energy expenditures should exist [5,30,31], but the effect of metabolic costs might be too small to detect without excessive replication. At 27°C, two groups of fish out of the five demonstrated very high DEN values and in the remaining three, energy expenditures were too high to allow positive net growth to occur. This supports the theory of an exponential increase in energy expenditures when temperature exceeds the normal range of growing temperatures [3,5,6,32]. Thus, 27°C seem to be close to the tolerance temperature for perch of this strain.

Our prediction that DEN of perch is affected by body size was, however, fulfilled. DEN of perch was found to increase significantly with increasing body size, which is in contrast with the data on percid fish presented by Bailey and Alanärä [32]. However, the percid data presented in that article is quite scattered and mainly focuses on sea bass *Dicentrarchus labrax* (Linnaeus) and sea bream *Sparus aurata* (Linnaeus). In accordance with the theoretical background provided earlier, perch seems to follow the same pattern of increased energy expenditures with increasing body size of fish as demonstrated for other species such as cod *Gadus morhua* (Linnaeus) [45,46], several different salmonid species and flatfish [32].

One question that must be addressed in connection with the method used to achieve different sized fish of the same age by growing them in different temperatures before the body size experiment is whether this treatment caused a compensatory growth of the fish kept in the low temperature. Most existing information on compensatory growth is connected to feed restriction of the fish, and knowledge about effects and duration of compensatory growth is quite scattered [47]. In this study, the fish kept in low temperature between the temperature and the body size experiments were never feed restricted. Growth compensation may, however, have occurred after the temperature was increased due to the previous temperature restriction. In earlier studies of compensatory growth after temperature manipulation in salmonid fish, growth compensation was complete in four [48], ten [49] and approximately 20 weeks [50]. In our study, the fish had 14 weeks to recover from the temperature restriction before the body size experiment started. This should have allowed for growth compensation to occur and to subside again. Growth rates of small fish during experimental round one was in fact lower than that of small fish in round two, indicating that growth compensation due to the restricted temperature between the experiments was not occurring at that stage. Furthermore, the condition factors of fish in experimental round one did not increase significantly from the start to the end of the round which also indicates that no compensatory growth occurred at that point.

In the present study, small groups of fish were used (four to eight individuals per group depending on study and treatment). Dominance hierarchies in small groups of fishes are often established through aggressive behaviour of dominant individuals towards subordinate individuals [51,52]. Aggressive behaviour in small groups of perch has been observed in a few cases [53] but often no aggression can be observed [54]. Whether aggressive behaviour leads to dominance hierarchies in perch is unclear.

When dominance hierarchies are established, feed intake of subordinate individuals is reduced and energy expenditures of both dominant and subordinate fish are increased due to aggressive acts and stress responses [52]. In a study performed by Strand et al. [38], fish held in small groups had significantly lower feed intake, but also higher feed efficiency (lower energy expenditures) than solitary individuals. This indicates that dominance hierarchies were not the reason for the lower feed intake of fish in small groups in the study performed by Strand et al. [38]. Furthermore, perch is a schooling species, finding security in numbers. Thus the results obtained by Strand et al. [38] and the social preferences of the species make the occurrence of dominance hierarchies in the groups used in this study unlikely. Groups of fish may also compete for limited resources. However, during the study, the fish were constantly over-fed, thus competition for feed should not have occurred.

Rearing densities may also affect performance of cultured fish. In this study, rearing densities were deliberately maintained low (2-5 kg · m<sup>-3</sup> in the temperature study and 3-8 kg · m<sup>-3</sup> in the size study) to avoid crowding and water quality deterioration. In the size experiment the size classes and the number of fish included in the groups in each size class were designed to produce an even rearing density of fish in the experimental tanks and to reduce the risk of crowding when large fish were used. Therefore the number of fish per tank had to be reduced as size of the fish increased. Furthermore, in the study performed by Strand et al. [38], fish held in groups of 4 and 12 individuals (2-6 kg · m<sup>-3</sup>) demonstrated high growth rates, thus the rearing densities used in this study was sufficient to provide adequate conditions for good growth of the fish.

In the temperature experiment, growth rates and feed intake increased, and energy requirement decreased, from the first experimental round to the final round. The same trend could be noted for growth of perch in the body size experiment. As both experiments were performed during late spring and early summer, the increase in feed intake and growth with time may be the result of a release of a winter suppression of appetite and growth. Similar seasonal increases in feed intake and growth at constant temperatures have previously been noted for perch [39,40]. Nevertheless, the main results regarding the effect of temperature and body size on the growth, feed intake, and energy requirements of juvenile perch are not affected by the differences between the rounds.

In conclusion, the prediction that TGC of perch would be unaffected by temperature and body size was not fulfilled. TGC proved to be significantly affected both by temperature and body size of the fish in a similar manner as is SGR. The advantages with TGC for growth model construction thus seem to be less apparent than earlier believed. In contrast, DEN was predicted to be affected by both temperature and body size of the fish, but was only found to be significantly affected by body size. DEN was not affected by temperature at or below optimal temperatures for growth, but as temperature increased further, energy expenditures seemed to increase exponentially.

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