

Influence of body weight, swimming characteristics, and water temperature on the cost of swimming in brook trout (*Salvelinus fontinalis*)

Ming Tang, Daniel Boisclair, Chantal Ménard, and John A. Downing

Abstract: We performed respirometry experiments to estimate the spontaneous swimming costs of brook trout (*Salvelinus fontinalis*) for 24 combinations of fish weight (3.5, 17, and 32 g), water temperature (4, 12, and 18°C), and respirometer size (27, 54, and 108 L). Fish swimming characteristics were estimated for each experiment using videocamera recordings and image analysis. Under our experimental conditions, average swimming characteristics of fish, such as swimming speed and turning and acceleration rates, varied from 2.5- to 29-fold. Our data, alone or combined with similar published results on brook trout weighing 1 g, indicated that fish weight was the only variable that could explain a statistically significant proportion of the variations of spontaneous swimming costs for that species ($r^2 = 0.91$). Our work confirms, with a wider range of experimental data, that spontaneous swimming costs of fish are 3- to 22-fold (8-fold average difference) more energy demanding than predicted by forced swimming models developed using fish swimming at constant speeds and directions in flumes.

Résumé : Nous avons réalisé des expériences respirométriques visant à estimer les coûts de la nage spontanée de l'omble de fontaine (*Salvelinus fontinalis*) pour 24 combinaisons de masse des poissons (3,5, 17 et 32 g), de température de l'eau (4, 12 et 18°C) et de taille de respiromètres (27, 54 et 108 L). Les caractéristiques de nage des poissons ont été estimées, pour chaque expérience, à l'aide d'enregistrements par vidéocaméras et d'analyses d'images. Sous nos conditions expérimentales, les caractéristiques de nage moyennes dont la vitesse de nage, les taux de virage et d'accélération ont varié par un facteur de 2,5 à 29. Nos données, seules ou combinées avec des résultats similaires publiés pour des ombles de fontaine de 1 g, ont indiqué que la masse des poissons est la seule variable qui peut expliquer une proportion statistiquement significative des coûts de la nage spontanée pour cette espèce ($r^2 = 0,91$). Nos travaux confirment, avec une gamme plus étendue de données expérimentales, que les coûts de la nage spontanée des poissons sont 3 à 22 fois (8 fois en moyenne) plus élevés que ceux prédits par les modèles de la nage forcée développés avec des poissons nageant à des vitesses et dans des directions constantes.

Introduction

Estimation of fish swimming costs is of key importance for many ecological studies. Models and variables that represent the energetic expenditures associated with movements performed by fish to feed, migrate, and escape predators are inherent components of optimal foraging, habitat quality, and bioenergetic models (Ware 1975; Kitchell et al. 1977; Hughes and Dill 1990). The importance of the cost of swimming in ecological studies is further illustrated by the number of approaches developed to estimate fish movements under field situations (radiotracking of fish position:

Holliday et al. 1974; estimation of the frequency of contractions of axial muscles or estimation of tail beat frequency: Ross et al. 1981; Weatherley et al. 1982; video observations: Ménard 1991; Boisclair 1992a). All approaches that attempt to transform fish movements into swimming costs require equations that describe the relationship between energy expenditures, fish attributes (fish weight, muscular or swimming activity), and environmental variables (water temperature). Consequently, the validity of these approaches and equations determines the quality of the predictions made by a wide range of ecological models.

Fish swimming costs have long been presumed to increase with swimming complexity (Beamish and Dickie 1967). Empirical models developed by Boisclair and Tang (1993) provided a quantitative framework for formalizing this expectation. These models showed that fish weight and average speed could explain a large fraction of swimming costs ($0.76 < R^2 < 0.80$). Furthermore, they suggested that, for specific combinations of fish weight and average speed, the cost of swimming for fish allowed to change their speed and direction (spontaneous swimming in a rectangular aquarium)

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may be 6–14 times more expensive than for fish forced to swim at a unidirectional and constant speed (forced swimming in a flume).

The magnitude of the difference between spontaneous and forced swimming costs has been attributed to the added cost of performing accelerations and turns (Webb 1991; Boisclair and Tang 1993). This led to the hypothesis that swimming characteristics other than speed could contribute to explaining the variation in spontaneous swimming costs (Krohn and Boisclair 1994). This hypothesis, however, could not be tested using the original data set gathered by Boisclair and Tang (1993) because swimming speed was the only swimming characteristic available. Experimental evidence combining respirometry data and detailed assessments of swimming characteristics of brook trout (*Salvelinus fontinalis*) confirmed predictions of the magnitude of the difference in the energetic cost between spontaneous and forced swimming (Krohn and Boisclair 1994; Tang and Boisclair 1995). These analyses also showed that variables such as the variance in speed and the average turning rate may explain a fraction of the variation in spontaneous swimming costs equivalent to, and sometimes larger than, average speed. However, these experiments focused on relatively small brook trout (1.2 g wet weight) with few experiments performed on brook trout of 5–10 g wet weight. Despite the expected influence of fish weight on metabolism (Brett and Glass 1973; Kitchell et al. 1977; Beamish 1978; Boisclair and Tang 1993), no data are currently available to assess the relative effect of fish weight and a complete suite of swimming characteristics on spontaneous swimming costs. Furthermore, no experimental data have been produced to test the predictions made by the model proposed by Boisclair and Tang (1993) for different fish size-classes.

The objectives of our study were to (i) evaluate the relative influence of fish weight, swimming characteristics, and water temperature on spontaneous swimming costs of brook trout and (ii) contribute to the development of a more powerful and general model that would allow the quantification of the cost of spontaneous movements for fishes with a carangiform or subcarangiform swimming mode.

Methods

Experimental design

The influence of water temperature, fish body mass, and swimming characteristics on the cost of spontaneous swimming was quantified by measuring oxygen consumption for fish of different sizes kept at three water temperatures and under conditions that induced them to display different swimming characteristics. This was achieved by performing 24 respirometry experiments with juvenile brook trout having a mean weight of 3.5 (SD = 0.4), 17.3 (SD = 6.1), and 32.2 (SD = 8.2) g wet at water temperatures of 4, 12, and 18°C using respirometers of 27 (30 × 30 × 30 cm), 54 (60 × 30 × 30 cm), and 108 L (120 × 30 × 30 cm). This approach was adopted because the volume available for swimming has a significant influence on fish swimming characteristics (Tang and Boisclair 1993; Krohn and Boisclair 1994). Each experiment was one combination of a water temperature and a respirometer size except for the largest fish, which were not tested in the 27-L respirometer because it severely restricted fish movements (longest dimension of the respirometer <1.5 fish body length). Fish swimming characteristics (speed, acceleration, and turning rates) were estimated using the

stereocinematographic method (Ménard 1991; Boisclair 1992a, 1992b). Young-of-the-year brook trout were selected as the subject of our work because individuals from a standard size and homogeneous inbred strain were easily obtained from a fish farm (Réserve La Petite Nation, Quebec). Furthermore, this permitted the combination of the results of the present study with those of similar experiments performed in our laboratory using brook trout averaging 1.2 (SD = 0.15) g (Tang and Boisclair 1995).

Experimental procedure

Estimation of spontaneous swimming costs

Fish were acclimatized to a given water temperature using a 500-L Living Stream™ aquarium (model LSW 700). During acclimation, water temperature was increased or decreased 1°C·day⁻¹ until it reached the desired level. Fish were maintained at that temperature for more than 14 days prior to an experiment. For experiments performed at 4°C, fish were fasted for 4 days prior to an experiment to avoid the confounding effects of digestive processes on respiration (Brett 1964; Brett and Groves 1979). The fasting period was set at 3 days for temperatures at 12°C and at 2 days at 18°C.

The respirometers consisted of Plexiglas boxes with lids. Three sides of the respirometers were covered with black tape to reduce outside disturbance and to improve fish observability. The respirometers were placed in a second LSW 700 to ensure precise control of water temperature during the experiments. Two water pumps were installed in the respirometers: pump A was used for mixing and maintaining a homogenous oxygen concentration within the respirometer during an experiment, and pump B allowed a connection between the inside and outside of the respirometers.

Four young-of-the-year brook trout were transferred from the acclimation tank to their respective respirometer 24 h before the onset of an experiment (hereafter referred to as the stabilization period). The number of fish used in our experiments was selected to ensure that significant respiration (considering the precision of our oxygen meter (Intab 565, ±0.005 ppm)) could be estimated for all fish sizes and water temperatures tested and for all volumes of aquaria employed. Because agonistic behaviour could unduly increase estimates of respiration rates, experiments were interrupted when persistent agonistic behaviour was observed. Following the introduction of fish into the respirometer, it was sealed without residual air bubbles. During the stabilization period, pump B generated a small exchange between the respirometer and the holding tank. This circulation of water maintained 75–80% oxygen saturation inside the respirometer. At the beginning of an experiment, pump B was connected to the oxymeter, thereby preventing new water from leaking into the respirometer from the holding tank. Initial oxygen concentration was measured using two steps. First, pump A was turned on for 1 min to homogenize oxygen concentration inside the respirometer. Second, pump B transferred water from the respirometer to the probe of the oxymeter and back to the respirometer. Water from the respirometer never contacted air during this process. Additional measurements of oxygen concentration were taken every 30–60 min using this same procedure. Pump A was not turned on between oxygen measurements in order to minimize fish disturbance.

An experiment was terminated when fish had consumed more than 0.5 ppm oxygen or after 12 h of observation. No observations were made below oxygen concentrations of 7.6 ppm. This limit was imposed to minimize the influence of low oxygen concentration on fish behaviour. Water temperature never varied by more than 0.5°C during an experiment. At the end of an experiment, fish were immediately removed from the respirometer and their weight (±0.005 g wet) and total length (±0.05 cm) measured individually. Biological oxygen demand (BOD) inside the respirometer filled

with water was determined within 24 h of each experiment using the same procedure as described above but without fish.

Estimation of swimming characteristics

Fish swimming characteristics were estimated from the temporal variation of fish positions in an x,y,z Cartesian coordinate system. This procedure required the filming and computer analysis of the movements executed by fish during each experiment.

Fish movements in the respirometers were filmed with a pair of videocameras (Panasonic WV-BL602) through a glass window (0.3×1.5 m) located on the side of the LSW 700. The cameras were oriented in parallel and separated by 10 cm. Images obtained by the two cameras were synchronized and combined side by side into a single image by a videoprocessor (Panasonic Quad WJ-450). Time of recording was printed by a time and date camera titler (Panasonic WJ-810) precise to ± 0.005 s. The final images were sent to a videocassette recorder (Sony EV-C3). Fish were filmed $10\text{--}50$ min \cdot h $^{-1}$ depending on the duration of the experiment (2.5–12 h). We recorded a total of 120 min of film per experiment. Photoperiod during our experiments ranged from 16 h light : 8 h dark to 14 h light : 10 h dark. Experiments were performed only during the lighted period of the day. During the lighted period of the day, two fluorescent lights located above the respirometers were turned on to homogenize lighting conditions and to improve the quality of the images.

Images recorded were analyzed using the Jandel Video Analysis Software (Java). Calibrations necessary to transform images filmed in fish x,y,z positions were performed using the method described by Boisclair (1992a, 1992b) and Krohn and Boisclair (1994). The position of a fish was quantified by four pairs of coordinates (the x and the y coordinates of the head and tail of the fish, respectively). For each experiment, we selected 50 sequences of 10 s of filming. These sequences were distributed at random over the complete duration of an experiment. For each sequence, individual fish inside the respirometer were classified as swimming or resting. The resting mode was assigned to fish moving less than 0.5 cm \cdot s $^{-1}$ for 3 consecutive seconds. The coordinates of one fish defined as swimming during a complete sequence was estimated at 1-s intervals during 10 successive seconds. This procedure allowed us to estimate 10 successive fish positions per sequence and 500 fish positions for each experiment.

Computations

Estimation of spontaneous swimming costs

Spontaneous metabolism (C_R , milligrams oxygen) of an average fish during a specific experiment was calculated as

$$(1) \quad C_R = (D[O_2] - \text{BOD}) \times V/4$$

where $D[O_2]$ is oxygen depletion (milligrams oxygen per litre) during an experiment, BOD is the biological oxygen demand of the water (milligrams oxygen per litre), V is the volume (litres) of the respirometer, and 4 is the number of fish inside the respirometer. Spontaneous swimming costs (C_S , milligrams oxygen per hour) were estimated as

$$(2) \quad C_S = (C_R - (\text{SMR} \times t))/(t \times P_t)$$

where SMR is the standard metabolic rate (milligrams oxygen per hour) of a fish, t is the duration (hours) of the experiment, and P_t is the proportion of time that fish spent swimming (see eq. 4). Because C_S corresponds to the respiration rate of fish excluding respiration associated with standard metabolism and digestion (fish were fasted), this value is presumed to represent only the cost of swimming (i.e., that of performing external movements).

SMR was determined with a model (eq. 3) that we developed using data from Job (1955) on standard metabolism of brook trout

($0.19\text{--}54.1$ mg $O_2\cdot$ h $^{-1}$) weighing 5–1000 g held at water temperatures ranging from 5 to 20°C:

$$(3) \quad \log_{10}\text{SMR} = 0.85\log_{10}W + 0.04T - 1.45$$

where W is the mass of the fish (grams wet weight) and T is the water temperature (degrees Celsius). In the experiments performed by Job (1955), the fish were sometimes fasted for as little as 12 h. This protocol may not be sufficient to eliminate oxygen consumption associated with digestion processes. Furthermore, SMRs were defined as the lowest rate of oxygen consumption of fish during any 2-h interval in a 24-h period. The setup used by Job (1955) (described by Fry and Hart 1948) allowed fish to swim freely. This situation implies that the SMR estimates produced by eq. 3 may represent maximum values (including unspecified costs of digestion and spontaneous activity) and consequently that our measures of activity costs should be interpreted as minimum values.

The P_t was estimated as

$$(4) \quad P_t = \left(\sum_{k=1}^k P_k \right) / (k \times 240)$$

where P_k is the total number of seconds that fish were in the swimming mode during 1 min sampled at random from within every 5 min of filming, k is the number of times that P_k was estimated during an experiment ($k = 120$ min of filming per experiment/5-min intervals = 24), and 240 is the maximum number of seconds that fish can be active per minute (4 fish per respirometer \times 60 s per minute). The time available for swimming is here defined as $k \times 240$ (5760 s). When more than one fish was in the swimming mode during a given second, the number of seconds added to P_k was equal to the number of fish swimming.

Swimming characteristics

Fish movements were described using three characteristics: speed, acceleration, and turning rates. Swimming characteristics were estimated from the displacements of a fish in an x,y,z coordinate system during a given time period (generally 1–2 s). A complete description of the geometric formulae used to estimate fish swimming characteristics from successive x,y,z positions of the tail and head of a fish was presented by Tang and Boisclair (1993).

Data analysis

Spontaneous swimming costs

Comparison of spontaneous swimming costs among experiments was performed using a permutation procedure consisting of four steps. (i) A total of 12 000 pseudo-values of spontaneous swimming costs were created for the 24 experiments (further referred to as nominal sets of pseudo-values). Each set of 500 pseudo-values was generated by adding 500 error values to the respiration rate estimated during a specific experiment. Error values were randomly chosen from a normal distribution having a mean of zero and a standard deviation of 0.007. The standard deviation was estimated using the instrumental error (0.005 mg $O_2\cdot$ L $^{-1}$) of the respirometer, the number of oxygen readings necessary to estimate fish respiration (four: two readings for total respiration and two readings for BOD), and the property that over 99% of observations from a normal distribution are within ± 3 SD of the mean ($0.005 \times 4/3 = 0.007$). (ii) Variations in respiration rates among the 24 sets of pseudo-values were tested using a parametric three-way analysis of variance (ANOVA). The F values were calculated for fish weight, water temperature, and aquarium size. The interaction terms were not tested because it was expected that they would greatly complicate our simulations and have no effect on our interpretation of the existence of significant variations in spontaneous swimming costs among experiments. (iii) An additional series of 49 three-way

Table 1. Experimental conditions, proportion of available time that fish were engaged in swimming activity (P_t), and average (subscript a) or variance in (subscript v) swimming characteristics among experiments.

Experiment	T (°C)	V (L)	W (g)	SSC (mg O ₂ ·h ⁻¹)	P_t (%)	S_a (cm·s ⁻¹)	S_v	A_v	TR _a (°·s ⁻¹)	TR _v
1	4	27	3.79	0.58	44.7	4.18	7.5	4.8	43.2	1715
2	4	54	4.25	0.71	66.3	5.64	12.0	13.1	37.0	1485
3	4	108	4.66	0.89	37.2	5.06	3.7	4.4	26.1	975
4	4	27	13.82	2.07	59.7	8.46	40.4	42.5	54.7	1968
5	4	54	14.26	1.80	29.5	3.79	5.7	4.4	30.6	1442
6	4	108	10.86	5.24	15.8	3.81	4.5	3.9	32.0	1982
7	4	54	34.83	9.12	41.4	8.77	34.6	35.9	48.5	2050
8	4	108	31.19	12.07	14.4	7.05	6.6	4.7	24.6	573
9	12	27	3.87	1.08	57.0	6.79	18.6	26.1	53.9	1949
10	12	54	3.08	1.17	42.7	5.61	17.0	17.1	43.5	1742
11	12	108	3.50	1.37	81.9	6.78	8.6	12.9	43.4	1447
12	12	27	11.20	2.73	40.3	5.22	10.2	7.9	48.7	1946
13	12	54	13.39	5.41	46.1	10.27	74.9	44.7	55.7	2475
14	12	108	13.27	3.74	49.9	13.48	84.0	86.2	54.3	2905
15	12	54	28.40	9.13	19.7	7.01	10.9	17.2	40.1	1628
16	12	108	31.77	20.29	13.7	7.08	18.6	15.1	37.6	2410
17	18	27	3.64	0.71	54.6	8.09	37.5	43.9	63.4	2656
18	18	54	3.70	0.78	89.3	8.88	15.8	19.3	58.6	1819
19	18	108	3.55	1.32	57.5	8.79	22.1	26.8	48.9	1967
20	18	27	14.09	1.65	68.7	7.40	20.1	27.0	60.1	2036
21	18	54	16.42	2.91	77.4	6.64	12.8	11.8	48.8	1860
22	18	108	16.19	2.37	78.6	8.25	21.3	17.4	45.9	2359
23	18	54	40.13	6.62	77.2	9.00	109.3	21.7	60.8	2879
24	18	108	41.56	12.06	68.2	12.81	102.9	87.1	53.3	2710

Note: T , water temperature; V , aquarium volume; W , mean fish weight; SSC, spontaneous swimming costs; S , swimming speed; A , acceleration; TR, turning rate.

ANOVAs were executed. Each ANOVA was done using 24 reconstructed sets of swimming costs pseudo-values (500 pseudo-values per set). Reconstruction was performed by redistributing 12 000 swimming costs pseudo-values at random into 24 groups. (iv) Among-experiment variations were declared significant when the F value of the ANOVA performed using the nominal swimming costs pseudo-values was greater than 95% of the 49 F values obtained using the reconstructed sets. Similarly, the statistical significance of the influence of fish weight, water temperature, and aquarium size was determined by comparing their F values obtained using the nominal swimming costs pseudo-values with the respective sets of 49 F values calculated using reconstructed sets.

Swimming characteristics

Among-experiment variations in swimming characteristics were tested using a permutation procedure similar to that used for spontaneous swimming costs but with two differences: first, we did not have to use pseudo-values to perform the tests (the sets of swimming characteristics estimated from fish coordinates were used directly) and, second, the nominal set of data for each experiment contained 190 swimming characteristics instead of 500 spontaneous swimming costs values. Homogeneity of the variance in the swimming characteristics among experiments was assessed using Bartlett's test performed following a permutation procedure (Sirois and Boisclair 1995). Variations in the proportion of time that fish spent in the swimming mode were assessed using a three-way ANOVA without replicates.

Models

The relationships (linear and logarithmic) between spontaneous swimming costs, water temperature, fish weight, and swimming characteristics were developed using stepwise multiple regression analysis. The average and the variance in each swimming charac-

teristic were used as independent variables to explain variations in spontaneous swimming costs (Sokal and Rohlf 1995). One exception to this rule was acceleration rates, since they are always expected to average zero.

Results

Spontaneous swimming costs

Spontaneous swimming costs ranged from 0.58 to 20.29 mg O₂·h⁻¹·fish⁻¹ (Table 1). Spontaneous swimming costs varied with fish weight ($p < 0.02$), water temperature ($p < 0.02$), and respirometer size ($p < 0.02$). The proportion of time used by fish for swimming ranged from 13.7 to 89.3% (Table 1) and varied with temperature ($p = 0.0028$) but was independent of fish weight ($p = 0.19$) and respirometer size ($p = 0.81$).

Swimming characteristics

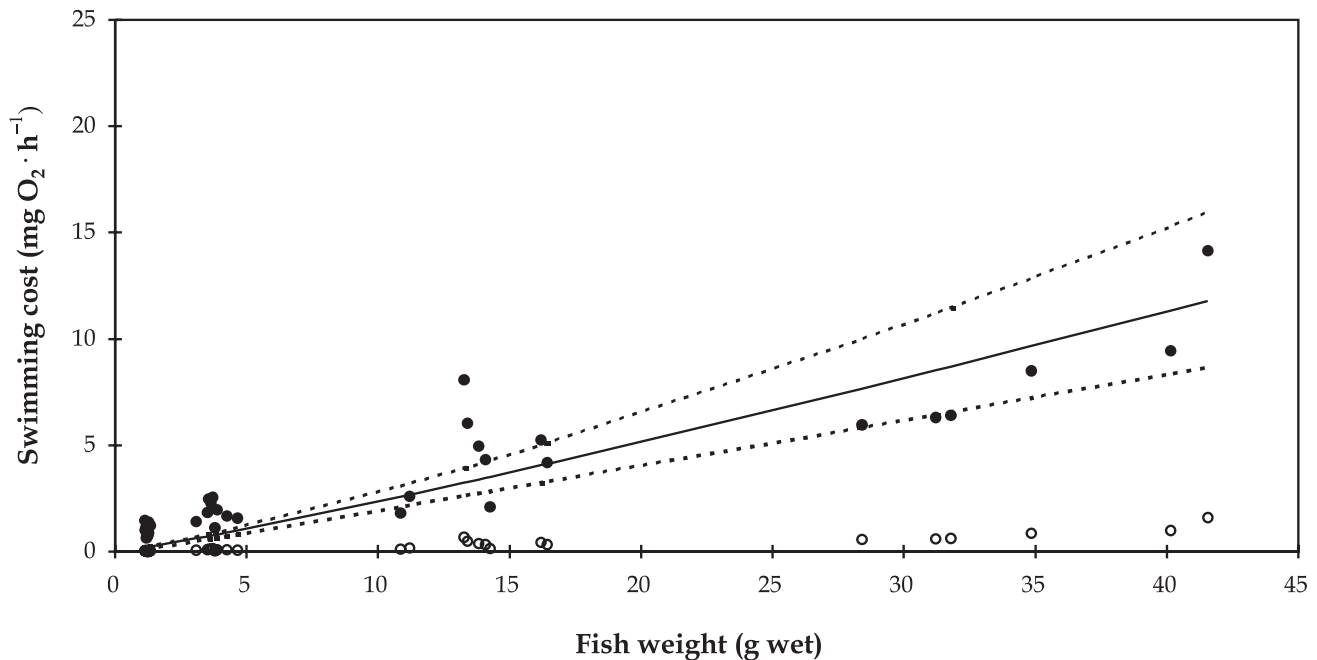
Average swimming speed ranged from 3.79 to 13.48 cm·s⁻¹ (Table 1). Fish swimming speed varied with fish weight ($p < 0.02$), water temperature ($p < 0.02$), and respirometer size ($p < 0.02$) and tended to increase with water temperature ($p < 0.01$).

Average turning rate ranged from 24.56 to 63.39°·s⁻¹ (Table 1) and tended to increase with water temperature ($p < 0.0002$) and decrease with respirometer size ($p < 0.0009$). Average turning rate was significantly influenced by fish weight ($p < 0.02$), water temperature ($p < 0.02$), and respirometer size ($p < 0.02$).

Table 2. Models to estimate spontaneous swimming costs (C , $\text{mg O}_2 \cdot \text{h}^{-1}$) of brook trout using fish weight (W , g wet) as an independent variable.

Model	r^2	p	n
Our study			
Allometric model: $\log_{10}C = 1.035\log_{10}W - 0.645$	0.81	<0.0001	24
Linear model			
$C = 0.319W - 0.453$	0.66	<0.0001	24
$C = 0.265W - 0.120$	0.79	<0.0001	23
Combination of our study and data from Tang and Boisclair (1995)			
Allometric model: $\log_{10}C = 1.131\log_{10}W - 0.759$	0.91	<0.0001	42

Fig. 1. Comparison between the predictions made by the allometric model that we developed (solid line; broken lines are 95% CI) by combining our data with those of Tang and Boisclair (1995) and predictions of spontaneous (solid circles) and forced swimming (open circles) using the models of Boisclair and Tang (1993).



The variances of speed (3.67–109.33), acceleration rates (3.88–87.06), and turning rates (573–2905) were significant among experiments ($356.48 < \chi^2 < 2022.09$, $p < 0.02$) (Table 1). The variance in speed tended to increase with fish weight ($p < 0.011$), and the variance in the turning rate tended to increase with water temperature ($p < 0.004$).

Models

Our experiments allowed us to develop relationships between spontaneous swimming costs and fish weight (Table 2). The slope of the allometric model that we obtained ($r^2 = 0.81$) was not significantly different from unity ($p > 0.05$), indicating the presence of a direct proportionality between spontaneous swimming costs and fish weight. Using a linear model, fish weight explained 66% of the variation in spontaneous swimming costs. No descriptor of fish swimming characteristics, alone or combined with fish weight, using an allometric or linear model, explained a significant fraction of variations in spontaneous swimming costs. Dixon's test performed using the residuals of our model indicated that experiment 16 represented an outlier ($p < 0.05$) (Sokal and Rohlf 1995). Exclusion of this experiment re-

sulted in a linear model in which fish weight explained 79% of variations in spontaneous swimming costs (Table 2).

Combination of the data from our 24 experiments with those of Tang and Boisclair (1995) (18 experiments) slightly increased the range of fish weight included in our analysis (from 3.1–41.6 to 1.2–41.6 g) but had no effect on the range of swimming characteristics that we used. The three experiments of Tang and Boisclair (1995) performed at 21°C were excluded from our analysis because such temperatures may negatively affect the behaviour of brook trout and complicate the interpretation of the respiration rates of these fish. The data set of 42 experiments confirmed the existence of a strong relationship between spontaneous swimming costs and fish weight (Table 2). The allometric model that we obtained suggested that fish weight explained 91% of the variation in spontaneous swimming costs (Table 2). The slope of this model (1.13, SD = 0.06) was statistically different from unity ($p < 0.05$).

Discussion

Our analyses indicate that, in certain models, fish weight

can explain 91% of the variation in spontaneous swimming costs. Neither water temperature nor fish swimming characteristics contributed to the models, a finding that contrasts with published studies on the cost of spontaneous swimming. For instance, the empirical analysis performed by Boisclair and Tang (1993) suggested that swimming speed could explain 60% of the variation in spontaneous swimming costs for three fish species. Similarly, Krohn and Boisclair (1994) and Tang and Boisclair (1995) reported that characteristics such as swimming speed and average turning rate could explain from 35 to 83% of the variance in spontaneous swimming costs of brook trout. The difference between the structure of the model that we found and that presented in published studies may be related to the range of the independent variables used to develop the models. However, the range of average swimming speed observed in our experiments ($3.8\text{--}13.5\text{ cm}\cdot\text{s}^{-1}$) is similar to that used in the empirical analysis of Boisclair and Tang (1993) ($0.4\text{--}8.3\text{ cm}\cdot\text{s}^{-1}$) and found by Tang and Boisclair (1993) ($6.4\text{--}11.1\text{ cm}\cdot\text{s}^{-1}$) in 1- to 27-m^3 enclosures. Furthermore, our range of speed is even larger than that observed by Krohn and Boisclair (1994) ($2.3\text{--}6.6\text{ cm}\cdot\text{s}^{-1}$) and Tang and Boisclair (1995) ($4.0\text{--}9.7\text{ cm}\cdot\text{s}^{-1}$). In fact, the ranges that we obtained for all swimming characteristics (turning rate, variance in turning rate, variance in speed, variance in acceleration) are larger than those in other studies on the spontaneous swimming costs of brook trout. One key element may be that our study also covers the widest relative range of fish weight published so far to model spontaneous swimming costs. In other studies, fish weight varied 1.2-fold (Tang and Boisclair 1995) to 12.5-fold (Boisclair and Tang 1993). In our study, fish weight varied 38-fold among experiments. With the exception of our own work, the only other study in which fish weight explained a significant fraction (16%) of spontaneous swimming costs was the empirical analysis of Boisclair and Tang (1993), and it is also the data set that contained, on a relative basis, the second most variable range of fish weight (8–100 g wet, 12.5-fold difference). This suggests that the structure of the model that we found is largely determined by the range of the variables that we used.

We compared the allometric model obtained combining our data with those Tang and Boisclair (1995) with the model proposed by Boisclair and Tang (1993). For that purpose, we used fish weight and mean swimming speed values (from this study and those of Tang and Boisclair 1995) as inputs to the model of Boisclair and Tang (1993) and compared the predictions of this model with the predictions of our allometric model (Fig. 1). Predictions produced by the model of Boisclair and Tang (1993) tended to parallel those of our allometric model. However, these predictions differed, on average, by 83.5% (1.6–152%). Two factors may contribute to explaining the numerical difference between these models. First, the empirical model of Boisclair and Tang (1993) for spontaneous swimming was developed for fish ranging from 8 to 100 g wet weight. Hence, some of the predictions described above have been made outside the range appropriate for using this model. Exclusion of predictions for fish weighing less than 8 g decreased the relative difference between both models to an average of 48.6%. Second, the model of Boisclair and Tang (1993) was developed using

results from three fish species other than brook trout. In addition, the protocols used to estimate swimming speed (using grids and different visual approaches) were very different for each study. It is currently difficult to assess if a single model can be appropriate for estimating the cost of spontaneous swimming for many fish species or for evaluating the effect of sampling protocols on the predictions made by the models.

Despite structural and numerical differences between the models cited above, our study confirms that the cost of spontaneous swimming, for given fish weight and swimming speed combinations, is larger than that of forced swimming. While forced swimming is defined as a movement in which fish speed and direction are constant (as swimming in a flume), fish in our experiments, as under most natural conditions, could accelerate and turn. The energetic implications of these differences can be quantified by comparing oxygen consumption predicted by our allometric model with predictions made by the forced swimming model developed by Boisclair and Tang (1993). The forced swimming model of Boisclair and Tang (1993) uses fish weight and swimming speed as independent variables and was developed for fish weight ranging from 1.8 to 100 g wet and swimming speed from 0.3 to $20\text{ cm}\cdot\text{s}^{-1}$. The comparison between our spontaneous model and the forced model of Boisclair and Tang (1993) was made using values of fish weight and speed obtained during our experiments. Spontaneous swimming costs predicted by our model were 3- to 22-fold larger than predictions made by the forced swimming model (average of 8.2-fold) (Fig. 1). Hence, our observations confirm, with a wider range of experimental data on spontaneous swimming (see Krohn and Boisclair 1994; Tang and Boisclair 1995), that use of forced swimming models may greatly underestimate the cost of swimming for fish that perform changes in speed and direction. This situation may have an equally strong effect on predictions made by many ecological models. Forced swimming models have been used to estimate the energetic value of a habitat for fish (expected energy acquired by fish under given environmental conditions: Feldmeth and Jenkins 1973; Braaten et al. 1997) and the behaviour that fish should adopt to maximize or optimize their energy gain (optimal swimming speed under a given set of environmental conditions: Ware 1975; Dabrowski et al. 1988). Forced swimming models have also been integrated into bioenergetic models and currently represent the standard approach that allows the use of values of fish swimming speed to assess the energy requirements of fish populations (Stewart et al. 1983; Hewett and Johnson 1992; Rand et al. 1993). Considering the magnitude of the difference that we observed between predictions made by forced and spontaneous swimming models, our work suggests that many ecological models that depend on estimates of swimming costs may underestimate total energy expenditures for fish that perform changes in speed and direction. This may result in an overestimation of optimal swimming speed values and in an underestimation of fish consumption rates predicted by bioenergetic models. By extension, an underestimation of fish swimming costs may also cause an overestimation by bioenergetic models of the carrying capacity of aquatic systems and of the fish stocking rate that may be sustainable in these systems.

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