The effect of turbulence on the cost of swimming for juvenile Atlantic salmon (*Salmo salar*)[1]

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Abstract: Fish activity costs are often estimated by transforming their swimming speed in energy expenditures with respirometry models developed while forcing fish to swim against a flow of constant velocity. Forced swimming models obtained using a procedure that minimizes flow heterogeneity may not represent the costs of swimming in rivers characterized by turbulence and by a wide range of instantaneous flow velocities. We assessed the swimming cost of juvenile Atlantic salmon (*Salmo salar*) in turbulent flows using two means (18 and 23 $cm \cdot s^{-1}$) and two standard deviations of flow velocity (5 and 8 $cm \cdot s^{-1}$). Twenty respirometry experiments were conducted at 15 °C with fish averaging 10 g. Our results confirmed that swimming costs are affected by the level of turbulence. For a given mean flow velocity, swimming costs increased 1.3- to 1.6-fold as turbulence increased. Forced swimming models underestimated actual swimming costs in turbulent flow by 1.9- to 4.2-fold. Spontaneous swimming models overestimated the real cost of swimming in turbulent flow by 2.8- to 6.6-fold. Our analyses suggest that models in which both the mean and the standard deviation of flow velocity are explicitly represented are needed to adequately estimate the costs of swimming against turbulent flows.

Résumé : Les coûts d'activité des poissons sont souvent estimés en transformant leur vitesse de nage en dépenses énergétiques avec des modèles respirométriques développés lorsque les poissons nagent contre un écoulement d'une vitesse constante. Cependant, les modèles de nage forcée obtenus en utilisant une procédure qui minimise l'hétérogénéité de l'écoulement peuvent ne pas représenter les coûts de nage dans des rivières caractérisées par une turbulence, et ainsi, par une grande étendue de vitesses instantanées de l'écoulement. Nous avons évalué le coût de la nage de juvéniles du saumon atlantique (*Salmo salar*) dans un écoulement turbulent en utilisant deux moyennes (18 et 23 $cm \cdot s^{-1}$) et deux écarts types de vitesse de l'écoulement (5 et 8 $cm \cdot s^{-1}$). Nous avons effectué 20 expériences respirométriques à une température de l'eau de 15 °C avec des poissons d'une masse moyenne de 10 g. Nos résultats ont confirmé que les coûts de la nage sont affectés par les niveaux de turbulence. Pour une vitesse moyenne donnée de l'écoulement, les coûts de la nage ont augmenté par un facteur de 1,3 à 1,6 alors que la turbulence augmente. Les modèles de la nage forcée ont sous-estimé les coûts effectifs de la nage en écoulement turbulent par un facteur de 1,9 à 4,2. Les modèles de la nage spontanée ont sur-estimé les coûts réels de la nage par un facteur de 2,8 à 6,6. Nos analyses suggèrent que des modèles dans lesquels la moyenne et l'écart type de la vitesse de l'écoulement sont représentés de façon explicite sont requis pour estimer les coûts de la nage contre un écoulement turbulent.

Introduction

Bioenergetic models can be applied to quantify fish habitat quality using the net energy gain obtained by a fish under specified environmental conditions (Hayes et al. 2000). In suitable habitats, fish have a positive balance between the energy acquired from their environment and that required for metabolic expenditures and physiological maintenance (Fausch 1984). Bioenergetic modeling involves the estimation of consumption, growth, metabolism, excretion, and egestion. Although activity metabolism is the least understood component of fish bioenergetic models, it has been argued to represent a large and variable proportion of fish energy budget (Boisclair and Leggett 1989; Boisclair and Sirois 1993; Rowan and Rasmussen 1996). Hence, inappropriate assumptions about activity metabolism may have a strong influence on the accuracy of the predictions of net energy gain and habitat quality values generated by bioenergetic models (Ney 1993; Boisclair 2001).

Fish activity metabolism may be estimated by quantifying fish behaviour and transforming the characteristics of fish behaviour (types and numbers of movements) in energy expenditures. This approach has been used to estimate the ac-

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tivity metabolism of fish in lakes (Lucas et al. 1991; Sirois and Boisclair 1995; Briggs and Post 1997). Estimation of activity metabolism for fish living in rivers represents a particular challenge because of the unknown metabolic consequences for fish of having to swim against a turbulent flow (Roy et al. 1999; Boisclair 2001). The cost of performing feeding motions from the riverbed towards the water surface to capture prey items drifting in the water flow is often estimated using forced swimming models (Puckett and Dill 1985; Sabo et al. 1996). These models are obtained using flume respirometers designed to minimize flow heterogeneity (Bainbridge 1958; Brett 1964; Beamish 1978). The experimental conditions used to develop forced swimming models resemble the conditions found in rivers because fish swim against a flow. However, these models focus on steady swimming and do not account for the costs of performing changes of speed and direction. Changes of speed and direction have been suggested to incur a 3- to 22-fold increase in fish respiration rates relative to predictions made by forced swimming models (Boisclair and Tang 1993; Tang et al. 2000). Spontaneous swimming models adequately account for the costs of performing accelerations and turns, but they have been developed and used with fish swimming in absence of flow (Trudel and Boisclair 1996; Aubin-Horth et al. 1999; Tang et al. 2000).

Turbulence is the state of a flow characterized by the superposition of intense small-scale motions in all directions on a main large-scale flow (Vogel 1994). Turbulence may be perceived as a partly random, partly structured, temporal variation of flow velocity at one point in space (Kirkbride 1993). Turbulence may also be perceived as the spatial heterogeneity of flow velocities at a given time (Bradshaw 1985). As such, the description of turbulence depends on the temporal and spatial scales at which it is observed. Turbulence and, in particular, its descriptor, turbulence intensity (standard deviation of the flow velocity divided by the mean flow velocity), may be expected to vary with the temporal scale (e.g., ms or min) used to measure flow velocity and standard deviation of flow velocity at one point in space. Similarly, because of the spatially heterogeneous nature of turbulent flow, turbulence intensity estimated at a small spatial scale (1 cm^3) may be different from that estimated at a larger spatial scale (1 dm^3).

The turbulence of the flow in rivers may be an important factor influencing the activity costs of fish in these environments (Fausch 1993; McLaughlin and Noakes 1998). However, turbulence is not taken into account by either forced or spontaneous swimming models. The objectives of this study were (*i*) to determine the effect of turbulence on fish swimming costs, (*ii*) to compare the cost of swimming in turbulent flow to the costs predicted by forced and spontaneous swimming models, and (*iii*) to propose a new model to estimate the energetic cost of swimming in a turbulent flow.

Material and methods

We attained our objectives by performing 20 respirometry experiments during which we subjected individual fish to four types of turbulent conditions (a combination of two means and two standard deviations of the flow velocity). We performed five experiments per flow condition at a water temperature of 15 °C. Fish respiration rates obtained under the different turbulent conditions were compared with predictions made by forced and spontaneous swimming models (Boisclair and Tang 1993). This strategy was adopted because our experimental setup was not designed to provide and does not allow laminar flow or flow without turbulence. As such, we preferred to use, as a reference for comparisons, the 40 years of data on forced and spontaneous swimming available in the literature and used by Boisclair and Tang (1993) to develop general forced and spontaneous swimming models.

Fish

Juvenile Atlantic salmon (age-1+ *Salmon salar*; JAS) were selected for our study because their natural habitat encompasses gravel-bed rivers characterized by highly turbulent flows. The behaviour of JAS comprises so-called “sit-and-wait” periods in which JAS swim just above the substrate, often at the downstream edge of a rock, used as a protection against the turbulent flow. The rock preferentially used by a territorial JAS is referred to as its “home-rock”. The sit-and-wait behaviour represents the largest part of the time budget of JAS (>80%; F. Burton and D. Boisclair, unpublished data). JAS also perform “attacks”, which are feeding motions from the riverbed towards the water surface, or in the water column, in which they capture drifting invertebrates (Kalleberg 1958). During these motions, JAS experience rapid changes in the structure of flow. JAS were also used for our work because the abundance of wild Atlantic salmon is decreasing (Bardonnet and Baglinière 2000). This situation is alarming, particularly considering that these fish supported extensive and valuable commercial and recreational fisheries. It is expected that an improved assessment of the costs of habitat utilization for JAS would contribute to the development of models and management strategies of riverine environments better adapted to protect this species.

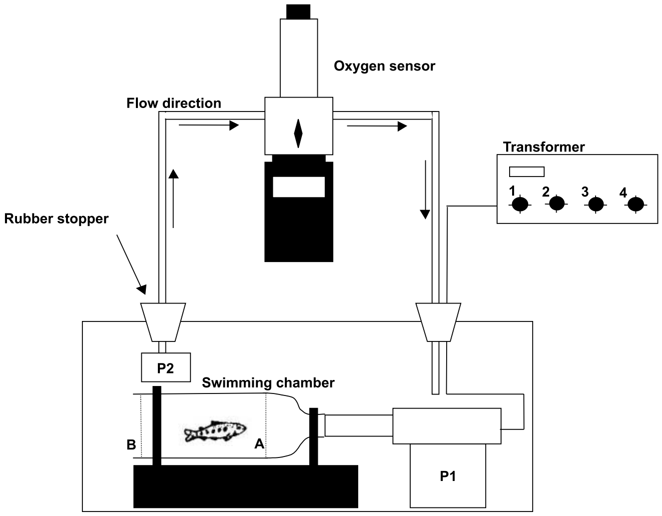
The Pisciculture de Tadoussac (operated by the Société de la Faune et des Parcs du Québec, Canada) provided the JAS used for our experiments. These were F_1 generation fish from the crossing of wild genitors that originated from the Sainte-Marguerite River (Saguenay Region, Québec, Canada). The juveniles were transferred to the Université de Montréal and kept in a 500-L Living Stream aquarium (model LSW 700; Frigid Units Inc., Toledo, Ohio) at 15 °C for a period of 1 month before beginning the experiments. This temperature was selected because it corresponded to the mean summer temperature of the Sainte-Marguerite River (Burton and Boisclair, unpublished data). The pH of the water was 7.8. Total hardness was 116 $mg \cdot L^{-1}$ $CaCO_3$, and water alkalinity was 83 $mg \cdot L^{-1}$ $CaCO_3$. The water was kept oxygen-saturated by airstones. Fish were fed daily with commercial food pellets (Corey Feed Mills Ltd., Fredericton, New Brunswick). The mean mass of the fish used for our respirometry experiments was 10.09 g wet (total number of fish used in our experiments (*N*) = 20, standard deviation (SD) = 0.33 g wet; mean total length (TL) = 10.8 cm, SD = 0.4 cm).

Experimental design

The respirometer consisted of a Plexiglas® box having a volume of 24 L (60 cm × 20 cm × 20 cm) with a lid that could be hermetically sealed. The respirometer was placed in a 500-L Living Stream aquarium to maintain a water temperature of 15 °C during the experiments. The respirometer contained two pumps and a bottle-shaped swimming chamber. The size of the respirometer was dictated by the size of the two pumps and that of the swimming chamber used. The pumps were inserted in the respirometer to insure that oxygen could not be introduced in the respirometer by the water flowing in the pumps. The size and the shape of the swimming chamber were selected to insure that fish could not avoid the flow and to minimize the influence of wall effects on our fish. Such wall effects may, at times, create vortices or more laminar flows near solid surfaces. Hence, flow structure closer to walls may be different from that in the center of a swimming chamber. Using a much smaller swimming chamber would have meant that fish would have been closer to the walls of the swimming chamber and more prone to wall effects difficult to describe or quantify. The narrow neck of the swimming chamber was connected to a pump (model 1750; Jacobs Canada Inc., Mississauga, Ont.) that generated the turbulent flow in the swimming chamber by recirculating water within the respirometer (Fig. 1). This pump is hereafter referred to as pump 1. Another pump (model 402; Powerhead, Montréal, Québec; hereafter referred to as pump 2) served two purposes. Before an experiment, pump 2 was used to create a water exchange between the respirometer and the aquarium and, hence, provide oxygenated water to the respirometer. During an experiment, pump 2 was used to transfer water from the respirometer to the oxygen meter. The swimming chamber contained two grids. The grids consisted of nylon mesh of 9 cm in diameter perforated with 2 mm × 2 mm holes. The grids were located in the "upstream" and "downstream" sections of the swimming chamber. The upstream grid was used to produce a spatially uniform, fine turbulence flow structure within the swimming chamber (Tritton 1988). The downstream grid was designed to force the fish to remain in the swimming chamber without interfering with the flow.

Turbulence in the swimming chamber was created by modulating the electric current that powered pump 1. Four components of the electric current were adjustable: (1) the maximal electric current that determines the maximal flow velocity, (2) the minimal electric current that determines the minimal flow velocity, (3) the frequency of pulsation between a reduction of the electric current to introduce a pulsation of the water flow, and (4) the duration of the reduction of the electric current to manipulate the duration of low- and high-speed flow conditions. Flow structures were quantified using an Acoustic Doppler Velocimeter (ADV; Sontek, San Diego, Calif.). The ADV allowed us to record the three orthogonal velocity vectors of the flow (streamwise, *U*; vertical, *V*; lateral, *W*) at a frequency of 25 Hz. The volume sampled by the ADV (0.25 cm^3) is located 5 cm away from its probe so that the perturbation of the measured flow by the probe is minimized. This volume (cylinder of 0.9 cm horizontally and a radius of 0.6 cm) was judged appropriate for our purposes because it resembled the product of the surface area of the cross section of the head and the length of the head of the fish used. The volume sampled by the ADV was therefore similar to the volume of the head of the fish used. The ADV permitted us to define the settings of the components of the electric current that could create four different flow conditions determined by two mean streamwise flow velocities $\bar{u}$ (low flow condition = 18 cm·s^{-1}; high flow condition = 23 cm·s^{-1}) and two standard deviations of the streamwise flow velocity u_{SD} (low turbulence = 5 cm·s^{-1}; high turbulence = 8 cm·s^{-1}). The four experimental flow structures were selected for our experiments because they corresponded to flow conditions commonly used by JAS in the Sainte-Marguerite River (Guay et al. 2000; E.C. Enders and D. Boisclair, unpublished data). Fish activity costs were quantified by measuring the oxygen depletion over time with an oxygen meter (model 565 (Intab, Stenkullen, Sweden); ±0.005 mg O_2·L^{-1}).

Fig. 1. Schematic representation of the experimental setup used during the respirometry experiments performed to estimate the cost of swimming in a turbulent flow. A transformer modulated the electric current that powered a pump (P1), which created a turbulent flow in the swimming chamber against which a fish would swim. A second submerged pump (P2) continuously transferred water from the swimming chamber to the oxygen sensor to measure the oxygen uptake by a fish. The swimming chamber contained two grids. The "upstream" grid (A) was used to produce a spatially uniform fine turbulence flow structure within the swimming chamber, and the "downstream" grid (B) was designed to force the fish to remain in the swimming chamber.



Experimental procedure

Characteristics of flow structures

Turbulence was quantified at the beginning and end of the suite of experimental observations (five experiments) aimed at testing the effect of one of the four specific flow conditions on fish respiration rate. Turbulence was quantified in the absence of fish to avoid interference caused by fish on our recordings. For every flow condition, six velocity time series (three at the beginning and three at the end of a suite of experimental observations) were recorded for a period of 5 min. Between each velocity time series, the apparatus used to create the turbulent flow was completely shut down. This strategy was adopted to verify the repeatability and the stability of the flow structures created by our apparatus for given settings of the electric current that powered the pump.

Respirometry

Respirometry experiments were performed using a single fish at a time. A fish was selected at random from our stock of experimental fish, kept separately, and not fed for 2 days before the experiment to avoid increased metabolic rates resulting from digestion (Brett and Groves 1979). Twenty-four hours before the beginning of an experiment, the fish was introduced into the swimming chamber to allow it to adapt to the experimental conditions. After this introduction, the respirometer was sealed without residual air bubbles. During this adaptation phase, pump 2 generated a water exchange between the respirometer and ambient water of the aquarium. At the beginning of the experiment, pump 2 was connected to the oxygen meter, preventing an external water supply, and pump 1 was started to create the turbulent flow structures in the swimming chamber. Oxygen concentration was measured at the beginning of the experiment, after which it was measured every 30 min for the duration of the experiment (6 h) for a total of 13 oxygen concentration measurements.

We monitored fish behaviour during each experiment to insure that they were continuously swimming. Every 10 min, an image of the position held by the fish within the swimming chamber was automatically registered with a Sony Webcam (Sony Electronics Inc., Oradell, N.J.). In addition, during the last 30 min of the experiment, the fish was continuously filmed by a video camera (WV-BL602; Panasonic Canada Inc., Lachine, Québec). Hence, our procedure presumes that if a fish is always in a swimming position in a series of images registered at 10-min intervals and if it swims continuously during the last 30 min of an experiment, it was continuously swimming during the 6 h of the experiment. Analysis of the images and of the films collected during our 20 experiments indicated that fish were always swimming in the central section of the swimming chamber. No fish settled at the bottom of the swimming chamber or was observed against the upstream or downstream grid of the swimming chamber. Consequently, we are proceeding with the assumption that during our experiments, fish were continuously swimming against the flow structures created by our apparatus.

An experiment always ended after 6 h. This 6-h period was chosen because performing longer (few hours but without provoking fatigue; see Discussion) rather than shorter experiments (few minutes) may allow oxygen depletion estimated during the respirometry experiments to include the repayment of an oxygen debt incurred by the recourse by fish to anaerobic metabolism. No observation was made under 7.6 mg $O_2 \cdot L^{-1}$ to minimize the influence of low oxygen concentration on the fish behaviour (Beamish 1978). At the end of an experiment, the fish was removed from the respirometer, anaesthetized (clove oil; 0.6 mg$\cdot L^{-1}$), weighed (g wet), and measured (TL, cm). The biological oxygen demand (BOD) was determined within 6 h of an experiment using the same procedure but without fish.

Computations

We estimated the cost of swimming against a turbulent flow in three steps. Firstly, we estimated the total metabolic rate of fish (C_R, mg $O_2 \cdot h^{-1}$) as

$$(1) \qquad C_R = \Delta O_2 / \Delta t \cdot V_W - \text{BOD}$$

where ΔO_2 is the difference in oxygen concentration between two consecutive oxygen concentration measurements (mg $O_2 \cdot L^{-1}$), Δt is the time interval of 0.5 h between two consecutive oxygen concentration measurements, V_W (22.6 L) is the volume of water in the respirometer excluding the volume of our pumps and swimming chamber, and BOD is the biological oxygen demand by micro-organisms in the water (mg $O_2 \cdot h^{-1}$). BOD ranged from 0.001 to 0.004 mg $O_2 \cdot h^{-1}$. Because we measured oxygen concentration within the swimming chamber at 30-min intervals over 6 h, we obtained 12 C_R values per experiment. Secondly, we calculated the mean (further referred to as C_M, mg $O_2 \cdot h^{-1}$) and the standard deviation of the C_R values obtained for each experiment. Thirdly, the cost of swimming against a turbulent flow (C_A, mg $O_2 \cdot h^{-1}$) was estimated as

$$(2) \qquad C_A = C_M - \text{SMR}$$

where SMR is the standard metabolic rate of a fish (mg $O_2 \cdot h^{-1}$). The standard metabolic rate was determined by a model that we developed using data from Brett and Glass (1973) on the standard metabolism of juvenile sockeye salmon (*Oncorhynchus nerka*) weighing 4–10 g and held at a water temperature of 15 °C

$$(3) \qquad \text{SMR} = 0.227 M^{0.653} \; (n = 5;\ r^2 = 0.86;\ p < 0.05)$$

where M is the body mass of the fish (g wet). SMR values were obtained by extrapolating the relationship between oxygen consumption and mean flow velocity from forced swimming experiments to zero velocity. According to eq. 3, SMR for the fish used in our experiments ranged from 1.00 to 1.07 mg $O_2 \cdot h^{-1}$.

Statistical analysis

The repeatability of each of the four experimental flow structures created by our apparatus was tested using one-way analysis of variance (ANOVA). Such ANOVA was performed to compare the mean streamwise flow velocities during the three times series recorded before a suite of experimental observations. The analysis was also done for the three velocity time series obtained after a suite of experimental observations. The stability of the turbulent flow structures was tested using a one-way ANOVA comparing the mean flow velocities before with those after a suite of experimental observations. During this analysis, the three velocity time series obtained before or after a suite of experimental observations were used as replicates. The repeatability and the stability of the standard deviations of the flow velocities were tested using the same approach with Levene's test of the equality of variances. This test was selected because it has been argued to be more robust and not dependent on the assumption of normality compared with, for example, the Bartlett's test of equality of variances (Scherrer 1984).

We confirmed the periodicity of the pulsating flow using a power spectrum analysis (Lapointe et al. 1996). Every 5-min velocity time series measured with the ADV were filtered using a Gausian filter. The filtered time series was decomposed in frequencies using a Fourier transformation (Legendre and Legendre 1998). The power spectrum analysis measures the variance contributions from different frequencies within the velocity time series. The total variance of the time series is presented as the area under a relationship between the variance associated to a frequency and the frequency (referred to as a power spectrum). Spikes in the power spectrum indicate a periodicity with the corresponding frequency.

Low- and high-speed flow events within the velocity time series were identified using conditional analysis. These events were defined as velocity fluctuations above or below the mean streamwise velocity that lasted more than 0.75 s (Lu and Willmarth 1973).

Swimming costs were compared among the four different flow structures with a two-way ANOVA using mean flow velocity and standard deviation of flow velocity as classification variables. The five replicates of swimming costs for each flow structure allowed us to test the statistical significance of the interaction term of this analysis (mean flow velocity × standard deviation of flow velocity).

The activity costs that we estimated while fish were swimming against a turbulent flow were compared with predictions made by the forced and the spontaneous swimming models developed by Boisclair and Tang (1993). Both models were inputted with the mass of the fish and the mean flow velocity used during our experiments. Activity costs predicted by the forced or spontaneous models were compared with observed activity costs using model II regression analysis. The null hypothesis in this analysis was that there is no statistically significant difference between predicted and observed activity costs. The slope of the regression line was tested against an expected value of unity, and the intercept was tested against an expected value of zero. The statistical significance and the 95% confidence intervals of the slope and the intercept of the major axis estimates were tested with 999 permutations (Legendre and Legendre 1998).

Results

Characteristics of flow structures

The means and the standard deviations of the streamwise flow velocities recorded were consistent with the targeted values (Table 1). The mean streamwise flow velocities ranged from 18.02 to 18.32 $cm \cdot s^{-1}$ for the low flow condition (target = 18 $cm \cdot s^{-1}$) and from 23.02 to 23.09 $cm \cdot s^{-1}$ for the high flow condition (target = 23 $cm \cdot s^{-1}$). The standard deviation of the streamwise flow velocity under the low turbulent conditions ranged from 5.06 to 5.16 $cm \cdot s^{-1}$. Corresponding values under the high turbulent conditions ranged from 7.92 to 8.27 $cm \cdot s^{-1}$ (Table 1). The mean vertical flow velocities ranged from –0.70 to 0.44 $cm \cdot s^{-1}$ for low flow velocities and from –0.10 to 0.12 $cm \cdot s^{-1}$ for high flow velocities. The standard deviation of the vertical flow velocity ranged from 4.79 to 5.04 $cm \cdot s^{-1}$ under the low turbulent conditions and from 6.93 to 7.64 $cm \cdot s^{-1}$ under high turbulent conditions. Corresponding values for the mean lateral flow velocities ranged from –0.45 to 0.49 $cm \cdot s^{-1}$ for low flow and from 0.20 to 0.32 $cm \cdot s^{-1}$ for high flow conditions. The standard deviation of the velocities under the lateral flow ranged from 5.41 to 5.62 $cm \cdot s^{-1}$ under low turbulence and from 7.50 to 7.71 $cm \cdot s^{-1}$ under high turbulence conditions.

For any given flow condition, the mean streamwise flow velocity $\bar{u}$ and the standard deviation of streamwise flow velocity u_{SD} did not vary significantly among the three recordings performed before (variation = 0.1–1.8%) or after (variation = 0.1–1.8%) a suite of experimental observations (Repeatability test: $\bar{u}$, $0.656 < p < 0.998$; u_{SD}, $0.196 < p < 0.989$). Similarly, for any given flow condition, the mean streamwise flow velocity $\bar{u}$ and the standard deviation of streamwise flow velocity u_{SD} obtained before a suite of experimental observations did not vary significantly (variation = 0.0–2.0%) from values estimated after a suite of experimental observations (Stability tests: $\bar{u}$, $0.917 < p < 0.998$; u_{SD}, $0.464 < p < 1.000$). These results suggest that the flow structures created by our apparatus were repeatable and stable.

The spike at 0.17 Hz in the power spectrum analysis confirmed the presence of a dominant period of 6 s within the velocity time series (Fig. 2). However, the power spectra also showed the occurrence of a variety of frequencies, signifying the presence of a fully developed turbulent flow. The examination of the velocity time series allowed us to identify from two to five low-speed flow events/min and five high-speed flow events/min. The mean duration of the flow events was 1.0 s. The standard deviation of the duration of the flow events ranged from 0.20 to 0.29 s (Table 2).

Swimming costs

Swimming costs varied threefold among our experiments, ranging from 1.46 ($\bar{u}$ = 18 $cm \cdot s^{-1}$; u_{SD} = 5 $cm \cdot s^{-1}$) to 4.42 mg $O_2 \cdot h^{-1}$ ($\bar{u}$ = 23 $cm \cdot s^{-1}$; u_{SD} = 8 $cm \cdot s^{-1}$; Fig. 3). These values corresponded to a factor ranging from 1.4 to 4.3 times SMR. Swimming costs tended to increase with mean flow velocity ($p < 0.01$) and with the standard deviation of the flow velocity ($p < 0.01$). The interaction between the mean and the standard deviation of flow velocity was also significant ($p < 0.01$), indicating that an increase of standard deviation of flow velocity did not have the same effect for the low and high flow conditions. An increase of the standard deviation of flow velocity from 5 to 8 $cm \cdot s^{-1}$ increased activity metabolic rates by factor of 1.3 at a low flow conditions. This factor was 1.6 at high flow conditions (Table 3).

Comparison between observed swimming costs and predictions by forced and spontaneous swimming models

Predictions of activity costs obtained using the forced swimming model tended to underestimate observed activity costs. At low flow conditions, the forced swimming model underestimated the observed cost of swimming of JAS subjected to turbulent flows by a factor ranging from 1.9 (u_{SD} = 5 $cm \cdot s^{-1}$) to 2.4 (u_{SD} = 8 $cm \cdot s^{-1}$). Corresponding values at high flow conditions ranged from 2.6 (u_{SD} = 5 $cm \cdot s^{-1}$) to 4.2 (u_{SD} = 8 $cm \cdot s^{-1}$; Table 4). The 95% confidence interval of the intercept of the regression model between observed and predicted respiration rates ranged from 0.55 to 0.74. This intercept was statistically different from zero ($p = 0.001$). The 95% confidence intervals of the slope of the regression model between observed and predicted respiration rates ranged from 0.07 to 0.13. This slope was significantly different from unity ($p = 0.001$).

Activity costs predicted by the spontaneous swimming model of Boisclair and Tang (1993) always overestimated swimming costs in turbulent flows (Fig. 4). At the low flow velocity, the spontaneous swimming model overestimated the

Table 1. Ranges of the mean flow velocity and the standard deviation of the flow velocity ($cm \cdot s^{-1}$) during the six 5-min velocity time series. Ranges of minimum and maximum flow velocity ($cm \cdot s^{-1}$) for the streamwise U (u_{min}, u_{max}), vertical V (v_{min}, v_{max}), and lateral W (w_{min}, w_{max}) velocity vectors in the four different flow conditions and the ranges of their standard deviations (u_{SD}, v_{SD}, w_{SD}, respectively) are also presented.

Velocity vector	Low velocity – low turbulence	Low velocity – high turbulence	High velocity – low turbulence	High velocity – high turbulence
Range $\bar{u}$	18.02–18.18	18.26–18.32	23.02–23.08	23.02–23.09
Range u_{SD}	5.06–5.16	8.16–8.27	5.07–5.15	7.92–8.08
u_{min}	3.11–4.63	0.27–1.64	3.47–5.64	0.35–0.90
u_{max}	34.21–35.36	36.34–38.94	34.47–36.88	42.24–44.85
Range $\bar{v}$	–0.70–0.34	–0.42–0.44	–0.10–0.10	–0.10–0.12
Range v_{SD}	4.79–4.94	6.93–7.05	4.81–5.04	7.14–7.64
v_{min}	–23.02–(–18.74)	–25.83–(–22.04)	–29.77–(–27.35)	–31.41–(–28.39)
v_{max}	20.61–22.95	21.52–24.26	27.84–31.45	29.20–30.65
Range $\bar{w}$	0.15–0.19	–0.45–0.49	–0.20–0.10	0.30–0.32
Range w_{SD}	5.41–5.57	7.50–7.69	5.42–5.62	7.53–7.71
w_{min}	–26.27–(–20.38)	–27.49–(–22.31)	–21.71–(–35.37)	–24.95–(–30.61)
w_{max}	22.64–23.82	25.08–28.23	29.62–33.31	29.04–35.74

Fig. 2. Relationship between the spectral density and the frequency of the streamwise velocity vector U of the time series for four different flow conditions (two mean water velocities $\bar{u}$ of 18 and 23 $cm \cdot s^{-1}$ and two standard deviations u_{SD} of 5 and 8 $cm \cdot s^{-1}$).

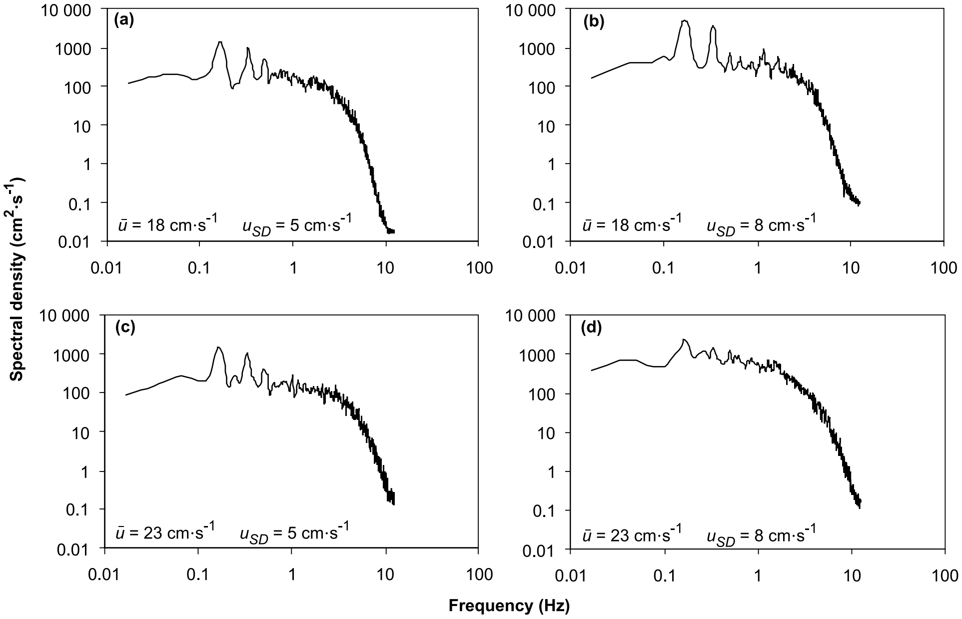
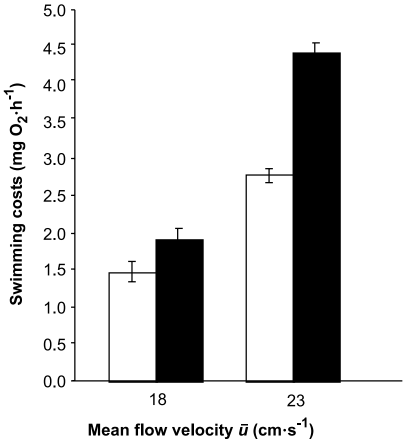


Table 2. Number and duration of low- and high-speed flow events for each of the four turbulent conditions.

	Low velocity – low turbulence	Low velocity – high turbulence	High velocity – low turbulence	High velocity – high turbulence
Number of low-speed flow events/min	2	3	2	5
Number of high-speed flow events/min	5	5	5	5
Mean duration (s)	1	1	1	1

swimming costs in a turbulent flow by a factor ranging from 6.6 (u_{SD} = 5 $cm \cdot s^{-1}$) to 5.0 (u_{SD} = 8 $cm \cdot s^{-1}$). The overestimation of respiration rates predicted by the spontaneous model was decreased to factors ranging from 4.5 (u_{SD} = 5 $cm \cdot s^{-1}$) to 2.8 (u_{SD} = 8 $cm \cdot s^{-1}$) at high flow conditions. The 95% confidence intervals of the intercept associated with the regression model between observed and predicted oxygen consumption rates ranged from 7.11 to 9.15. The intercept of

Fig. 3. Swimming costs of juvenile Atlantic salmon (*Salmo salar*) under four turbulent conditions defined by the mean flow velocity ($\bar{u}$) and the standard deviation of flow velocity (u_{SD}). Low turbulence conditions (u_{SD} of 5 cm·s^{-1}) are represented by open bars and high turbulent conditions (u_{SD} of 8 cm·s^{-1}) are represented by solid bars. Vertical lines represent 95% confidence intervals.



this regression model was significantly different from zero ($p = 0.001$). The 95% confidence interval of the slope of the relationship between observed and predicted activity costs ranged from 0.73 to 1.44. This slope was not significantly different from the expected value of 1 ($p > 0.05$).

Discussion

Our analyses indicate that the swimming costs of JAS in turbulent flow may significantly increase as mean flow velocity and standard deviation of the flow velocity increase. In our experiments, swimming costs increased by an average factor of 1.5 as mean flow velocity increased from 18 to 23 cm·s^{-1}. The effect of mean flow velocity on fish respiration rates is not surprising as it is imbedded in all swimming cost models currently available (Beamish 1978; Boisclair and Tang 1993; Tang et al. 2000). We also found that swimming costs for a given mean flow velocity may increase with the standard deviation of the flow velocity. In our study, fish respiration rates increased, on average, by a factor of 2.1, as the standard deviation of the flow velocity increased from 5 to 8 cm·s^{-1}. Our analyses also showed that the effect of increasing the intensity of the turbulence of flow may increase as mean flow velocity increases. As the standard deviation of the flow velocity increased from 5 to 8 cm·s^{-1}, swimming costs of JAS increased by a factor of 1.3 at a mean flow velocity of 18 cm·s^{-1} and by a factor of 1.6 at a mean flow velocity of 23 cm·s^{-1}.

Our work may be taken as an indication that not only mean flow velocity, but also standard deviation of flow may be required to adequately estimate the cost of swimming under turbulent conditions. However, our data do not really allow us to fully evaluate the ultimate cause of the variation of fish respiration rates among our treatments. Although our methods focus mostly on the mean and the standard deviation of flow velocity, any other characteristic such as the number and the intensity of the flow events may affect the metabolic rates of fish. In our study, experimental treatments did not only vary in terms of mean and standard deviation of velocity, but also in terms of the number of events per minute (particularly low-speed flow events). This is expected because the descriptors of turbulence are expected to be correlated: high turbulence is expected to have more flow events per unit of time and a higher SD flow/mean flow than low turbulence; high velocity is expected to have faster flow and more events per unit of time than low velocity. In our study, among-experiment variability in flow structure was expressed by more low-speed events in high turbulence conditions (3–5/min) than in low turbulence conditions (2/min; high-speed events were always 5/min). Similarly, more events occurred under high-speed conditions (5 low-speed events/min) than under low-speed conditions (3 low-speed conditions/min). Because the descriptors of flow are interrelated, it is presently impossible with the few data that we have to assess the relative effect of mean flow, standard deviation of flow velocity, and the number of flow events (and, potentially, the magnitude of flow events or the type of flow event, high or low) on fish respiration. Our present contribution is limited to providing estimates of the effect that turbulence may have on fish respiration, notwithstanding its ultimate cause.

The applicability of our results to field situations depends on the ability of our experimental design to reflect natural conditions found in rivers and streams and on the validity of the assumptions that we used to estimate fish swimming costs. Activity metabolism is generally estimated using forced swimming experiments seeking to minimize heterogeneity of flow velocity and direction (Brett 1965; Beamish 1978) or using spontaneous activity experiments in absence of flow (Boisclair and Tang 1993; Krohn and Boisclair 1994; Tang and Boisclair 1995). Because rivers are characterized by temporally heterogeneous flow, we expected that using an experimental design that does not only allow flow to be present but to be varied may better represent natural flow conditions faced by the fish. Both mean and standard deviation of the flow velocity used during our experiments were chosen to represent a subset of the natural conditions encountered by JAS. The two experimental mean flow velocities ($\bar{u}$ = 18 and 23 cm·s^{-1}) are within the range of focal point and microhabitat velocities used by JAS (DeGraaf and Bain 1986; Morantz et al. 1987; Guay et al. 2000). The experimental standard deviations of 5 and 8 cm·s^{-1} were adopted following field observations of habitat selected by JAS in the Sainte-Marguerite River (Enders and Boisclair, unpublished data). Natural flow conditions comprise realistic flow structures such as temporal successions of fast- and slow-moving flow events extending over the whole water column (Kirkbride and Ferguson 1995; Ferguson et al. 1996). In gravel-bed rivers, flow events lasting from 0.5 to 5 s have been shown to occur at 5- to 30-s intervals (Roy et al. 1999). Consequently, we controlled the electric current powering the pump that created a pulsating flow such that our apparatus produced slow flow events of a mean duration of 1 s at 6-s intervals. Hence, we performed our experiments under combinations of mean flow velocity, standard deviation of the flow velocity, duration of flow events, and interval between flow events that are within the range found under natural conditions.

Table 3. Number of respirometry experiments (N) per flow condition (combinations of mean flow velocity $\bar{u}$ and standard deviation of the flow velocity (u_{SD})), mean fish mass (M), costs of swimming (C_A) in the corresponding turbulent flow condition, and standard deviation (SD) of C_A among the five experiments.

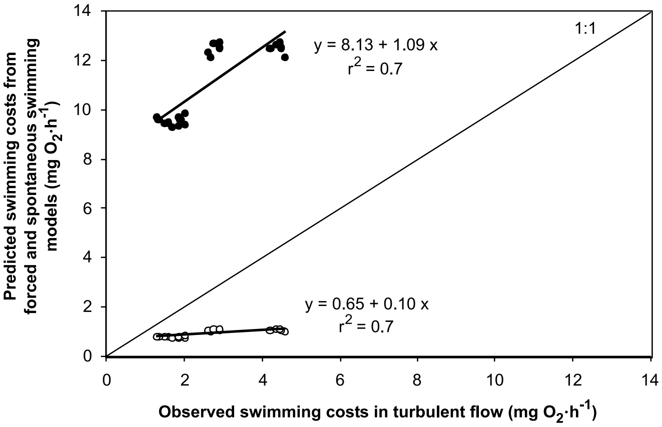
N	$\bar{u}$ (cm·s^{-1})	u_{SD} (cm·s^{-1})	M (g)	C_A (mg O$_2$·h^{-1})	SD of C_A (mg O$_2$·h^{-1})
5	18	5	10.01	1.46	0.17
5	18	8	10.15	1.91	0.08
5	23	5	10.09	2.77	0.12
5	23	8	10.13	4.42	0.15

Table 4. Comparisons between the observed activity metabolic rate for given combinations of mean flow velocity ($\bar{u}$) and standard deviation of the flow velocity (u_{SD}) and the predictions of forced and spontaneous swimming model of Boisclair and Tang (1993) implemented with mean flow velocity.

$\bar{u}$ (cm·s^{-1})	u_{SD} (cm·s^{-1})	Factor 1	Factor 2
18	5	1.9	6.6
18	8	2.4	5.0
23	5	2.6	4.5
23	8	4.2	2.8

Note: Factor 1 represents the factor by which the predictions of the forced swimming model underestimated observed activity metabolic rates. Factor 2 represents the factor by which spontaneous swimming model overestimated observed activity metabolic rate.

Fig. 4. Comparison between the observed swimming costs of juvenile Atlantic salmon (*Salmo salar*) of 10 g under four different turbulent conditions (two mean flow velocities $\bar{u}$ of 18 and 23 cm·s^{-1} and two standard deviations u_{SD} of 5 and 8 cm·s^{-1}) and the swimming costs predicted by the forced (open circles) and the spontaneous (solid circles) swimming models of Boisclair and Tang (1993).



However, our results do not cover the complete range of conditions that may be encountered in natural environments. Furthermore, flow characteristics other than those that we studied may affect fish swimming costs. For instance, Webb (1993*a*) described that "ground effects" created by solid structures, such as the walls of our swimming chamber, increase lift, reduce drag, and therefore decrease swimming costs. Fish from our experiments may have been subjected to such effects. In view of our objectives, the presence of ground effects may not affect the relevance of our results to field situations. In their natural habitat, JAS spend most of their time swimming just above the substrate (sit-and-wait behaviour). However, the difference between the ground effects perceived by fish in our swimming chamber and those experienced by fish under natural conditions and the effect of such a difference on the applicability of our results to field situations represents a more important issue for which we have no immediate solution. Similarly, because we measured flow velocity only in one central point of the swimming chamber, we cannot describe the form and size of the vortices that may have been present in our swimming chamber. Theoretically, the upstream grid introduced in the swimming chamber should prevent the occurrence of large vortices or recirculation zones that would decrease the energy expenditure of fish (Tritton 1988). Although the existence of such recirculation zones in our swimming chamber should be assessed to better interpret our results, two lines of evidence suggest that JAS were not subjected to a significant effect of vortex. First, negative streamwise flow velocities were not observed in our swimming chamber. This indicates that during our experiments, JAS were not submitted to a counter-streamwise flow. Second, the vertical (V) and lateral (W) flow velocity components were highly variable (range = –31.41 to 31.45 cm·s^{-1}) and directionally unstable (from negative to positive values). This suggests that fish were not subjected to directionally stable conditions that characterize recirculation zones (Vogel 1994). Consequently, the swimming costs estimated may not be representative of those incurred by JAS when they hold position on the downstream end of a rock (where vortices and recirculation zones are expected to occur). However, the respiration rates obtained may adequately represent the cost of swimming against a turbulent flow (with similar mean and standard deviation of flow velocity) while JAS perform the attack phase of their feeding motions to capture prey items.

During our experiments, JAS were continuously swimming over a 6-h period. However, in their natural environment, JAS may swim against a turbulent flow only during shorter time periods than those used in our experiments (attacks directed towards invertebrates that drift in the flow, aggressive interactions, habitat exploration). Although we recognize that the duration of our experiments may have been demanding to the fish, within-experiment variation in oxygen consumption rates during 30 min (C_R) ranged from 3.8% to 11.6%. Furthermore, we found no relationship between C_R and time since the beginning of an experiment ($0.01 < r^2 < 0.134$; $0.24 < p < 1$). Hence, our experimental conditions did not appear to cause any functionally or statistically significant fatigue to the fish used.

The method used to estimate fish swimming costs is based on the assumption that the standard metabolic rate (SMR) of Atlantic salmon is adequately represented by that of sockeye salmon of similar sizes (Brett and Glass 1973). The use physiological models developed for one species to predict bioenergetic attributes of another species may produce potentially misleading estimates (Ney 1993). Our use of the SMR data of sockeye salmon for Atlantic salmon was motivated by the absence of SMR data specific to Atlantic salmon, by the availability of a large data set for sockeye salmon, and by the taxonomic (both salmonids), morphological (body mass–length relation), physiological (preferred water temperature), and ecological (juvenile stages in riverine freshwater) similarities between both species. However, it may be hypothesized that SMR for similar-sized fish held at a same water temperature vary among different salmonid species. To our knowledge, the only data that may allow us to test this hypothesis are the SMR data of Job (1955) for brook char (*Salvelinus fontinalis*) ranging from 5 to 2000 g at 15 °C. Job (1955) estimated SMR as the lowest hourly respiration rates of fish held in a rectangular respirometer during 24 h. Applying the SMR model of brook trout to the fish size used in our experiments, we obtained SMR values ranging from 1.02 to1.12 mg $O_2 \cdot h^{-1}$. Corresponding values obtained with the model based on data collected for sockeye salmon, and used during our computations, ranged from 0.99 to 1.07 mg $O_2 \cdot h^{-1}$. The 2.4–4.5% difference between SMR obtained for two different species of salmonids suggests that the use of the SMR model of sockeye salmon to predict the SMR of Atlantic salmon may have a minor effect on our estimates of swimming costs.

Forced and spontaneous swimming models are presently the most commonly used models to estimate the swimming costs of fish. Comparisons between predictions made by these models and our estimates of the cost of swimming under turbulent flow allowed us to assess the effect of turbulence of swimming energetics. However, it is useful to compare models that are subjected to similar assumptions. Three basic assumptions are shared by all swimming cost models. Firstly, all types of models assume that experimental conditions allow fish to swim in a manner that may mimic their swimming in the field. Experimental approaches differ with respect to the probability that this assumption may be true. For instance, during forced swimming experiments, fish are forced to swim against a flow of constant velocity and direction (no acceleration and no turns are allowed). Such flow is rarely present in the field. Therefore, fish may rarely swim at a constant speed and direction, whether against a flow or in a body of water without any flow. In turbulent swimming experiments, fish are forced to swim against a turbulent flow, which does exist in the field. During spontaneous swimming experiments, fish control their swimming speed. They are also allowed to freely perform accelerations and turns. As such, spontaneous swimming models may be expected to be the closest to natural conditions for fish living in habitats that have no significant flow (lakes, ponds, etc). Secondly, all models assume that within the range of the duration of the experiments performed, the length of an experiment (h) has no effect on the validity of the respiration rates obtained (i.e., respiration rates/h estimated over 30 s is identical to respiration rates/h estimated over 6 h). Forced and turbulent swimming experiments are particularly susceptible to this assumption because experiments often require that fish swim continuously for hours, which may not correspond to the natural behaviour of most fish species. Both types of approaches assume that if fish continue to swim for the complete duration of an experiment and if respiration rates do not significantly increase or decrease through time, then fish are not fatigued and their respiration rates adequately represent swimming costs under the experimental conditions. As such, when developing swimming cost models, combinations of swimming intensity and duration of the experiments are selected to avoid fatigue. Spontaneous swimming experiments are not affected by this assumption because fish are free to swim or to remain immobile. Thirdly, all models assume that swimming costs are adequately estimated by measuring oxygen consumption by fish. This assumption also presumes that the energy required to swim comes mostly from the aerobic metabolism. If anaerobic metabolism contributes to fish swimming costs, then the potential exists for oxygen consumption rates to underestimate actual swimming costs. However, the absolute or relative contribution of aerobic and anaerobic metabolism is difficult to establish and is rarely estimated. Yet, anaerobic metabolism could theoretically interfere with estimates of fish swimming costs obtained by measuring oxygen consumption by fish under forced, turbulent, or spontaneous swimming experiments. Indeed, even under spontaneous swimming experiments, fish may occasionally perform intense accelerations that may require anaerobic metabolism. The interference caused by anaerobic metabolism is circumvented by modulating the experimental flow velocities and the duration of the experiments to minimize the expression of anaerobic metabolism. It is expected that avoiding extreme velocities may minimize the use by fish of anaerobic metabolism. Furthermore, performing longer (few hours but without provoking fatigue) rather than shorter experiments (few minutes) may allow oxygen depletion estimated during the respirometry experiments to include the repayment of an oxygen debt incurred by the recourse to anaerobic metabolism. Hence, the three approaches to estimate or model fish swimming costs rest on the same basic assumptions.

Generally, the three approaches employ the same strategy (selection of experimental flow velocities, assessment of trends of fish respiration rates during experiments, selection of the duration of experiments) to measure, avoid, and minimize the effects of these assumptions. Another element common to all three approaches is that fish respiration rates are modeled using fish mass, flow velocity, or fish swimming speed. This facilitates the comparison among models, although it may be necessary for fish living in turbulent flows, as illustrated by our work, to add descriptors of the complexity of flow (e.g., standard deviation of flow) to this list of independent variables. Providing evidence that the inclusion of such descriptors in swimming cost models for fish living under turbulent conditions may not only be necessary, but also achievable, may constitute the most important contribution of our work. It is our contention that the comparisons that we performed among the different models is justified not only from a fundamental perspective, but also from a functional perspective. Although it may be conceptually obvious that using forced swimming models to estimate the cost of swimming for fish swimming against a turbulent flow may be incorrect, a number of recent studies used this approach because of the lack of quantitative information about the effect that turbulence may have on fish swimming costs. The comparisons that we performed among swimming models allow users of such models to readily assess the functional and quantitative consequences of our work on estimates produced by the most commonly used models.

The swimming costs estimated under our experimental conditions were 1.9- to 4.2-fold larger than those predicted using a forced swimming model and 4.2- to 6.6-fold smaller than those predicted by a spontaneous swimming model. The higher respiration rates estimated under turbulent conditions relative to predictions made by forced swimming conditions are consistent with the suggestion of Webb (1982) and Boisclair and Tang (1993) that unsteady swimming (including changes in speed and direction) is more energetically costly than steady swimming (no changes in speed and direction). Changes in swimming speed and direction that must be performed under turbulent conditions may be expected to cause a substantial increase in the energy costs compared with steady swimming at the same average speed. Adjustments undertaken by fish with their fins to maintain their position in the water column are also expected to increase activity costs (Weatherley et al. 1982; Gauthier 1998; McLaughlin and Noakes 1998). The extensive use of fins provides stability but also increases drag (Webb 1993*b*), and as illustrated by our work, it increases energy expenditure at a same mean flow velocity. McLaughlin and Noakes (1998) noted a temporal variability in the tail beat frequency and amplitude of young-of-the-year brook trout observed in a natural stream. They suggested that these adjustments corresponded to the fluctuations of the flow velocity, which may increase the energetic costs for swimming against a turbulent flow. Our results are consistent with their suggestion.

Activity costs predicted by the forced swimming model that we used are expected to increase with swimming speed raised to a power of 1.21 (Boisclair and Tang 1993). An exponent greater than one suggests a relatively higher increase of activity cost with a given increase of swimming speed. Therefore, it may be hypothesized that the estimation of activity costs with instantaneous flow velocities instead of the mean flow velocity would improve the accuracy of the predictions made by the forced swimming model (e.g., peaks in flow velocities could lead to an important increase of the activity costs estimated using a model in which velocity has an exponent of 1.21). We tested this hypothesis by estimating the oxygen consumption rates predicted by the forced swimming model using flow velocity data recorded at 25 Hz (Table 5). Our results indicated that the use of instantaneous flow velocity, instead of the mean flow velocity, increased activity costs predicted by the forced swimming model by 2–6%. This analysis confirms that the use of forced swimming models in bioenergetic modeling of riverine fish species may underestimate actual cost of swimming in turbulent flow even when these models are implemented with instantaneous measures of flow velocity.

Our data suggest that the cost of swimming in a turbulent flow may be higher than predicted by forced swimming models but lower than expected when using spontaneous swimming models. In our study, the difference between actual swimming costs and those predicted by the forced swimming model increased with the mean and the standard deviation of flow. Furthermore, the difference between actual swimming costs and those predicted by the spontaneous swimming model decreased with the mean and the standard deviation of flow. Because our laboratory experiments simulated flow conditions from the lower part of the turbulence spectrum that may be observed under natural environments, we anticipate that the difference between actual swimming costs observed in our study and those predicted by the forced swimming model may be much lower than those that could be found in more extreme turbulent conditions. Similarly, we expect that the difference between actual swimming costs observed in our study and those predicted by the spontaneous swimming model may be higher than those that could be found in more extreme turbulent conditions.

Table 5. Comparisons between the cost of swimming (C_A) predicted by the forced swimming model of Boisclair and Tang (1993) implemented with the mean flow velocity ($\bar{u}$; $u_{SD} = 0$) and predictions of this model implemented with instantaneous flow velocities recorded at 25 Hz (u_{SD} = 5 or 8 cm·s^{-1}).

$\bar{u}$ (cm·s^{-1})	u_{SD} (cm·s^{-1})	C_A (mg O$_2$·h^{-1})	Factor A
18	0	0.77	—
18	5	0.79	1.03
18	8	0.82	1.06
23	0	1.04	—
23	5	1.06	1.02
23	8	1.07	1.03

Note: Factor A represents the factor by which the predictions increased because of the use of the instantaneous instead of the mean flow velocities.

The major difference between the movements performed by fish during spontaneous swimming experiments and those observed under the turbulent conditions that we used do not appear to reside in the standard deviation of fish swimming speed (or flow velocity) but in the intensity of the changes in direction. The variance of speed estimated during spontaneous swimming experiments generally range from 3.7 to 109 cm^2·s^{-2} (Tang and Boisclair 1995; Tang et al. 2000). These values correspond to standard deviations of 1.9 to 10.5 cm·s^{-1}. However, during spontaneous swimming experiments, fish perform turns ranging from 30.9 to 63.5° (Tang and Boisclair 1995). Such turns were not performed under the experimental conditions that we used. Hence, for a given swimming speed, lowest costs may be predicted by a forced swimming model (low standard deviation of the flow velocity and small angles of turns), intermediate costs may be predicted by a turbulent model developed under conditions similar to those used in our experiments (turbulent flow with intermediate levels of standard deviation of the flow velocity, e.g., 5–8 cm·s^{-1}, and small angles of turns), and the highest costs may be predicted with spontaneous models (high standard deviation of flow velocity and more pronounced angles of turns). This situation may indicate that for a given mean flow velocity or swimming speed, forced, turbulent, and spontaneous swimming data obtained for increasing standard deviation of flow velocities or swimming speeds and increasing angles of turns may form a continuum of increasing swimming costs. In the context of estimating the activity costs of JAS in the field, we speculate that such ranking may mean that the forced swimming model may be adequate to estimate the cost of swimming for fish facing flows of minimized heterogeneity (e.g., sit-and-wait position of fish near the substrate), that the turbulent swimming model may be adequate for fish inhabiting turbulent flow conditions, and that the spontaneous swimming model may be adequate for fish in more stringent conditions (complex swimming motions, high turbulence). Estimation of the activity costs of fish in turbulent flows may therefore require more than one model.

Our results suggest that bioenergetic models aimed at estimating the costs of habitat use by fish living in turbulent environments may require a description of the behaviour of the fish, estimates of the mean and the standard deviation of the flow, and respiration models in which the effects of the mean and the standard deviation of flow velocity are explicitly represented. Such an approach should be extended to studies using video observations (Trudel and Boisclair 1996; Aubin-Horth et al. 1999), radio tracking (Bourke et al. 1996; Ovidio 1999), and physiological telemetry (electromyograms; Korsmeyer et al. 1997; Dewar et al. 1999) in turbulent environments. We anticipate that models using the mean and the standard deviation of flow velocity may provide estimates of the costs of habitat utilization by fish living in rivers that are more accurate than commonly used forced swimming models. As such, our study suggests that the use of models more adequately representing the cost of swimming against a turbulent flow may strongly affect estimates of the cost of swimming and the expected balance of the benefits and costs of habitat utilization in turbulent environments.

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