

The costs of habitat utilization of wild, farmed, and domesticated juvenile Atlantic salmon (*Salmo salar*)¹

Eva C. Enders, Daniel Boisclair, and André G. Roy

Abstract: We compared morphometry and total swimming costs of wild, farmed (first-generation hatchery progeny of wild progenitors) and domesticated (seventh-generation progeny of the Norwegian aquaculture strain) juvenile Atlantic salmon (*Salmo salar*). Respirometry experiments were performed to assess total swimming costs of fish ranging in size from 4.0 to 16.1 g wet mass at a water temperature of 15 °C. Fish were subjected to flow conditions of low and high turbulence. Total swimming costs increased significantly with intensity of turbulence and were, on average, 1.4 times higher at high than at low turbulence. Total swimming costs were 2.4- to 4.0-fold higher than predicted by forced swimming models developed under conditions that minimize flow heterogeneity. Total swimming costs of wild and farmed fish were not statistically different (average difference = 6.7%). Hence, swimming costs models developed using farmed fish may be used to estimate swimming costs of wild fish. However, domesticated fish had total swimming costs 12.0% to 29.2% higher than farmed or wild fish. This may be related to domesticated fish having deeper bodies and smaller fins.

Résumé : Nous avons comparé la morphométrie et les coûts énergétiques totaux de nage des juvéniles du saumon atlantique (*Salmo salar*) sauvages, piscicoles (première génération en pisciculture issue de géniteurs sauvages) et domestiques (septième génération en pisciculture issue de la souche d'aquaculture norvégienne). Les expériences respirométriques ont été réalisées afin d'estimer les coûts énergétiques totaux de poissons de 4,0 à 16,1 g à une température de 15 °C. Les poissons étaient soumis à une faible et une forte condition turbulente de l'écoulement. Les coûts énergétiques totaux de nage augmentaient significativement avec l'intensité turbulente; ils étaient en moyenne 1,4 fois plus élevés à forte turbulence qu'à faible turbulence. Les coûts énergétiques totaux de nage étaient de 2,4 à 4,0 fois plus élevés que ceux prédits par les modèles de nage forcée. Les coûts énergétiques totaux des poissons sauvages et piscicoles n'étaient pas significativement différents (différence moyenne = 6,7 %). Ainsi, les modèles de coûts énergétiques de nage développés avec les poissons piscicoles peuvent être utilisés afin d'estimer les coûts énergétiques des poissons sauvages. Cependant, les poissons domestiques avaient des coûts énergétiques totaux de 12,0 % à 29,2 % plus élevés que les poissons piscicoles ou sauvages. Ceci pourrait être relié au fait que les poissons domestiques avaient un corps plus haut et des nageoires plus petites.

Introduction

Swimming costs of stream-dwelling fish are generally estimated using forced swimming models (Hughes and Dill 1990; Sabo et al. 1996; Guensch et al. 2001). These models are derived from experiments conducted with fish swimming at a steady speed in a flume respirometer designed to minimize flow heterogeneity (Brett 1964; Beamish 1978). However, in their natural environment, stream-dwelling fish are confronted by highly turbulent flow. In these environments,

turbulence is associated with a wide range of instantaneous velocities to which fish have to continuously adjust their swimming speed and their body position to maintain their location in the surrounding flow field. It has been demonstrated recently that turbulence affects the behavior and swimming performance of stream-dwelling fish. Pavlov et al. (2000) observed a decrease in sustained and critical swimming speeds with an increase of turbulence intensity for two lowland fish species (*Gobio gobio* and *Rutilus rutilus*), indicating that the energy expenditures are higher in

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E.C. Enders^{2,3} and D. Boisclair. Université de Montréal, Département de sciences biologiques, C.P. 6128, Succursale Centre-ville, Montréal, QC H3C 3J7, Canada.

A.G. Roy. Université de Montréal, Département de géographie, C.P. 6128, Succursale Centre-ville, Montréal, QC H3C 3J7, Canada.

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²Corresponding author (e-mail: enderse@dfo-mpo.gc.ca).

³Present address: Fisheries and Oceans Canada, Ecological Sciences Section, P.O. Box 5667, St. John's, NL A1C 5X1, Canada.

Table 1. Number of respirometry experiments per flow condition for four groups of juvenile Atlantic salmon ((1) wild fish, (2) farmed fish from the Sainte-Marguerite River, (3) farmed fish from the Imsa River, and (4) domesticated fish), range of body mass, and total swimming costs under low and high turbulence intensities with the same mean flow velocity of $23 \text{ cm}\cdot\text{s}^{-1}$ and two different standard deviations of $5 \text{ cm}\cdot\text{s}^{-1}$ and $8 \text{ cm}\cdot\text{s}^{-1}$.

	Group 1	Group 2	Group 3	Group 4
Experiments per flow condition	8	8	5	6
Body mass (g)	4.15–13.02	4.90–16.01	3.95–16.11	7.73–14.06
Total swimming costs ($\text{mg O}_2\cdot\text{h}^{-1}$)				
Low turbulence intensity	2.10–4.40	2.68–6.00	2.11–6.59	3.99–6.25
High turbulence intensity	2.83–7.21	3.74–8.00	2.67–8.02	5.24–8.29

turbulent flow. In a preliminary study, we demonstrated that net swimming costs (total respiration rate of unfed fish minus the standard metabolism) of juvenile Atlantic salmon (*Salmo salar*; JAS) under fluctuating flow velocities may be two- to four-fold higher than those predicted by forced swimming models (Enders et al. 2003). For practical reasons, the respirometry experiments were performed with fish of hatchery origin. However, Fleming et al. (1994) demonstrated that cultured JAS diverged significantly from their principal wild founder population in body morphology, having smaller heads and fins and narrower caudal peduncles. The morphological differences that exist between wild and cultured fish may also affect swimming performance and, therefore, the applicability of swimming costs models developed using cultured fish to wild populations. This may, in turn, affect estimates of the net energy gain and the habitat quality values generated by bioenergetics models (Ney 1993).

The objectives of our study were (i) to compare morphometric variables among wild JAS, farmed JAS (first-generation hatchery progeny from wild progenitors), and domesticated JAS (seventh-generation progeny of a Norwegian aquaculture strain), (ii) to confirm the effect of flow turbulence on the energetic cost of swimming, and (iii) to quantify the differences that may exist in the total swimming costs (cost of swimming + standard metabolism) of the different groups of fish. This study was especially designed to assess the applicability of respirometry models developed with cultured JAS to wild JAS.

Materials and methods

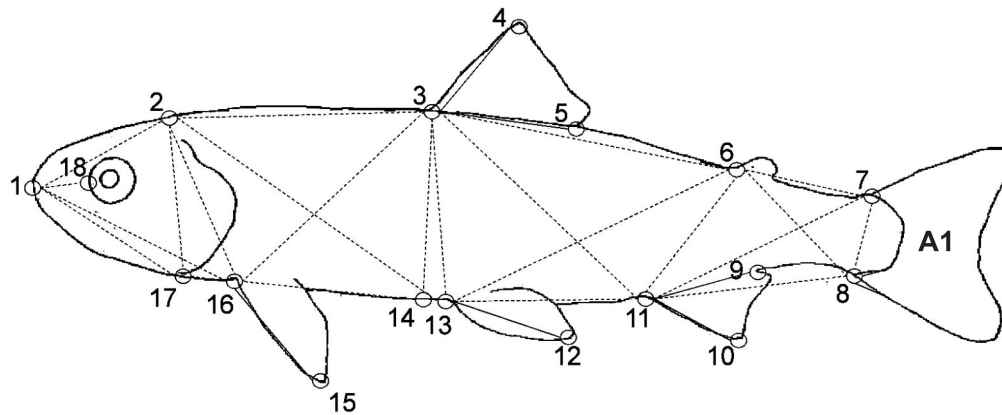
We accomplished our objectives by taking photographs of 20 individuals from each of the four groups of fish that differed in geographical origin (Canada or Norway) and degree of domestication (wild, farmed, or domesticated). From these photographs, we measured 30 morphometric variables describing different features of the body dimensions. Respirometry experiments were performed during which we subjected individual fish to two different types of turbulent flow characterized by the same mean flow velocity but two different standard deviations of flow velocity. Experiments were therefore performed under two levels of turbulence intensity (standard deviation/mean flow velocity). Total swimming costs (cost of swimming + standard metabolism) obtained for the two turbulence intensities were compared for four fish groups. All fish were adapted to a water temperature of $15 \text{ }^\circ\text{C}$ for a period of 3 weeks before starting the

respirometry experiments. The body mass of the fish used for our experiments ranged from 4.0 to 16.1 g wet mass (Table 1).

Fish

We obtained juvenile Atlantic salmon (JAS) for our experiments from four different sources. (1) Wild JAS from the Sainte-Marguerite River (Saguenay Region, Québec, Canada, $48^\circ 15' \text{N}$, $69^\circ 55' \text{W}$) were collected with a backpack electrofisher (model 12-B; Smith-Root Inc., Vancouver, Washington, USA). Fish were transferred to the laboratory at the Université de Montréal and kept in a 500-L Living Stream aquarium (model LSW 700; Frigid Units Inc., Toledo, Ohio, USA). Flow in these tanks was approximately $5 \text{ cm}\cdot\text{s}^{-1}$. Wild fish did not accept commercial pellets and were fed daily with red mosquito larvae (San Francisco Bay Brand™, Newark, California, USA). (2) Farmed JAS from the crossing of wild progenitors that originated from the Sainte-Marguerite River were obtained from the Pisciculture de Tadoussac (operated by the Société de la Faune et des Parcs du Québec, Canada). The juveniles were transferred to the Université de Montréal and kept under conditions (tank and flow velocities) identical to those of wild fish. However, farmed fish from the Pisciculture de Tadoussac were fed daily with commercial food pellets (Corey Feed Mills Ltd., Fredericton, New Brunswick, Canada). (3) Farmed JAS from the crossing of wild progenitors that originated from the Imsa River were provided by the Norwegian Institute of Nature Research (NINA) Research Station at Ims (Rogaland, Norway, $58^\circ 59' \text{N}$, $5^\circ 58' \text{E}$). The fish were kept in 1-m^2 tangential flow tanks supplied with flow-through freshwater from the Imsa River. The flow velocity in the tanks was approximately $5 \text{ cm}\cdot\text{s}^{-1}$. These fish were fed commercial food pellets (EWOS®, Bergen, Norway) using automatic feeders. (4) Domesticated JAS that originated from the Norwegian National Breeding Program at Sunndalsøra (Aquagen, Norway) were taken as eyed eggs to the NINA Research Station. The Sunndalsøra salmon were developed for the Norwegian fish farm industry and have been bred selectively since 1971 to attain certain characteristics such as increased growth, delayed maturity, and disease resistance. The first-generation fish were derived from 40 different wild salmon populations. However, after four generations, the stock was dominated by individuals coming from only one to three populations characterized by fast-growing and late-maturing fish. The fish that we studied were seventh generation of the first brood line (Gjedrem et al. 1991). The domesticated JAS were kept

Fig. 1. Location of 18 landmarks (open circles), 23 trusses (dotted lines), six fin lengths (solid lines), and the caudal fin area (A1): (1) anterior tip of snout at upper jaw; (2) most posterior aspect of neurocranium; (3) origin of dorsal fin; (4) distal tip of dorsal fin; (5) insertion of dorsal fin; (6) origin of adipose fin; (7) anterior attachment of dorsal fin membrane from caudal fin; (8) anterior attachment of the ventral membrane from caudal fin; (9) insertion of anal fin; (10) distal tip of anal fin; (11) origin of anal fin; (12) distal tip of pelvic fin; (13) origin of pelvic fin; (14) point of the ventral surface of the body directly below the anterior dorsal fin origin; (15) distal tip of pectoral fin; (16) origin of pectoral fin; (17) posterior-most point of the maxilla; and (18) anterior-most edge of the orbit.



under conditions (tank, flow velocities, food, feeding regime) identical to those of farmed fish of the Imsa River.

Morphometric measurements

Individual fish from each group ($n = 20$) were anaesthetized (clove oil; $0.6 \text{ mg}\cdot\text{L}^{-1}$) and placed left side up on a moist, blue carpet that had two rulers with millimetre scales along the lower and left edges. Anal, dorsal, and caudal fins were erected and small pieces of white paper were placed under the pectoral and pelvic fins to increase their visibility. Images were taken using a tripod and a video camera (ES610 fitted with a 50-mm lens; Canon Canada Inc., Mississauga, Ontario) set at a fixed distance of 40 cm from the fish. The images were analyzed using the image analysis software SigmaScan Pro 5.0 (Statistical Solutions, Saugus, Massachusetts, USA). Spatial coordinates of 18 morphometric landmarks as described in Winans (1984) and Swain et al. (1991) were taken (Fig. 1).

The 18 morphometric landmarks were used to calculate 23 interconnected distance variables defining different aspects of the dimensions of a fish (subsequently referred to as truss measurement; Fig. 1). The truss network is a series of measurements calculated between the landmarks that form a regular pattern of contiguous quadrilaterals or cells across the body. Compared with more conventional sets of measurements, the truss network has the advantage of providing an equal coverage of the entire body (Strauss and Bookstein 1982). In addition to the truss network, six fin measurements were calculated from the landmark coordinates, and the caudal fin area was measured. Consequently, we obtained 30 morphometric variables describing different aspects of body dimensions. To measure the precision of the digitizing approach, 10 individuals were measured five times. The standard deviation over the five replicates of every morphometric variable was estimated for each of the 10 fish. The average standard deviation over 10 fish was used as an estimate of measurement error. The measurement error was always less than 0.5 mm.

Principal components analysis was then used to describe the body shape independent of body size (Jolicoeur 1963). Therefore, all morphometric variables were log-transformed. This procedure allows body size, for which we are trying to control during our comparative analyses, to become an additive component of every variable. The first principal component of the log-transformed data was expected to represent a combination of the morphometric variables correlated to the general body size and was therefore removed from the data set. The dorsal fin height was the only morphometric variable that did not vary with body size. However, such variables dominate the subsequent shape components and artificially influence the importance of these variables. Therefore the dorsal fin height was omitted from the principal components analysis as suggested by Somers (1986). The loadings of the 29 remaining size-corrected morphometric variables from the second and third principal components were used to compare the four fish groups. The significance of the morphological differences between the four groups was assessed using multivariate analysis of variance (MANOVA) followed by Scheffé's post hoc test.

Respirometry

The respirometry system consisted of a transparent Plexiglas® container (24 L; 60 cm × 20 cm × 20 cm) with a lid that could be hermetically sealed. The respirometer was placed in a water bath to maintain water temperature of 15 °C during the experiments. The details of the experimental design are described in Enders et al. (2003) and are presented here only in a summarized version. The respirometer contained two pumps and a bottle-shaped swimming chamber. The shape of the swimming chamber was selected to ensure that fish could not avoid the water flow during the experiments. The narrow neck of the swimming chamber was connected to pump 1 (model 1750; Jacobs Canada Inc., Mississauga, Ontario), which generated the turbulent flow in the swimming chamber by recirculating water within the respirometer. The swimming chamber contained two grids.

The grids consisted of nylon mesh 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). Spatially uniform fine turbulence corresponds to small-scale turbulence without persistent eddies. The downstream grid was designed to force the fish to remain in the swimming chamber without interfering with the flow. Pump 2 (model 402; Powerhead, Montréal, Québec) served two purposes. Before an experiment, pump 2 was used to create water exchange between the respirometer and the aquarium, hence providing oxygenated water to the respirometer. During an experiment, pump 2 was used to transfer water from the respirometer to the oxygen meter. Fish swimming costs were quantified by measuring the oxygen depletion over time with an oxygen meter (InTap 565; Mettler Toledo, Mississauga, Ontario; ±0.01 mg O₂·L⁻¹).

Characteristics of flow structures

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, which determines the maximal flow velocity, (2) the minimal electric current, which determines the minimal flow velocity, (3) the frequency at which the current was reduced, which introduced pulsations into the water flow, and (4) the duration of the reduced current. Flow velocities were measured using an Acoustic Doppler Velocimeter (ADV; Sontek, San Diego, California, USA). The ADV allowed us to record the three orthogonal velocity components of the flow (streamwise, U ; vertical, V ; lateral, W) at a frequency of 25 Hz. The volume sampled by the ADV (0.25 cm³) is located 5 cm away from its probe so that the perturbation of the measured flow by the probe is minimized. Turbulence, quantified at the beginning of the suite of experiments in Canada and in Norway, was aimed at testing the effect of flow conditions on total swimming costs. Turbulence was quantified in the absence of fish to avoid interference caused by fish on the recordings. The presence of fish would not have changed the turbulence faced by the fish. However, if a fish had stayed in the swimming chamber, it would have interfered with the velocity measurements because the ADV measurements are based on the acoustic Doppler effect and the assumption that the particles in the flow have the same velocity as the flow. The fish, however, is actively swimming in chamber, having a ground speed of approximately zero. For every flow condition, a velocity time series was recorded for a period of 5 min. The ADV permitted us to define the settings of the components of the electric current that could create two different flow conditions determined by one mean streamwise flow velocity, \bar{u} (23 cm·s⁻¹) and two different standard deviations of the streamwise flow velocity, u_{SD} (low turbulence condition = 5 cm·s⁻¹; high turbulence condition = 8 cm·s⁻¹). Flow turbulence intensities (standard deviation/mean flow velocity) for each condition were 0.22 and 0.35, respectively. The means and the standard deviations were estimated from the 5-min velocity time series sampled at a frequency of 25 Hz. The two experimental flow conditions were selected for our ex-

periments because they are within the range of mean flow velocities (5–40 cm·s⁻¹; DeGraaf and Bain 1986; Guay et al. 2000) and the range of standard deviations of flow velocity (4–14 cm·s⁻¹) at the focal point of the JAS in nature (Enders et al. 2005). In this article, we use the term high turbulence to facilitate the presentation of our results and not to insinuate that the high turbulence represents a condition close to the maximum turbulence experienced by fish in the field.

Stability and repeatability tests with three velocity time series recorded at the beginning and end of a suite of experiments were conducted in a previous study. These tests demonstrated that our apparatus generates consistent and reproducible turbulent flow structures (Enders et al. 2003). The repeatability of each of the two experimental flow structures created by our apparatus was again tested using a one-way analysis of variance (ANOVA). This ANOVA was performed to compare the mean streamwise flow velocities during the time series recorded before a suite of experimental observations. The repeatability of the standard deviations of the flow velocities was tested using the same approach with Levene's test of the homogeneity of variance (SPSS Inc., Chicago, Illinois, USA).

Total swimming costs

We used a single fish selected at random from our stock of experimental fish for each experiment. The fish was not fed for 2 days before the experiment to avoid increased metabolic rates associated with 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 the introduction of the fish into the swimming chamber, the respirometer was sealed without residual air bubbles. No observation was made below 7.6 mg O₂·L⁻¹ to minimize the influence of low oxygen concentration on fish behavior (Beamish 1978).

We monitored fish behavior during each experiment to ensure that fish were continuously swimming. An image of the position held by the fish within the swimming chamber was automatically registered every 10 min with a web cam (Sony Electronics Inc., Oradell, New Jersey, USA). 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, we assume that if a fish is always in a swimming position during a series of images registered at 10-min intervals and if a fish swims continuously during the last 30 min of an experiment, then it was swimming continuously against the flow structures created by our apparatus. An experiment ended after 6 h, at which time the fish was removed from the respirometer, anaesthetized (clove oil; 0.6 mg·L⁻¹), weighed (g wet mass), and measured (total length, cm). The biological oxygen demand (BOD) was determined within 6 h of an experiment using the same procedure but without fish.

The total oxygen consumption rate of the fish (V_{O_2} ; mg O₂·h⁻¹) was estimated as

$$(1) \quad V_{O_2} = \Delta O_2 / \Delta t \cdot V_W - BOD$$

where ΔO_2 is the difference in oxygen concentration between two successive measurements (mg O₂·L⁻¹), Δt is the

time interval of 0.5 h between two consecutive measurements, V_W (22.6 L) is the volume of water in the closed respirometer, and BOD is the biological oxygen demand by microorganisms in the water ($\text{mg O}_2\cdot\text{h}^{-1}$). Because we measured oxygen concentration within the swimming chamber at 30-min intervals over 6 h, we obtained 12 VO_2 values per experiment. We then calculated the total swimming costs (C_R ; cost of swimming + standard metabolism) as the mean of the VO_2 values obtained for each experiment.

Before statistical analyses, total swimming costs and body masses were log-transformed, and the residuals were tested for normality using graphical probability plots and for homogeneity of variance using Levene's test. A two-way ANOVA was performed to determine the effect of the fish groups and the turbulence intensities on the total swimming costs. In these analyses, body mass was used as a covariate. Scheffé's post hoc test was used to verify which of the four fish groups were significantly different. The two-way ANOVAs were performed using SuperANOVA 1.11 statistical packages (Abacus Concepts Inc. 1991).

Results

Comparison of the morphometric variables for the four different fish groups

Principal components analysis indicated differences in body shape among the four groups of fish (Fig. 2a). The first principal component (PC1) summarized the strong correlations between the morphometric variables and the total body length ($r^2 = 0.88$, $p = 0.001$). The second and third principal components (PC2 and PC3) described the variation in body shape, statistically independent from total body length ($r^2 = 0.07$, $p = 0.15$ and $r^2 = 0.00$, $p = 0.86$, respectively). PC1 accounted for 76.3% of the total variance in the morphometric variables. PC2 explained 6.8% and PC3 accounted for 5.0% of the total variance in morphometric variables (Table 2). PC2 involved a contrast between body depth, caudal fin area, and measurements in the head region. Domesticated fish had positive scores on PC2, indicating a deep body shape with smaller caudal fins and smaller heads, whereas the wild fish and farmed fish from the Sainte-Marguerite River had negative scores on PC2, indicating slender bodies with greater caudal fins and larger heads. The body height of domesticated JAS was 7.9% to 8.6% larger than that of wild JAS. The caudal fin and the head of domesticated JAS were on average 16.7% and 26.7% smaller than those of wild JAS. In this respect, farmed fish from the Imsa River were intermediate between farmed fish from the Sainte-Marguerite River and domesticated fish. The four groups showed significant differences for the PC2 (MANOVA, $F_{[3,79]} = 135.2$, $p < 0.001$). PC3 was defined by tail length and dorsal and anal fin lengths. Farmed fish from the Sainte-Marguerite River scored positively on PC3, indicating shorter tail lengths and smaller dorsal and anal fin lengths, whereas the wild fish and farmed fish from the Imsa River tended to score negatively on PC3, indicating longer tail lengths and larger dorsal and anal fin lengths. The tail lengths of farmed JAS from the Sainte-Marguerite were 19.3% to 17.9% shorter than those of wild JAS. The dorsal and anal fin lengths of farmed JAS of the Sainte-Marguerite

were on average 26.6% and 3.4% smaller than those of wild JAS. Domesticated fish did not score on PC3. Mean PC3 scores differed significantly between the four fish groups (MANOVA, $F_{[3,79]} = 31.2$, $p < 0.001$). Scheffé's post hoc test showed that PC3 scores of wild JAS differed significantly from those of farmed and domesticated JAS ($p < 0.01$). The PC3 scores of farmed fish were significantly different from those of domesticated JAS ($p < 0.01$). However, the PC3 scores of the two groups of farmed JAS from the Sainte-Marguerite River and the Imsa River were not significantly different ($p = 0.98$).

Characteristics of flow structures

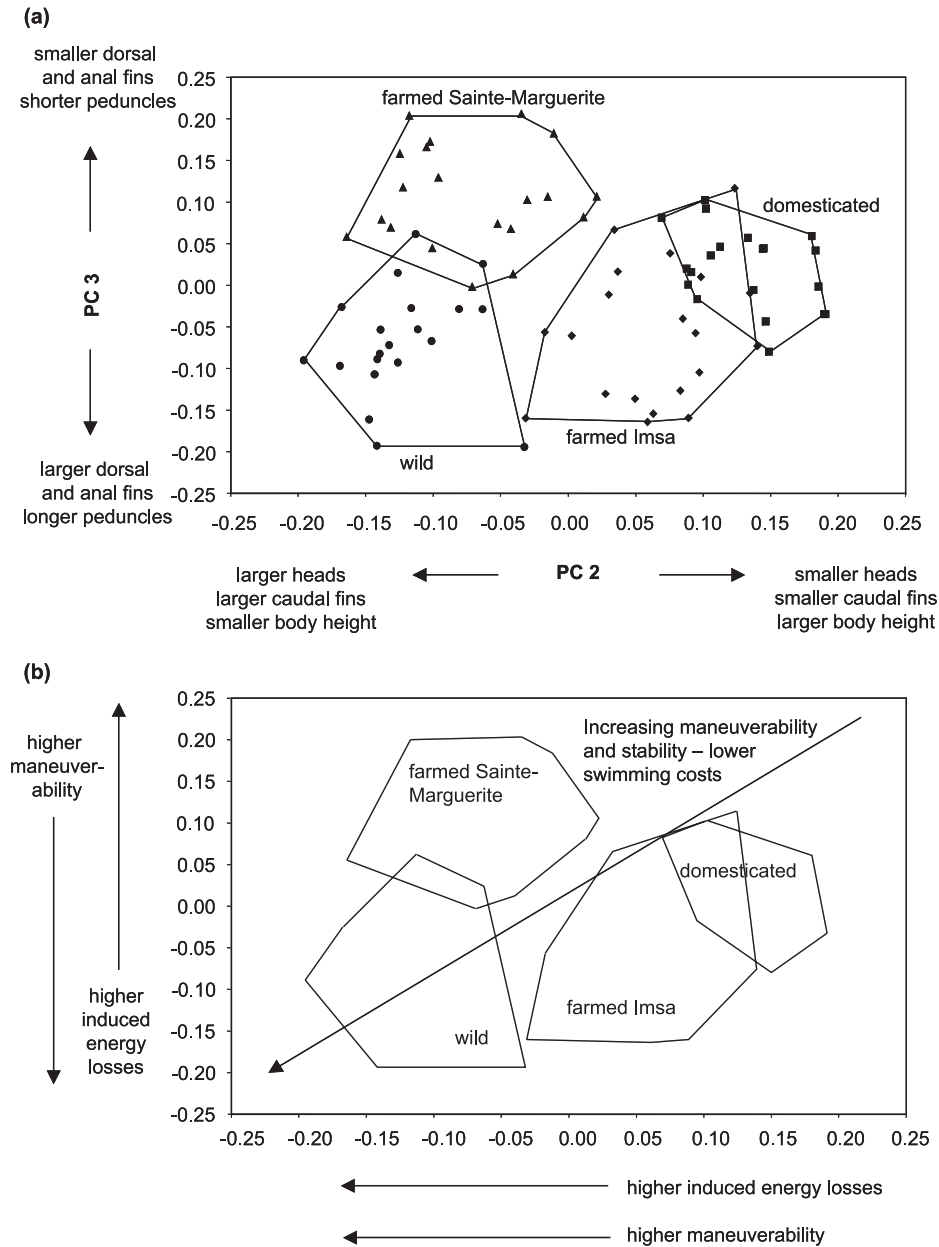
The mean values of the streamwise flow velocities obtained for the two different turbulent conditions were consistent with the targeted value of $23 \text{ cm}\cdot\text{s}^{-1}$ (Table 3). The mean streamwise flow velocities ranged from 23.01 to $23.04 \text{ cm}\cdot\text{s}^{-1}$. Standard deviations of the streamwise flow velocity ranged from 5.13 to $5.15 \text{ cm}\cdot\text{s}^{-1}$ under low turbulent conditions (target = $5 \text{ cm}\cdot\text{s}^{-1}$). Corresponding values for the high turbulent conditions (target = $8 \text{ cm}\cdot\text{s}^{-1}$) ranged from 7.99 to $8.07 \text{ cm}\cdot\text{s}^{-1}$. The turbulence intensity was 0.22 for the low turbulence condition and 0.35 for the high turbulence condition. The mean vertical flow velocities ranged from -0.15 to $0.92 \text{ cm}\cdot\text{s}^{-1}$, with the standard deviation of the vertical flow velocity ranging from 4.92 to $7.56 \text{ cm}\cdot\text{s}^{-1}$. The mean lateral flow velocities were close to zero, ranging from 0.09 to $0.33 \text{ cm}\cdot\text{s}^{-1}$ with standard deviations between 5.41 and $7.69 \text{ cm}\cdot\text{s}^{-1}$.

The time series of the streamwise flow velocity for the two flow conditions clearly indicated that the flow created by our apparatus was turbulent with a range of velocity fluctuations (Fig. 3). For the two turbulence conditions, \bar{u} did not vary significantly among the recordings performed for the four velocity time series (variation = 0.1% , ANOVA, $F_{[3,30003]} = 0.05$, $p = 0.98$). Similarly, for any given flow condition, u_{SD} obtained for the two velocity time series did not vary significantly (variation = 0.4% , Levene's statistic $_{1,15000} = 2.50$, $p = 0.12$, and variation = 1.0% , Levene's statistic $_{1,15000} = 0.55$, $p = 0.81$, respectively). These results confirmed our previous findings that the turbulent flow structures created by our apparatus were repeatable and stable (Enders et al. 2003).

Total swimming costs

Total swimming costs varied fourfold among treatments depending on fish body mass (Fig. 4). The predicted total swimming costs for a 10-g wild JAS at low turbulence intensity ($3.80 \text{ mg O}_2\cdot\text{h}^{-1}$) was 45.9% lower than the predicted value for high turbulence intensity ($5.55 \text{ mg O}_2\cdot\text{h}^{-1}$; Table 4). Total swimming costs differed among the four groups of fish (ANOVA, $F_{[3,38]} = 7.20$, $p = 0.0006$) and increased with turbulence intensity ($F_{[1,38]} = 0.01$, $p = 0.0001$) and body mass ($F_{[1,38]} = 0.03$, $p = 0.0001$). The interaction terms between fish group, turbulence intensity, and body mass were not significant ($0.66 < p < 0.95$) and indicated that the direction of the effect of turbulence intensity and body mass on total swimming costs was similar among fish groups. Total swimming costs of wild fish were not significantly different from those of farmed fish (difference ranging from 2.3%

Fig. 2. (a) Principal components analysis of the morphometric variables of wild fish (●), farmed fish from the Sainte-Marguerite River (▲), farmed fish from the Imsa River (◆), and domesticated fish (■). Morphometric variables, which have loadings on principal component axes 2 and 3, are noted, and arrows indicate the direction of the correlation. (b) Arrows indicate the direction of maneuverability, and induced energy losses increase because of the morphometric variables expressed on principal component axes 2 and 3.



to 11.2%, $p = 0.08$). Similarly, the total swimming costs of the two groups of farmed fish (Sainte-Marguerite River and Imsa River) were not significantly different ($p = 0.73$). However, the total swimming costs for wild fish vs. domesticated fish differed significantly ($p = 0.0001$). Total swimming costs predicted for a 10-g wild fish were 29.2% lower under low turbulence intensity and 15.2% lower under high turbulence intensity than the total swimming costs for domesticated fish (Fig. 5). Total swimming costs predicted for a 10-g farmed fish were also significantly different from those for domesticated fish ($p = 0.01$). The total swimming costs for a 10-g farmed fish were 12.5% (high turbulence in-

tensity) to 16.2% (low turbulence intensity) lower than those for a domesticated fish of the same mass.

Discussion

The morphology of the domesticated JAS has been shown to be different from that of the wild fish, with the head being smaller, the body more robust, and rayed fins smaller (Fleming and Einum 1997). In contrast, wild fish have a more slender body shape and larger fins than domesticated JAS. Our work supports these findings by showing that domesticated fish have deeper bodies and smaller caudal fins and

Table 2. Loadings of the morphometric variables along the first, second, and third principal component axes (PC1, PC2, and PC3, respectively).

Variable	PC1	PC2	PC3	Description
1–2	–0.137	–0.217	0.036	Forehead length
2–17	–0.176	0.013	0.023	Head depth 1
2–16	–0.175	0.020	0.096	Head depth 2
2–14	–0.196	0.016	0.070	Head to pelvic fin
2–3	–0.215	0.009	0.141	Head to dorsal fin
3–16	–0.209	0.145	0.073	Dorsal to pectoral fin
3–14	–0.207	0.301	0.067	Body depth
3–13	–0.198	0.226	0.051	Dorsal to pelvic fin
3–11	–0.198	0.013	0.052	Dorsal to anal fin
3–6	–0.205	–0.146	0.022	Dorsal to adipose fin
6–13	–0.201	0.015	0.032	Pelvic to adipose fin
6–11	–0.199	0.143	–0.065	Anal to adipose fin
6–8	–0.193	0.085	<i>0.209</i>	<i>Adipose to caudal fin ventral insertion</i>
6–7	–0.174	–0.013	<i>0.217</i>	<i>Adipose to caudal fin dorsal insertion</i>
7–11	–0.171	–0.053	0.004	Caudal fin dorsal insertion to anal fin
7–8	–0.206	0.002	0.062	Caudal fin dorsal to caudal fin ventral insertion
8–11	–0.180	–0.052	0.038	Anal fin to caudal fin ventral insertion
11–13	–0.197	–0.057	0.149	Pelvic fin insertion to anal fin insertion
13–16	–0.207	0.038	0.017	Pectoral to pelvic fin
16–17	–0.132	0.597	0.144	Length between premaxilla and pectoral
1–16	–0.139	–0.175	0.070	Snout to below pectoral
1–17	–0.135	–0.254	0.015	Snout to below premaxilla
1–18	–0.153	–0.333	–0.006	Snout to orbit
3–5	–0.155	0.160	<i>–0.586</i>	<i>Dorsal fin length</i>
10–11	–0.211	–0.023	–0.151	Anal fin height
9–11	–0.166	0.105	<i>–0.641</i>	<i>Anal fin length</i>
12–13	–0.193	–0.167	–0.050	Pelvic fin length
15–16	–0.135	–0.082	–0.042	Pectoral fin length
A1	–0.254	–0.309	–0.134	Caudal fin area

Note: Morphometric variables are the distances between the landmarks numbered in Fig. 1. The morphometric variables with important loadings (threshold = 0.2) along PC2 are indicated in bold and along PC3 in italic.

Table 3. Ranges of the mean flow velocity, standard deviation (SD), and minimum and maximum streamwise U , vertical V , and lateral W flow velocity components ($\text{cm}\cdot\text{s}^{-1}$) under low and high turbulence intensities.

		U	V	W
Low turbulence intensity ($0.22 \text{ cm}\cdot\text{s}^{-1}$)	Mean	23.01–23.04	–0.04–0.92	0.09–0.10
	SD	5.13–5.15	4.92–5.09	5.41–5.59
	Minimum	5.23–5.64	–27.64 to –21.89	–26.88 to –21.71
	Maximum	34.98–37.58	21.84–29.73	28.19–28.23
High turbulence intensity ($0.35 \text{ cm}\cdot\text{s}^{-1}$)	Mean	23.01–23.04	–0.15 to –0.01	0.29–0.33
	SD	7.99–8.07	7.35–7.56	7.69–7.70
	Minimum	0.17–0.90	–30.32–29.56	–29.61 to –29.76
	Maximum	44.85–46.91	29.52–30.34	29.95–32.45

heads than wild fish. These morphological differences may affect total swimming costs.

Numerous studies have compared the swimming performance of species characterized by large differences in body morphology (Lighthill 1971; Videler 1993; Webb and Gerstner 2000). However, very little is known about the energetic consequences of relatively minor differences in morphology and shape observed among morphs of a given species. In fact, most studies on swimming performance have focused on steady swimming and fast starts in low-

turbulence flumes or still water. Our results were obtained for fish swimming in highly heterogeneous flow. In turbulent water, costs of swimming may require an assessment of the costs of stabilizing the swimming trajectory in the face of turbulence-induced disturbances. There are no data on the energy costs of stabilization. However, maneuvers that dominate routine swimming time activity budgets (Webb 1991; Krohn and Boisclair 1994; Tang et al. 2000) have been argued to represent a mirror image of a behavior aimed at maintaining stability (Webb 2002). Flow visualization shows

Fig. 3. Velocity time series of 1 min (25 Hz) for the two different flow conditions with a mean flow velocity, \bar{u} , of $23 \text{ cm}\cdot\text{s}^{-1}$ and two standard deviations of the flow velocity, u_{SD} , of (a) $5 \text{ cm}\cdot\text{s}^{-1}$ and (b) $8 \text{ cm}\cdot\text{s}^{-1}$ in the swimming chamber in which juvenile Atlantic salmon (*Salmo salar*) swam during the respirometry experiments.

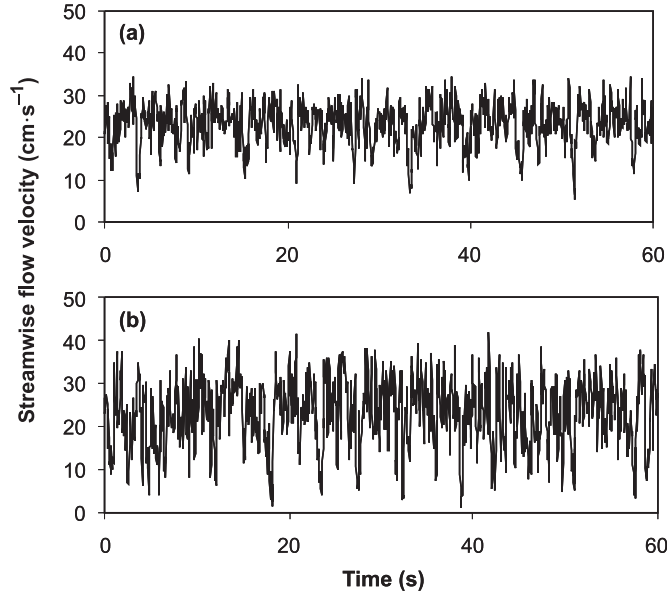
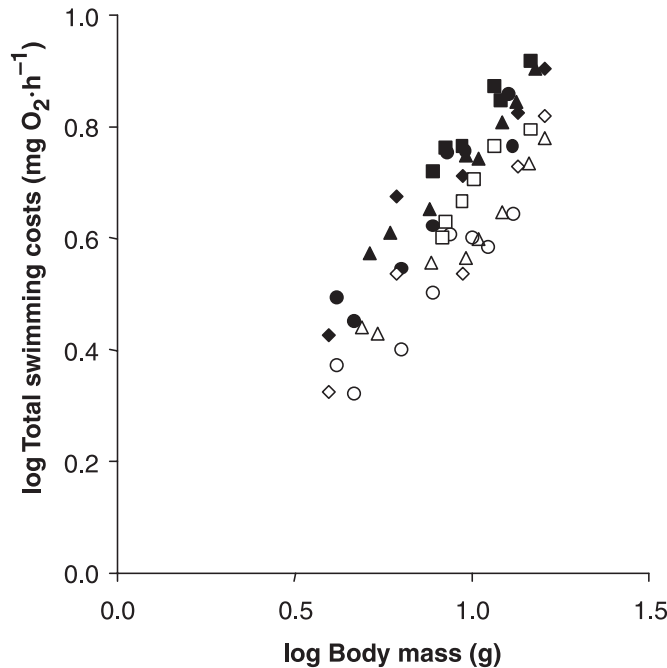
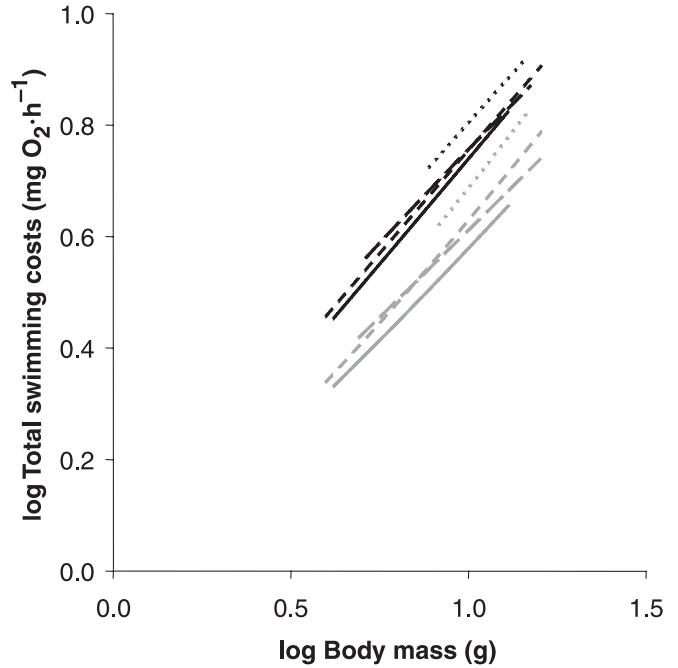


Fig. 4. Total swimming costs of wild fish (●), farmed fish from the Sainte-Marguerite River (▲), farmed fish from the Imsa River (◆), and domesticated fish (■) under low (open symbols) and high (solid symbols) turbulence intensity.



that maneuvers often involve substantial energy losses in vortex rotation (Drucker and Lauder 2003), and hence high induced energy costs are expected. Mechanics and metabolic studies of routine swimming show over tenfold increases in

Fig. 5. Regression lines representing the relationship between body mass and total swimming costs of wild fish (—), farmed fish from the Sainte-Marguerite River (---), farmed fish from the Imsa River (- - -), and domesticated fish (.....) under low (shaded lines) and high (solid lines) turbulence intensity.



energy costs compared with those expected for rectilinear swimming at the same mean speed (Weatherley and Gill 1987; Webb 1991; Boisclair and Tang 1993). It may be expected that stabilizing swimming postures incur similar energy costs. These could outweigh those of rectilinear swimming, so that explanations for the observed differences in swimming costs may be sought in terms of likely effects of morphology on stability.

Numerous effectors are involved in both maneuvers and stability: the body, median fins including the caudal fin, and the paired fins (Webb 2002). The caudal fin may be particularly important in stability because it is large and lies at a large distance from the centre of mass. In general, stability and maneuverability may be facilitated by large caudal, dorsal, and anal fins providing opportunities for large correction forces and a longer caudal peduncle increasing caudal fin torques (Weihs 2002). Larger body depth may reduce the tendency to slip, which is an adaptation to reduced steady swimming costs, but may add to correction costs following a disturbance (Lighthill 1971). Thus, stability is expected to improve as values become smaller for both PC2 and PC3. As a result, wild fish with the most negative values of PC2 and PC3 (smaller body depth and larger fins) may be expected to have the lowest stability costs and hence the lowest swimming costs in turbulent flow. The farmed JAS from the Sainte-Marguerite River with large tails but smaller dorsal and anal fins would be expected to have reduced stability and swimming costs higher than those of the wild fish. Similarly, higher swimming costs of farmed JAS of the Imsa River compared with wild JAS are consistent with intermediate-sized tails. Domesticated JAS with the highest swimming costs had the

largest positive values for PC2 and hence smaller tails and large body heights. Our observations suggest that these characteristics may have the largest consequence on the control of stability and on energetic costs of swimming in turbulent flow. Although there is uncertainty in matching shape and stability, arguments based on the costs of stability may provide the most coherent hypothesis to explain the observed variations in swimming costs among wild, farmed, and domesticated JAS.

Total swimming costs varied with turbulence intensity and among the four groups of fish. The total swimming costs increased by an average factor of 1.4 as standard deviation of the flow velocity increased from 5 to 8 cm·s⁻¹ and as turbulence intensity increased from 0.22 to 0.35. Furthermore, total swimming costs increased with body mass. The effect of body mass and mean flow velocity is well established and is included in all swimming costs models currently available (Beamish 1978; Brett and Groves 1979; Farrell et al. 2003). However, our results indicated that descriptors of flow turbulence such as the standard deviation of the flow velocity or the turbulence intensity may be required to adequately estimate the total swimming costs under turbulent flow conditions. JAS live in gravel-bed rivers characterized by highly turbulent flow. Estimates of swimming costs derived from experiments with minimized flow heterogeneity, such as forced swimming models, may therefore underestimate the actual cost of swimming of JAS in their natural environment. Enders et al. (2003) estimated the magnitude of the effect of turbulence on fish respiration rates by comparing the swimming costs incurred by fish under turbulent flows with those predicted by the forced swimming model of Boisclair and Tang (1993). This analysis indicated that forced swimming models might underestimate swimming costs in turbulent flows by a factor ranging from 2 to 4. Such comparative analysis cannot be performed with the results of the present study because the models of Boisclair and Tang (1993) were developed to estimate net swimming costs (total respiration rate of unfed fish minus the standard metabolic rate of fish). In the present study, we estimated only the total swimming costs of unfed fish. Comparisons between total swimming costs and net swimming costs would be misleading. Calculations of net swimming costs from our data would have required an estimate of standard metabolic rate (SMR) for each fish group. Because such data do not exist for the four fish groups studied and because SMR may vary among fish of different origins within a species (Boily and Magnan 2002; Grisdale-Helland et al. 2002; Trudel et al. 2004), we did not perform the calculation of potentially misleading net swimming costs for our four fish groups. Consequently, in the present study, we estimated the magnitude of the effect of turbulence on fish respiration rates by developing a new forced swimming costs model. This model was based on the data set used by Boisclair and Tang (1993) with the exceptions that the dependent variable was not net swimming costs but total swimming costs and that temperature was added as an independent variable. Indeed, before developing their model, Boisclair and Tang (1993) subtracted from published total swimming costs the SMR values provided in the papers they used to perform the empirical analysis. Hence, the development of a new forced swimming model (forced total swimming costs (FTSC), mg O₂·h⁻¹) simply required

the reversal of the computational approach used by Boisclair and Tang (1993). This procedure resulted in the development of the following FTSC model

$$(2) \quad \log_{10}\text{FTSC} = 0.96\log_{10}M + 0.23\log_{10}\bar{u} + 0.67\log_{10}T - 1.85$$

where FTSC is the total swimming costs under minimized flow heterogeneity (mg O₂·h⁻¹), M is the body mass of fish (g wet), \bar{u} is the mean flow velocity (cm·s⁻¹), and T is the water temperature (°C). Body mass explained 79% of the variance in the FTSC model ($F_{[3,114]} = 162.35$, $R^2 = 0.81$, $p < 0.0001$). The new FTSC model predicted that the total swimming costs of a 10-g fish swimming at a speed of 23 cm·s⁻¹ in a flow with minimized flow heterogeneity characterizing forced swimming experiments and at a water temperature of 15 °C should be 1.58 mg O₂·h⁻¹ (95% confidence intervals: 1.35–1.85 mg O₂·h⁻¹). The total swimming costs that we estimated for 10-g wild JAS swimming against our low and high turbulence intensities were, respectively, 2.4-fold (3.80 mg O₂·h⁻¹) and 3.5-fold (5.55 mg O₂·h⁻¹) higher than predicted by the FTSC model (Table 4). Differences between the predictions by the FTSC model and our observations were more pronounced for domesticated JAS, ranging from 3.1-fold (low turbulence intensity, 4.91 mg O₂·h⁻¹) to 4.0-fold (high turbulence intensity, 6.31 mg O₂·h⁻¹). Observations on fish behavior suggested that swimming in a turbulent flow should increase the swimming costs of fish (McLaughlin and Noakes 1998; Pavlov et al. 2000). Our study therefore supports the suggestion that total swimming costs in flow of fluctuating velocities are 2.4- to 4.0-fold higher than in steady flow conditions.

Our results indicated that total swimming costs of wild and farmed JAS were not significantly different. We therefore conclude that swimming costs models obtained using farmed fish can be employed to estimate the swimming costs of wild fish. However, total swimming costs of wild and farmed JAS differed significantly from the total swimming costs of domesticated JAS. The differences were larger between wild and domesticated JAS (15.2% to 29.2%) than between farmed and domesticated JAS (12.5% to 16.2%). These results suggest that swimming costs models developed with wild or farmed fish should not be applied to domesticated fish, and vice versa.

The observed morphometric differences among the four fish groups may not be the only explanation for the differences in the total swimming costs. Three alternate hypotheses might explain the observed difference between the total swimming costs of wild and domesticated JAS.

First, this difference may result from a conditioning effect. Throughout their freshwater life, wild JAS are exposed to turbulent flow with mean focal point velocities of 5–40 cm·s⁻¹ (DeGraaf and Bain 1986). When feeding on invertebrate drift, fish are exposed to even higher mean flow velocities of 10–120 cm·s⁻¹ (Morantz et al. 1987). Therefore, wild JAS may be better conditioned to swim against the experimental flow than farmed or domesticated fish. Conditioning improves growth rate and food conversion efficiencies and changes condition factor and body composition (see Davison (1997) for a review). JAS increased their sprint performance when exposed to flows of 1–2 body

Table 4. Total swimming costs and 95% confidence intervals (in parentheses) of 10-g fish under two turbulence intensities characterized by the same mean flow velocity of 23 cm·s⁻¹ and two different standard deviations of 5 cm·s⁻¹ and 8 cm·s⁻¹.

	Group 1	Group 2	Group 3	Group 4
Total swimming costs (mg O ₂ ·h ⁻¹) under low turbulence intensity	3.80 (3.41–4.24)	4.14 (3.91–4.38)	4.32 (3.54–5.26)	4.91 (4.62–5.22)
Factor A	2.4	2.6	2.7	3.1
Total swimming costs (mg O ₂ ·h ⁻¹) under high turbulence intensity	5.55 (4.91–6.27)	5.70 (5.48–5.93)	5.65 (4.74–6.73)	6.39 (6.13–6.66)
Factor B	3.5	3.6	3.6	4.0

Note: Four fish groups were compared: (1) wild fish, (2) farmed fish from the Sainte-Marguerite River, (3) farmed fish from the Imsa River, and (4) domesticated fish. Observed total swimming costs were compared with predictions of a new forced swimming model developed. Factor A represents the factor by which the predictions of the forced swimming model underestimated observed total swimming costs under low turbulence intensity, and factor B is under high turbulence intensity.

lengths (BL)·s⁻¹ (McDonald et al. 1998). Unconditioned JAS sustained swimming for 231 s in a flow of 38 cm·s⁻¹ (5–8 BL·s⁻¹), whereas fish conditioned to 1 BL·s⁻¹ sustained swimming for a longer period of 294 s, and fish conditioned to 2 BL·s⁻¹ sustained swimming for an even longer period of 324 s. Our findings that total swimming costs of wild JAS are lower than those of domesticated fish, regardless of the turbulence intensity, are consistent with the hypothesis that conditioning may have provided an advantage to wild fish. However, farmed JAS from the Imsa River and domesticated JAS were raised and held in flow tanks characterized by identical flow velocities. Hence, despite similar conditioning, total swimming costs of farmed fish were significantly different from those of domesticated fish. In addition, although wild and farmed fish experienced different conditioning, we found no significant difference between total swimming costs for these two groups of fish. These comparisons suggest that variables other than conditioning may play a more important role in determining swimming costs. This interpretation is supported by our observation that none of the fish from the four groups was fatigued or exhausted by the experimental conditions. JAS of all groups seemed to be physically capable of swimming continuously over a 6-h period. In their natural environment, JAS likely swim against turbulent flow during shorter time periods to attack invertebrate drift, to explore habitat, or to defend their territory. Therefore, the duration of the experiment may be seen as energetically demanding for the fish. Despite the high demand, fish from the four groups did not show any signs of exhaustion, such as drifting back against the downstream grid. Furthermore, we did not observe a relationship between C_R and time since the beginning of the experiment ($0.00 < r^2 < 0.19$, $0.22 < p < 1.00$). Hence, our experimental conditions did not appear to cause significant fatigue to any of the fish groups during the experiment.

Second, differences in total swimming costs among fish groups may be due to differences in body composition among these groups (Kleiber 1975). Differences in body composition may be related to differences in diet among the fish groups studied. Although we have no data regarding the body composition of the fish studied, it may be hypothesized that this trait differed between wild and farmed or domesticated fish owing to differences in diet: wild fish were fed natural prey items, whereas farmed and domesticated fish were fed with commercial diets. This hypothesis is supported by the study of McDonald et al. (1998), who found

2.2 times higher lipid concentrations in aquaculture JAS than in wild JAS. We are not aware of any study investigating the difference in lipid concentrations between farmed and domesticated JAS. Adipose tissue is metabolically inert relative to lean tissue and does not significantly contribute to the overall metabolism (Hayward 1965). As such, we would expect individuals with high lipid concentrations to have lower mass-specific standard metabolic rates than lean individuals. The results of our study are contrary to the expectation based on the effect of body composition on standard metabolic rate. We observed the highest mass-specific total swimming costs in domesticated, presumably more lipid rich, JAS. Although it is difficult to predict the effect of body composition on mass-specific total respiration rate, another argument suggests that body composition may have played a relatively minor role in our study. Farmed and domesticated fish were held under the same rearing conditions during their entire lives and they were fed the same diet. This suggests that they should have similar body composition. Yet, the farmed fish had mass-specific total respiration rates significantly lower than those of domesticated fish, and the farmed fish (presumably high fat composition) had mass-specific total respiration rates similar to those of wild fish (presumably low fat composition). Hence, body composition may not have had a large effect in our study.

Finally, it may be hypothesized that differences in total swimming costs among the four groups of JAS may be due to SMR that differ among these groups. Variations of SMR between different fish species have been well established (Herrmann and Enders 2000; Steffensen 2002). Trudel et al. (2004) demonstrated that SMRs might also vary, depending on body mass and water temperature, from 0% to 200% among closely related species of Pacific salmon (*Oncorhynchus* spp.). However, only a few studies considered within-species variation of SMR. Boily and Magnan (2002) concluded that there was a statistically significant difference between the SMR of brook charr (*Salvelinus fontinalis*) having different body shapes. Their work does not provide the data required to quantify the magnitude of the difference between fish having different body shapes. Hence, our data do not allow us to reject the hypothesis that SMR variations among the four different groups of JAS may have influenced the total swimming costs.

The observed higher total swimming costs of domesticated JAS may result in higher costs of habitat utilization and ultimately reduce survival rate of domesticated JAS

once they have escaped into a natural environment. Our study may provide additional support for the suggestion that the invasion of escaped domesticated salmon in natural environments may not only increase the competition for natural resources, but also result in a change in the fitness of wild populations through a decrease in swimming efficiency in turbulent flow if interbreeding occurs.

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