Relationship between individual variation in morphological characters and swimming costs in brook charr (*Salvelinus fontinalis*) and yellow perch (*Perca flavescens*)

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Summary

The objective of this study was to examine if individual variation in morphological characters is related to swimming costs in wild and domestic brook charr, and in wild yellow perch. Our results indicate that absolute swimming cost was higher in wild and domestic brook charr individuals having a stout body shape, and these individuals are therefore less efficient swimmers. These results are consistent with field observations that described relationships between individual variation in morphology and habitat use in salmonids. Further analyses indicated that standard metabolic rates were higher in individuals having a stout body shape, and that net swimming cost was not related to body shape. Accordingly, the higher swimming cost of stout individuals is probably an indirect consequence of an increase in standard metabolic rate. In wild yellow perch, absolute and net swimming costs were higher in individuals having a stout body shape and a low aspect caudal fin, and standard metabolic rate was not related to body shape. Therefore, in contrast to brook charr, individual variation in the swimming cost of yellow perch appears to be related to morphological characters that affect drag and thrust forces, which is consistent with previously published inter-specific observations.

Key words: brook charr, *Salvelinus fontinalis*, yellow perch, *Perca flavescens*, swimming cost, standard metabolic rate, morphology, body shape.

Introduction

Individual variation in body shape and fin morphology is often correlated with habitat use in freshwater fish populations (e.g. Robinson and Wilson, 1994; Snorrason et al., 1994). Based primarily on studies that investigated interspecific relationships between morphology and swimming ability (Webb, 1982, 1984a,b), such intra-specific relationships between morphology and habitat use are often assumed to reflect individual specialization to meet locomotor demands associated with habitat use (e.g. Bourke et al., 1997; Dynes et al., 1999; McLaughlin and Grant, 1994). While there are numerous examples of correlations between habitat use and variation in morphological characters, there is no direct empirical evidence to support the existence of a functional relationship between individual variation in morphology and swimming efficiency within a species.

Variation in morphological characters can affect swimming ability in three different ways; it can affect the ability to perform precise maneuvers, the ability to perform powerful acceleration, or the energetic cost of sustained swimming (Webb, 1982). Morphological characters that are likely to affect the energetic cost of sustained swimming are those related to thrust production and to drag forces such as body shape, caudal peduncle depth, the size and aspect ratio of the caudal fin (Webb, 1982; Webb and Weihs, 1986). Of these, the overall body shape of fishes is particularly interesting because of its possible link with energy reserves. The accumulation of energy reserves may lead to an overall body shape that is more stout and less elongated, which can potentially increase drag forces and, as a consequence, swimming costs. Such a conflict between the accumulation of energy reserves and locomotor efficiency is well documented in small birds, where the accumulation of fat causes an increase in the energetic cost of flight (Chai and Millard, 1997), which may even lead to an increase in mortality caused by predation (Gosler et al., 1995).

In this study, we analyzed metabolic and morphological data obtained as part of another study (P. Boily, D. Boisclair and P. Magnan, unpublished results) to investigate the existence of functional relationships between individual variation in morphological characters and swimming costs. For this purpose, we used wild and domestic brook charr (*Salvelinus fontinalis*), a species for which individual variation in morphology is often correlated to habitat use (Bourke et al.,

1997; Dynes et al., 1999; McLaughlin and Grant, 1994; McLaughlin, 2001). Charrs in general can exhibit high levels of phenotypic plasticity and may not be representative of most teleosts. Therefore, we also used the yellow perch (*Perca flavescens*), an unrelated freshwater species that lives in similar oligotrophic lakes and has a swimming mode similar to brook charr (Scott and Crossman, 1974; Lindsey, 1978; Webb, 1984a).

Materials and Methods

Animals and holding conditions

Three groups of fish were used in this study: wild brook charr (WBC), domestic brook charr (DBC) and wild yellow perch (WYP). The size of the fish had to be less than 30 g in order to swim freely in respirometers. WBC were collected from the littoral zone of Lake Charme (Mastigouche Reserve, Quebec, Canada) in May 1995, DBC were obtained from a commercial fish farm in June 1995 and WYP were collected in October 1995 from the littoral zone of Lake Hertel (Mont Saint-Hilaire, Quebec, Canada).

All fish were maintained in large temperature-controlled, dechlorinated freshwater tanks. Water quality was tested regularly throughout the study and fish appeared to be in good health. The photoperiod was maintained at 12 h:12 h L:D and fish were fed *ad libitum* once a day with commercial trout pellets (WBC and DBC) or equal parts of commercial trout pellets and Tetramin flakes (WYP). When fishes were first brought to the laboratory, the water temperature was set to a value similar to that of their origin. Gradually, water temperature was adjusted by 1 °C per day to the coldest experimental water temperature, i.e. 8 °C for DBC and 12 °C for WYP as they did not swim consistently at 8 °C in preliminary experiments. Because of the limited number of individuals from the WBC group that had an appropriate size, metabolic rate measurements on this population were obtained only at 12 °C. To minimize mortality, water temperature was changed from the coldest to warmest temperatures (from 8 or 12 °C, to 16, 18 and 20 °C). The experiments began after fish had acclimated to laboratory conditions for 2 months and were completed less than 3 months afterwards. After the 2 month acclimation period, charr and perch seemed to behave and swim normally in their holding tanks, without any erratic movements as the experimenter approached. We assumed that any bias due to laboratory rearing conditions would be additive on fish behavior and physiological performances. Fish were acclimated to their experimental temperature for 6–12 days prior to measurements and any given fish was used at only one water temperature.

Open-flow respirometry system and experimental protocol

Respirometers were modified Blazka-type swim tunnels (3.37±0.03 l), similar to those described by Beamish et al. (1989), and for which the velocity profile is approximately rectilinear. Respirometers were connected to an open-flow system, through which fresh, oxygenated water flowed at a rate ranging from 20 to 80 ml min^{-1}, depending on the experimental temperature. Water velocities (15–35 cm s^{-1}) were adjusted by varying the voltage of the submersible pump that created water movement inside each respirometer; the relationship between pump voltage and water speed was calibrated using a miniature water speed meter (OTT, Kempten, Germany; blade number 2–3). A mildly electrified (0–5 V) metallic grid at the end of the swim tunnel was used to motivate the fish to swim against the water current. Respirometers were submerged into a temperature-controlled water tank (±0.5 °C). Water flowed continuously at a stable rate through all respirometers.

Six to eight respirometers were connected simultaneously to the respirometry system and a single fish was placed in each respirometer. Solenoid valves directed water flow so that the oxygen concentration of the water entering and leaving each chamber was measured once every hour. Oxygen concentration was measured by directing the water flow to sub-sampling chambers in which the temperature-compensated probe of an oxygen meter (YSI model 54) was located. A computer using a BASIC program (W. Beamish, personal communication) recorded outputs from oxygen meters. Oxygen meters were calibrated daily using air-saturated water maintained at the experimental temperature, and their accuracy was verified weekly using the Winkler titration method modified for small volumes (APHA, 1989). Water flow rate through each respirometer was measured twice daily. Rates of O_2 consumption ($\dot{M}_{O_2}$; mg O_2 h^{-1}) were corrected for the oxygen consumption occurring in empty respirometers and for the time lag associated with open-flow respirometry systems (Niimi, 1978).

Two days prior to experiments, between 16:00 h and 18:00 h, 6–8 individuals were isolated and fasted in a tank in which the water was recirculated from the respirometry system. On the day prior to the experiments, between 16:00 h and 18:00 h, fish were individually placed in a respirometer in which current speed was set at 15 cm s^{-1}. The following morning, starting at 08:00 h, rates of oxygen consumption were recorded while gradually increasing current speed every 2 h, by intervals of 5 cm s^{-1}, up to 35 cm s^{-1}. Fish swam normally in the respirometers, rarely touching the electrified grid, until current speed became too high for them to maintain a stable position. When this occurred, current speed was reduced to 15 cm s^{-1}, and fish were left in the respirometers overnight. The following morning, fish were killed with an overdose of MS-222, weighed (M) to the nearest 0.01 g, and measured to the nearest 0.05 mm for the following morphological characters: standard length (L_s), maximum width (W_{max}) and depth (D_{max}), length of pectoral fin (L_p), depth of caudal peduncle (D_p), length (L_c) and depth (D_c) of caudal fin. For each individual, maximum cross-sectional surface area (SA, in cm^2), assuming an ellipsoid shape, was calculated as:

$$SA = \pi W_{max} D_{max} \times 4^{-1}. \qquad (1)$$

When SA exceeded 10 % that of the respirometer, current speed was corrected for the solid-block effect, as described by Keen and Farrell (1994).

To avoid using individuals that used anaerobic metabolism to a significant extent, only data from individuals that swam consistently at at least three swimming speeds, for 2 h at each swimming speed, and for which the $\log_{10}\dot{M}_{O_2}$ increased linearly with swimming speed, were kept for further analysis; approximately 10 % of individuals were rejected because they did not meet these criteria. Furthermore, few DBC individuals and no WYP individuals were able to swim consistently at 8 °C. To maintain consistency between species and to avoid large variation in sample size between experimental water temperatures, only data obtained at 12 °C and higher were kept for further analyses, leaving a sample size of 10 WBC, 53 DBC and 57 WYP (Table 1).

Analyses

All morphological characters were significantly and linearly related to standard length ($P<0.05$). Accordingly, size-adjusted morphological characters (W_{max}', D_{max}', L_p', D_p', L_c' and D_c') were calculated as the residuals of the linear regression of each character as a function of L_s (Packard and Boardman, 1987). The aspect ratio of the caudal fin (AR_c) was calculated by dividing D_c by L_c. A body shape index (BSI) was calculated as the residuals of the following model:

$$\log_{10}M = a + b\log_{10}L_s,\qquad(2)$$

where a and b are fitted constants. This relationship was significant for all groups at all temperatures ($P<0.05$). Individuals with positive BSI values have higher masses than predicted according to their length, and are therefore more stout in shape than individuals with negative BSI values, which are more elongated. Size adjustments of morphological characters and calculations of BSI were performed separately at each experimental temperature to be consistent with the calculation of absolute and net swimming cost indices (see below).

For each individual, standard metabolic rate (SMR) was estimated using the following model:

$$\log_{10}\dot{M}_{O_2} = \alpha + \beta U,\qquad(3)$$

where α and β are fitted constants and U is the current speed. The intercept of α is the estimate of $\log_{10}$SMR, and SMR was calculated as 10^α. For each individual at each current speed, net swimming costs (Csw_net) were calculated by subtracting SMR from $\dot{M}_{O_2}$.

Measurements of $\dot{M}_{O_2}$ and of Csw_net were obtained at multiple current speeds for each individual. To eliminate pseudoreplication, an absolute swimming cost index (swCI) was calculated, for each individual, as the average of the residuals of Equation 3 applied separately to each group at each water temperature. A net swimming cost index (swCI_net) was calculated in a similar manner, by replacing $\log_{10}\dot{M}_{O_2}$ with $\log_{10}$Csw_net in Equation 3. These regressions were significant for all groups at all experimental temperatures ($P<0.05$). Individuals with positive values for these indices have on average higher $\dot{M}_{O_2}$ or Csw_net than predicted from current speed at a given water temperature, and therefore have higher

Table 1. *General morphological characteristics of the experimental fish*

Group (N)	Mass (g) mean ± S.D. (range)	Length (cm) mean ± S.D. (range)
DBC (53)	12.6±5.54 (5.8–27.6)	11.5±1.26 (9.5–14.5)
WBC (10)	19.4±4.62 (11.9–26.0)	13.5±1.02 (12.0–15.2)
WYP (57)	11.9±6.38 (4.4–27.0)	10.0±1.82 (7.2–13.8)

DBC, domestic brook charr; WBC, wild brook charr; WYP, wild yellow perch.

swimming costs than individuals with negative values. The difference between swCI and swCI_net is that swCI_net is independent of SMR. Analyses of variance indicated that both indices differed significantly among individuals, and individual repeatability values, calculated from the results of these analyses of variance (Lessells and Boag, 1987), were high (0.87 for swCI and 0.75 for swCI_net), indicating that these indices reliably reflect individual variation in swimming costs rather than random noise. Residuals were calculated at each water temperature separately, instead of including water temperature as a variable in the models, because the effects of current speed changed according to water temperature (P. Boily, D. Boisclair and P. Magnan, unpublished data). Similarly, an SMR index (SMRI) was calculated at each water temperature as the difference between the group mean and the individual's value of $\log_{10}$SMR. These calculations were done separately at each water temperature, and logarithmic values of SMR were used for consistency with the calculations of swimming cost indices. None of the indices (swCI, swCI_net, SMRI) changed significantly according to water temperature and nearly identical results were obtained if water temperature was included as an independent variable for the calculation of indices.

For each group of fish, stepwise multiple linear regression analyses (forward selection, $P<0.05$ to be included) were performed to test the significance of the effects of BSI and size-adjusted morphological characters on sw*CI*, sw*CI*_net and SMRI. In addition, standard length and water temperature were included as independent variables, to eliminate their potentially confounding effects. Standard length was used as a measure of body size, for consistency with size adjustments of morphological characters and calculations of BSI; nearly identical results were obtained if body mass was used instead. Furthermore, D_{max}', W_{max}' and D_p' were excluded from these analyses because they were highly correlated to BSI ($r>0.69$, $P<0.001$). All statistical analyses were performed using SYSTAT version 8.03 with a 5 % level of significance.

Results

For all three groups of fish (DBC, WBC and WYP), the absolute swimming costs index was positively related to the body shape index, indicating that, independently of variation in size and water temperature, fish with stout body shapes have

Table 2. *Results from stepwise, multiple linear regression analyses of the effects of body size, water temperature and morphological characters on the absolute swimming cost index*

Group	Variable	Coefficient	P	Overall r^2
DBC	BSI	1.49	<0.001	0.43
	$\log_{10}L_s$	1.24	<0.005	
WBC	BSI	2.25	<0.05	0.56
WYP	BSI	0.920	<0.05	0.63
	$\log_{10}L_s$	1.61	<0.001	
	T_w	0.0152	<0.005	
	$A\!R_c$	−0.756	<0.01	

DBC, domestic brook charr; WBC, wild brook charr; WYP, wild yellow perch; BSI, body shape index; L_s, standard length; T_w, water temperature; $A\!R_c$ aspect ratio of caudal fin.

higher swimming costs than slender individuals (Table 2). In addition, the absolute swimming costs index was negatively related to aspect ratio of the caudal fin in WYP, indicating that individuals with high-aspect caudal fins have lower swimming costs than individuals with low-aspect caudal fins. For both groups of charr, there was no significant relationship between the net swimming cost index and any morphological characters (Table 3). In contrast, the net swimming cost index was significantly related to the body shape index and to the aspect ratio of the caudal fin in WYP (Table 3) with coefficients, significance levels and r^2 values similar to those obtained for the absolute swimming cost index. These results suggest that the effects of morphological characters on swimming costs are dependent on standard metabolic rate (SMR) for brook charr but not for yellow perch. This was confirmed by the fact that standard metabolic rate index was positively related to the body shape index in both groups of charr, but not for the yellow perch (Table 4).

Table 3. *Results from stepwise, multiple linear regression analyses of the effects of body size, water temperature and morphological characters on the net swimming cost index*

Group	Variable	Coefficient	P	Overall r^2
DBC	NS			
WBC	NS			
WYP	BSI	1.55	<0.05	0.53
	$\log_{10}L_s$	1.88	<0.001	
	T_w	0.0180	<0.05	
	$A\!R_c$	−1.14	<0.01	

DBC, domestic brook charr; WBC, wild brook charr; WYP, wild yellow perch; BSI, body shape index; L_s, standard length; T_w, water temperature; $A\!R_c$ aspect ratio of caudal fin.
NS, no significance found for any variable.

Table 4. *Results from stepwise, multiple linear regression analyses of the effect of body size, water temperature and morphological characters on the standard metabolic rate index*

Group	Variable	Coefficient	P	Overall r^2
DBC	BSI	2.18	<0.001	0.38
	$\log_{10}L_s$	1.71	<0.01	
WBC	BSI	4.31	<0.05	0.52
WYP	$\log_{10}L_s$	1.05	<0.001	0.21

DBC, domestic brook charr; WBC, wild brook charr; WYP, wild yellow perch; BSI, body shape index; L_s, standard length.

Discussion

Our results indicate that the effect of individual variation in body shape on absolute swimming costs is similar for all three fish groups investigated, but that the mechanism underlying this relationship differs between species. In brook charr, wild and domestic, individuals that were stout in shape had higher absolute swimming costs than individuals that were slender in shape. These results are consistent with field observations indicating that young brook charr found in fast-running waters tend to be slender in shape compared to individuals found in slow-running waters (McLaughlin and Grant, 1994). At first sight, these results also appear to support the assumption that morphological differences of brook charr living in fast-running waters or in the pelagic zone of lakes reflect local specialization that favors sustained swimming by reducing drag forces (Bourke et al., 1997; Dynes et al., 1999; McLaughlin and Grant, 1994). Yet, further analyses indicated that this is not the case. Because absolute swimming costs are not independent of SMR, its relationship with the body shape index can be the result of higher drag forces or SMR values in individuals that are more stout. If the relationship between the absolute swimming costs and the body shape index is caused by variation in drag forces, then the net swimming cost index should also be positively related to the body shape index, which was not observed in our experimental brook charr. Our results therefore indicate that the relationship between the absolute swimming costs and the body shape index is not likely to be caused by drag forces, which is an assumption frequently made when discussing field observations of variation in morphology in relation to habitat use (Dynes et al., 1999; McLaughlin and Grant, 1994). Rather, this relationship is likely to be an indirect consequence of individual variation in SMR, which was confirmed by the positive relationship between the SMR and body shape indices for both groups of brook charr.

Our method to calculate a body shape index is very similar to methods commonly used to estimate condition in salmonids and other fish species (Chellappa et al., 1995; Simpson et al., 1992; Wootton and Mills, 1979). Therefore, the positive relationship between SMRI and the body shape index may

reflect a trade-off between two opposing selective forces. On the one hand, high levels of energy reserves could increase the fitness of individuals through higher reproductive investments; it is known that surplus energy is invested in growth and reproduction, and that higher fecundity and larger eggs increase survivorship rates (Moyle and Cech, 1996). On the other hand a higher body shape index could be disadvantageous because of the associated increase in maintenance costs (SMR), which also results in an increase in absolute swimming costs. This relationship between the SMR index and the body shape index could be the expression of a reaction norm (Stearns, 1992), allowing different individuals to use different habitats (i.e. stout individuals, the littoral zone, and slender individuals, the pelagic zone) (see Dynes et al., 1999; Proulx and Magnan, 2001). This reaction norm could still be present in the genetic expression of domestic brook charr because they have been reared in Québec hatcheries for less than a century. In this context, the trade off between higher reproductive investment and higher SMR could be balanced by the differential costs of foraging in these habitats, which are presumed to be lower in the littoral zone (lower swimming costs and higher habitat profitability; Héroux, 1998). Trade-offs between the accumulation of energy reserves and locomotor efficiency are well documented in small birds, where an increase in storage of energy reserves increases the cost of flight because of the excess weight (Chai and Millard, 1997), and may even lead to larger mortality rates due to predation (Gosler et al., 1995). The main difference with our results is that a better condition is not directly related to an increase in locomotion costs *per se*, but rather to an indirect increase in swimming costs because of higher SMR. This explanation of the mechanism involved in increasing SMR as the body shape index increases is speculative, however, because body shape indices can be poor predictors of body composition (Chellappa et al., 1995).

Similar to brook charr, the absolute swimming cost index of yellow perch was positively related to the body shape index. However, in contrast to brook charr, the net swimming cost index was also positively related to the body shape index, while the SMR index was not. Furthermore, both absolute and net swimming cost indices significantly increased as the aspect ratio of the caudal fin decreased. Taken together, these results suggest that, in yellow perch, the relationship between morphological characters and swimming costs is the result of variation in drag and thrust forces rather than variation in SMR. While the effect of subtle variation in morphology on drag and thrust forces can be hard to predict (Vogel, 1994), our results suggest that slender yellow perch individuals produce less turbulence and therefore less drag, and that yellow perch with high-aspect caudal fins produce thrust more efficiently, both of which would lead to lower swimming costs. Such relationships between body shape, caudal fin shape and swimming efficiency are well documented at the interspecies level (Webb, 1984b, 1988).

In conclusion, our results indicate that absolute swimming costs increase in stout individuals for all three fish groups investigated. While a similar trade-off between the accumulation of energy reserves and locomotion efficiency may be present in both species, the mechanism generating it appears to differ. In brook charr, the increase in swimming costs associated with a stout body shape is related to an increase in SMR, while this is not the case for yellow perch, where the increase in swimming cost may be the result of increased drag forces.

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