FULL PAPER

Distinguishing between juvenile anadromous and resident brook trout (*Salvelinus fontinalis*) using morphology

Geneviève R. Morinville · Joseph B. Rasmussen

Abstract Phenotypic variation linked to habitat use has been observed in fish, both between and within species. In many river systems, migratory and resident forms of salmonids coexist, including anadromous (migrant) and resident brook trout, *Salvelinus fontinalis*. In such populations, juvenile anadromous (migrant) brook trout, prior to migration, inhabit regions of higher current velocity than residents. Because it is more costly to occupy fast currents than slow currents, differences in morphology minimizing the effects of drag were expected between the two forms. As predicted, migrant brook trout were found to be more streamlined (narrower and shallower bodies) than resident brook trout, and these differences persisted into the marine life of the fish. Migrants also exhibited shorter pectoral fins, which facilitate pelagic swimming, indicating that migrants, prior to their migration to the sea, possess the appropriate morphology for swimming in open water habitats. The reported differences between migrants and residents were powerful enough to derive discriminant functions, using only five of the seven measured traits, allowing for accurate classification of brook trout as either migrants or residents with an overall correct classification rate of 87%. Importantly, this study contributes to the notion that a link exists between morphology, habitat use, metabolic costs and life-history strategies.

Keywords Fish shape · Habitat use · Coexistence · Salmonid · Metabolic costs · Energetics · Sea trout · Migration · Anadromy

G. R. Morinville · J. B. Rasmussen
Department of Biology, McGill University,
1205 Dr. Penfield Ave., Montreal,
QC, Canada H3A 1B1

G. R. Morinville (✉)
Rescan Environmental Services, Sixth Floor,
1111 West Hastings, Vancouver, BC, Canada V6E 2J3
e-mail: genevieve.morinville@mail.mcgill.ca

J. B. Rasmussen
Department of Biological Sciences, Water Institute for Semi-Arid Ecosystems (WISE), University of Lethbridge, 4401 University Dr. West, Lethbridge, AB, Canada T1K 3M4

Introduction

Phenotypic variation in morphological traits implicated in predator evasion, feeding and habitat use have been commonly reported in the literature. For example, crucian carp, *Carassius carassius*, increase their body depth as a defense mechanism against gape-limited piscivores (Holopainen et al. 1997; Pettersson & Brönmark

1999) and Arctic charr have evolved morphological adaptations in mouth and snout shape according to their benthivorous or planktivorous–piscivorous feeding behaviors leading to four sympatric morphs in an Icelandic lake (Skúlason et al. 1989).

Phenotypic variation linked to habitat use has been observed, both in warm-water stream fishes including cyprinids and percids (Wood and Bain 1995), and in salmonids, both within and between species (Riddell and Leggett 1981; Bisson et al. 1988; Swain and Blair 1989). It has been consistently demonstrated that fish inhabiting faster currents are more streamlined (shallow-bodied versus deep-bodied) than those inhabiting slow currents. A more streamlined morphology in fast water reduces swimming costs by minimizing the effects of drag (Pettersson and Brönmark 1999). Drag is influenced by fish shape, the square of the current speed and the Reynolds number (Re) of the fish (Vogel 1994). Re is positively related to fish size, the undisturbed velocity, and water temperature (kinematic viscosity). Pressure drag predominates at high velocities such that changes to a more streamlined body morphology, as indicated by the fineness ratio (ratio of standard length to body depth), leads to a reduction in the drag coefficient (Webb 1975; Blake 1983). A high ratio between span and length of their caudal fin ('aspect ratio') also reduces the effects of drag (Webb 1984, 1988).

Using field observations, Bisson et al. (1988) demonstrated that differences in fin size and body shape could predict the stream channel locations utilized by juvenile salmonids. Coho salmon, *Oncorhynchus kisutch*, prefering pools, possess a deep and laterally compressed body with large median and paired fins, facilitating transitory maneuvering ability. In contrast, steelhead trout, *Oncorhynchus mykiss*, possess a fusiform body shape with short median fins and large paired fins, allowing for efficient swimming in fast water, whereas cutthroat trout, *Salmo clarki*, morphology is intermediate to these species, consistent with its habitat preferences.

Within-species variations in morphology have also been reported. In Atlantic salmon, individuals inhabiting a river with higher average flow velocities were more streamlined in shape and had larger paired fins than those inhabiting a river with lower average flows (Riddell and Leggett 1981). Similarly, Taylor and McPhail (1985) found heritable morphological differences between interior and coastal populations of juvenile coho salmon. Interior populations were more streamlined in shape and possessed smaller median fins than coastal populations, most likely the result of their greater need for efficient swimming during migrations, because these interior populations originated from locations that were further away from the sea. Interestingly, anadromous (migrant) and non-anadromous counterparts have also been observed to differ morphologically such that the former is better suited for prolonged swimming (Taylor and McPhail 1986; Taylor and Foote 1991). Fish may thus evolve morphological adaptions specific to their life-history strategy and exhibit these adaptations throughout their life stages.

In certain rivers, brook trout populations comprise a mixture of anadromous (migratory) and resident forms (Thériault and Dodson 2003; Morinville and Rasmussen 2003, 2006). It has been suggested through various lines of support including bioenergetic and stable isotope analyses that in such populations, juvenile anadromous (migrant) brook trout, prior to migration, inhabit regions of higher current velocity in freshwater than residents (Morinville and Rasmusen 2003). A recent comparative study also tends to supports this—fast habitats were occupied more frequently in streams containing migratory brook trout (migrant-resident streams) relative to riffle habitats of streams comprising only resident trout (resident-only streams) (Morinville and Rasmussen 2006).

In the wild, brook trout tend to swim actively and feed in the water column and continue to swim against the current even in fast waters (Keenleyside 1962). As for other salmonids, trout occupying fast currents are expected to possess a more streamlined morphology in order to minimize the costs associated with swimming. Such observations have been reported for brook trout as early as in their first year of life (McLaughlin and Grant 1994), although the differences may not necessarily persist over time (Imre et al. 2001). Because brook trout migrate as early as at age 1+ (Thériault and Dodson 2003), it is likely

that morphological differences exist between juvenile anadromous (prior to migration) and resident brook trout. Distinguishing between the two forms at early life stages will allow for future studies investigating coexistence and ultimately, the underlying mechanisms of anadromy.

The main objectives of this study were thus to (1) determine whether coexisting anadromous (migrant) and resident brook trout differ in body morphology, (2) whether the observed differences coincide with habitat use expectations, and (3) whether any observed differences can be used as a tool for future field identification. It is predicted that within migrant-resident streams (streams with resident and anadromous forms), migrant brook trout will be more streamlined than residents. Specifically, it is predicted that resident brook trout will have wider and deeper bodies (higher drag morphology) compared to migrant brook trout. Fin sizes including caudal, pelvic and pectoral are also expected to differ between migrants and residents. Furthermore, it is predicted that resident fish from migrant-resident streams will be less streamlined than those of resident-only streams because of their previously reported differences in habitat use. We also predicted that any observed pre-migratory morphological differences between migrants and residents would persist (carry over) into the marine life of the fish. That is, sea trout migrants were expected to continue to differ morphologically from residents throughout their life stages.

Study site and methods

Study site

This study was conducted in the Ste. Marguerite River (SMR) system in the Saguenay region of Quebec, Canada (48°27′ N, 69°95′ W). The SMR flows into the estuarine Saguenay River that further empties into the St. Lawrence River. The SMR system is home to the largest anadromous brook trout population of the Saguenay River basin (Lesueur 1993). Populations of anadromous Atlantic salmon and brook trout, as well as resident brook trout, co-occur in the region.

Streams containing such populations of coexisting brook trout and Atlantic salmon will be referred as 'migrant-resident' streams. Anadromous brook trout down-migrate from mid-May to early-June, as early as age 1+ to the estuarine Saguenay River (Thériault and Dodson 2003). Stream reaches above man-made barriers, such as poorly constructed culverts and natural barriers, such as waterfalls, will be referred as 'resident-only' streams as these only contain resident brook trout.

Fish collection

The genus *Salvelinus* exhibits the least pronounced anadromy of salmonids (Power 1980). No obvious smoltification occurs in migrant brook trout (McCormick et al. 1985) making it very difficult to differentiate a migrant from a resident until the moment of migration. In migrant-resident streams, we distinguished migrants as trout captured in trap nets during the downstream migration period, whereas those captured in streams following the migration period were defined as residents. Tagging studies confirmed that this method was effective in separating migrants from residents (Thériault and Dodson 2003). Although the trout remaining in the system after migration are considered residents, an unknown proportion of these trout may actually consist of future migrants.

Migrants were captured from two migrant-resident streams, Morin (spring 2001–2003) and Portage (spring 2002). Migrants were also captured upon sea entry in the Saguenay River estuary every 2–4 weeks from the Ste. Marguerite Bay or from nearby Anse-de-Roche (both sites are located in the Saguenay River) between May and October of 2002. These trout will be referred to as sea trout.

All resident brook trout were captured beginning mid-June using a backpack electro-fisher (Smith-Root, Inc. model 12A), following the migration period. Residents were sampled in three migrant-resident streams including Morin (summer 2001–2003), Portage (summer 2002) and Édouard (summer 2002), and in two resident-only streams including Épinette (summer 2002) and La Prairie (summer 2002).

Morphological trait measurements

All fish morphological trait measurements were performed in the field. Both fork (FL; to the nearest mm) and standard length (SL; to the nearest mm) were measured for all brook trout. Previously reported empirical evidence and theory, in addition to logistical constraints, guided the selection of morphological traits to be measured. Morphological traits included maximum body depth (taken as distance from start of dorsal fin to start of pelvic fin), maximum body width (taken at front of dorsal fin), peduncle depth, caudal fin height, pectoral fin length and pelvic fin length (Imre et al. 2001; Peres-Neto and Magnan 2004). A needlepointed divider was employed to measure the length of each body trait. This involved stretching the divider to the desired length, subsequently placing the divider on field book paper, and tracing the distance between the two needle ends. These lines were then subsequently measured using calipers (to the nearest 0.05 mm). All fish were released live. This procedure was done in order to minimize fish handling time and any subsequent stress on the fish because of the numerous measurements being taken in the field. The same person (G.R. Morinville) took all measurements.

Morphological comparisons

In order to detect morphological differences between migrants and residents, all morphological traits were ln-transformed and regressed upon ln-transformed standard length for pooled migrants and residents of a migrant-resident stream (Morin) for years 2001–2003. Residuals obtained from these regressions were retained for further analyses. Individual *t*-tests were subsequently conducted for each morphological trait using the residuals to compare migrants and residents within a stream over the 3 years of study.

Comparisons between residents of migrant-resident and resident-only streams were also conducted because of their previously reported habitat use differences (Morinville and Rasmussen 2006). Linear regressions of each ln-transformed morphological trait upon were conducted for pooled residents captured in migrant-resident streams (Édouard, Morin and Portage) and resident-only streams (Épinett and La Prairie) in 2002. Residuals were retained from each morphological trait for subsequent *t*-tests comparing the two types of streams.

Discriminant function analysis (DFA) was conducted on 2002 data to assess whether the overall differences observed between (1) pooled migrants (Morin and Portage), (2) pooled residents of migrant-resident streams (Édouard, Morin and Portage), and (3) pooled residents of resident-only streams (Épinette and La Prairie) using all measured traits were powerful enough to accurately predict the life-history group to which an individual fish belonged. Residuals obtained from group-specific ln-transformed linear regressions of each morphological trait as a function of fish size (standard length) were retained for DFA, and all fish were reclassified according to the model generated by DFA to obtain the correct reclassification rate.

Finally, comparisons between residents of migrant-resident streams and sea trout were also conducted in order to determine whether any observed differences between migrants and residents persist post-migration, that is, whether the differences persist into the marine life of sea trout. Linear regressions of each ln-transformed morphological trait upon ln-transformed standard length were conducted for pooled residents captured in migrant-resident streams (Édouard, Morin and Portage) and for sea trout captured in the Saguenay River in 2002. Residuals were retained from each morphological trait for subsequent *t*-tests comparing residents and sea trout. All statistical analyses were conducted using SYSTAT (Version 10.2).

Comparisons of form drag between life-history forms

Form drag was estimated for the different life-history forms including migrant-resident migrants and residents, resident-only residents and sea trout captured in 2002 using two surrogate measures: (1) fineness ratio (ratio of standard length to maximum body depth, and (2) circular ratio (ratio of maximum body depth to maximum body width)

indicative of prolonged swimming (Webb 1975; Sibbing and Nagelkerke 2001). A higher fineness ratio indicates a more elongated body shape with a ratio of about 5 indicating low drag. A lower circular ratio indicates a more circular shaped body with a ratio of 1 indicating a perfect circle. Both the fineness and circular ratio were compared between residents from migrant-resident and resident only streams, migrants and sea trout using one-way analysis-of-variance (ANOVA) and subsequent pairwise Tukey comparisons.

Field identification and validation

An interactive stepping DFA (Alfonso 2004) was conducted using all possible size-free ratios of morphological traits of migrant and resident data from Morin 2002 in order to select the variables that best classified migrants and residents. The purpose of this was to develop a simple method, using the fewest number of size-free ratios, for discriminating between future migrants and residents well before the spring outmigration (i.e., during the previous summer when fish could be easily caught by electrofishing). Variables were selected using both statistical and biological information until an overall classification rate of at least 85% was achieved. The model incorporated size-free ratios rather than residuals (in comparison to that presented in earlier section) in order to simplify the model, and thus in the process, making it accessible to all field workers and fishery managers. The resultant function was then applied to fish captured in Morin in 2001 and 2003, in addition to trout captured in 2002 resident-only streams in order to assess the validity of the model.

Results

Fish collection

In total, 2561 fish were measured in the field across all sites and years. Migrants captured in traps installed on Morin Stream and Portage Stream and measured ranged in size between 93.3 mm and 117.9 mm (Table 1). Residents captured in migrant-resident streams (Édouard, Morin and Portage streams) ranged in length from 96.4 mm to 119.6 mm, while those from resident-only streams (Épinette and La Prairie streams) ranged in length from 101.9 mm to 113.1 mm. Sea trout captured in the Saguenay River, including sites in the Ste. Marguerite Bay and Anse-de-Roche, were larger, ranging in length from 149.7 mm to 164.2 mm.

Morphological comparisons

Migrants versus residents

Significant regressions were detected for pooled migrants and residents from Morin Stream for all ln-transformed morphological traits across all 3 years of study (Table 2). Residuals from these regressions consistently indicated that Morin Stream migrants were more streamlined than residents, possessing shallower maximum body depths and smaller body widths (Fig. 1). In addition, Morin migrants consistently had shorter pelvic and pectoral fins than residents, suggesting temporal persistence for these traits. In contrast, variations across years existed for both peduncle depth and caudal height. Peduncle depths of migrants were shallower than residents in two of the 3 years (2001 and 2003). Caudal heights were also shorter in two of the 3 years (2001 and 2002).

Migrant-resident stream residents versus resident-only stream residents

Significant regressions were detected for pooled residents from migrant-resident and resident-only streams for all ln-transformed morphological traits across all years (Table 3). Residuals from these regressions indicated that residents from migrant-resident streams were more streamlined than residents from resident-only streams, possessing shallower body depths and peduncle depths, and smaller body widths. In addition, migrant-resident stream residents had shorter caudal, pelvic and pectoral fins.

Migrants versus migrant-resident and resident-only stream residents

A complete DFA was used with the known a priori separation of migrants, migrant-resident

Table 1 Number and mean fork length (±1 SE) of sampled resident, migrant and young-of-the-year (YOY) brook trout from resident-only (res-only) and migrant-resident streams, and Saguenay River (sea) sampling sites

Site	Site type	Fish type	Year	Mean fork length (mm)	Range (mm)	N
Épinette	Resident-only	Resident	2002	101.9 ± 1.9	66–155	118
La Prairie	Resident-only	Resident	2002	113.1 ± 4.2	53–184	45
Édouard	Migrant-resident	Resident	2002	97.6 ± 1.9	60–218	175
Morin	Migrant-resident	Migrant	2001	93.3 ± 1.4	50–179	197
		Resident		116.8 ± 2.6	53–256	198
		Migrant	2002	96.6 ± 1.3	65–186	285
		Resident		98.2 ± 1.5	58–227	419
		Migrant	2003	100.1 ± 1.4	56–156	226
		Resident		96.4 ± 1.4	62–168	211
Portage	Migrant-resident	Migrant	2002	117.9 ± 3.9	63–264	110
		Resident		119.6 ± 13.9	51–195	11
Saguenay River	Sea	Sea trout	2001	149.7 ± 3.1	73–311	257
			2002	164.2 ± 3.5	79–275	192

and resident-only stream residents. Residents from both stream types showed the most overlap in multivariate space, but were distinct from migrants, with resident-only trout being most distinct from migrants ($U = 0.365$, $F_{6,12} = 112.7$, $P < 0.005$; Fig. 2). The DFA model correctly reclassified (jackknifed classification) 91% of migrants, 74% of resident-only residents and 65% migrant-resident residents for an overall correct classification of 74%. Only 2.3% of migrants were misclassified as resident-only fish and 6.5% as residents from migrant-resident streams. The lower classification rate of residents from resident-only streams stems mostly from misclassifying 24.5% of fish as migrant-resident residents; only 1.9% of resident-only fish were misclassified as migrants. A higher proportion of residents from migrant-resident streams were misclassified as migrants (11.7%) and an even larger proportion as residents from resident-only streams (23.8%), leading to the lowest classification rate overall.

Migrant-resident streams versus Saguenay River sea trout

Significant regressions were detected for pooled residents from migrant-resident streams and sea trout from the Saguenay River for all ln-transformed morphological traits (Table 4). Residuals from these regressions indicated that sea trout were more streamlined than residents from migrant-resident streams, possessing shallower

body depths and peduncle depths, in addition to smaller body widths. Sea trout also had shorter caudal, pelvic and pectoral fins.

Comparisons of form drag between life-history forms

Fineness ratios (standard length to maximum body depth) varied significantly (ANOVA: $F_{3,1354} = 291.9$, $P < 0.001$) between 2002 resident-only stream residents, migrant-resident stream residents, migrants and sea trout (all at $P < 0.001$; Fig. 3a). Similarly, the bodies of migrants and sea trout were significantly more circular (ratio of maximum body depth to maximum body width is closest to 1) than those of residents from migrant-resident and resident-only streams (ANOVA: $F_{3,1354} = 61.7$ $P < 0.001$; Fig. 3b). Although no statistically significant differences existed between migrants and sea trout ($P = 0.062$), significant differences were found between residents from migrant-resident and resident-only streams (both have $P < 0.001$). Overall, migrants and sea trout had the most elongated and circular body form, and thus possessed a drag-efficient morphology compared to residents from resident-only streams that possessed a less elongated and circular body form.

Field identification and validation

Using an interactive forward stepping DFA with Morin 2002 data, three size-free ratios

Table 2 Regression statistics from ln-transformed morphological trait length as a function of ln-transformed standard length, residuals and statistical comparisons using t-tests between brook trout migrants (M) and residents (R) of Morin Stream from 2001 to 2003 for six morphological traits

Year	Trait	n	Pooled regression		Life-history form	Residuals			P
			P	R^2		Mean	SE	t	
2001	Depth	197	<0.005	0.91	M	–0.067	0.0037	19.4	$P < 0.005$
		198			R	0.066	0.0058		
	Width	186	<0.005	0.88	M	–0.078	0.0050	18.6	$P < 0.005$
		198			R	0.073	0.0063		
	Peduncle	175	<0.005	0.94	M	–0.037	0.0046	11.3	$P < 0.005$
		198			R	0.033	0.0041		
	Caudal	168	<0.005	0.88	M	–0.086	0.0057	20.6	$P < 0.005$
		193			R	0.075	0.0054		
	Pelvic	172	<0.005	0.94	M	–0.028	0.0048	8.4	$P < 0.005$
		198			R	0.024	0.0040		
	Pectoral	173	<0.005	0.93	M	–0.021	0.0051	5.6	$P < 0.005$
		197			R	0.018	0.0048		
2002	Depth	285	<0.005	0.91	M	–0.058	0.0040	–21.2	$P < 0.005$
		419			R	0.040	0.0027		
	Width	285	<0.005	0.91	M	–0.042	0.0045	–12.9	$P < 0.005$
		417			R	0.029	0.0033		
	Peduncle	285	<0.005	0.91	M	0.0072	0.0049	2.29	$P = 0.022$
		419			R	–0.0049	0.0028		
	Caudal	248	<0.005	0.91	M	–0.066	0.0043	–19.6	$P < 0.005$
		401			R	0.041	0.0033		
	Pelvic	285	<0.005	0.92	M	–0.033	0.0039	–12.3	$P < 0.005$
		417			R	0.022	0.0026		
	Pectoral	285	<0.005	0.93	M	–0.035	0.0036	–13.3	$P < 0.005$
		418			R	0.024	0.0027		
2003	Depth	222	<0.005	0.73	M	–0.10	0.0033	33.6	$P < 0.005$
		211			R	0.11	0.0055		
	Width	222	<0.005	0.80	M	–0.069	0.0037	22.3	$P < 0.005$
		211			R	0.073	0.0053		
	Peduncle	223	<0.005	0.77	M	–0.072	0.0040	23.3	$P < 0.005$
		209			R	0.077	0.0051		
	Caudal	195	<0.005	0.88	M	0.011	0.0044	-2.92	$P = 0.004$
		205			R	–0.010	0.0056		
	Pelvic	225	<0.005	0.81	M	–0.053	0.0037	19.2	$P < 0.005$
		211			R	0.057	0.0043		
	Pectoral	225	<0.005	0.84	M	–0.045	0.0037	16.5	$P < 0.005$
		211			R	0.048	0.0043		

were selected using both statistical and biological information, including depth to standard length ratio (DEP_LTH), peduncle to caudal height ratio (PED_CAUD) and pectoral to standard length ratio (PECT_LTH). The following function was derived for Morin 2002 using the standardized within variance canonical discriminant functions, within sample means (m_{year}) and standard deviations (SD$_{year}$; Table 5) to classify brook trout as either migrant or resident:

$$
\begin{aligned}
F = {} & (0.728)(\text{DEP\_LTH} - m_{year})(\text{SD}_{year})^{-1} \\
& + (-0.719)(\text{PED\_CAUD} - m_{year})(\text{SD}_{year})^{-1} \\
& + (0.386)(\text{PECT\_LTH} - m_{year})(\text{SD}_{year})^{-1}
\end{aligned}
$$

(1)

If $F < 0$, trout are classified as migrant, and if $F > 0$, trout are classified as resident. This function correctly classified 94.3% of migrants and 81.8% of residents from Morin 2002 brook trout
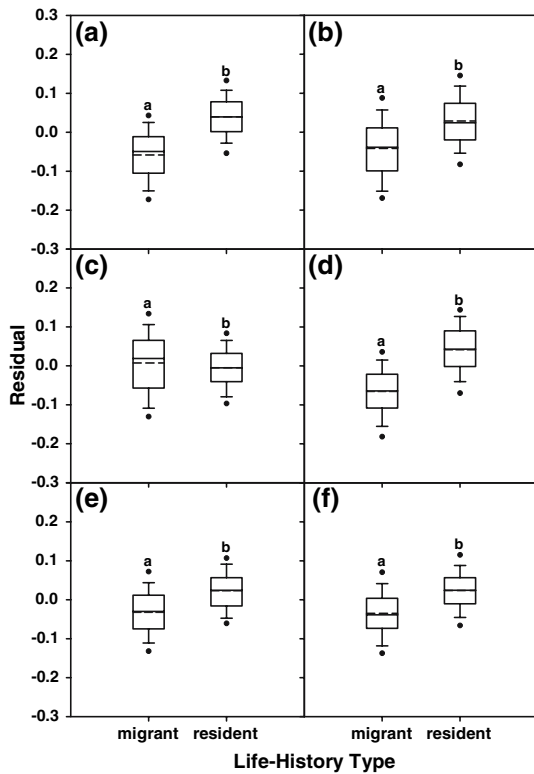
Fig. 1 Mean residuals (broken lines) of ln-transformed (**a**) body depth; (**b**) body width; (**c**) peduncle depth; (**d**) caudal fin height; (**e**) pelvic fin length; and (**f**) pectoral fin length regressed on ln-tranformed standard length for 2002 Morin Stream brook trout migrants and residents. Different letters indicate significant differences at $P < 0.05$ between life-history types
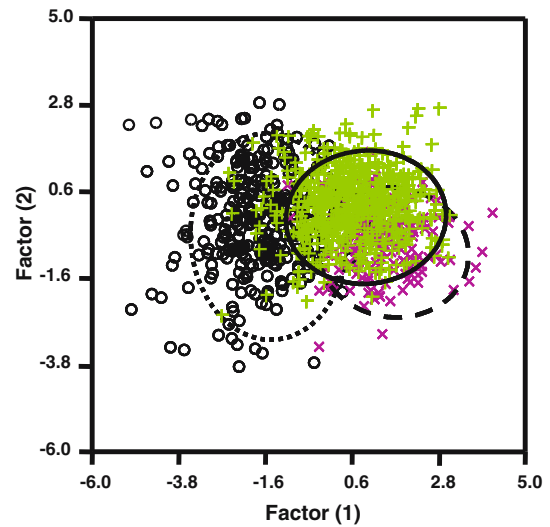

Fig. 2 Bivariate plot of the first two canonical variables of the linear discriminant function performed using migrants (circles, dotted line), resident-only stream residents (diagonal crosses; dashed line) and migrant-resident stream residents (crosses; solid line). Confidence ellipses are centred on the centroid of each life-history form. The first canonical variable (eigenvalue = 1.486) captured 94% of the difference among the groups. Significant differences existed between the three groups ($U = 0.365$, $F_{6,12} = 112.7$, $P < 0.005$). The model obtained correctly reclassified 91% of migrants, 74% of resident-only residents and 65% migrant-resident residents for an overall correct classification of 74%

Table 3 Regression statistics from ln-transformed morphological trait length as a function of ln-transformed standard length, residuals and statistical comparisons using *t*-tests between brook trout residents from 2002 pooled migrant-resident (Édouard, Morin and Portage streams; R) and pooled resident-only streams (Épinette and La Prairie streams; RO) for six morphological traits

Trait	Life-history form	n	Pooled regression		Mean	SE	t	P
			P	R^2				
Depth	RO	163	<0.005	0.95	0.044	0.0047	11.3	$P < 0.005$
	R	602			–0.012	0.0023		
Width	RO	162	<0.005	0.93	0.018	0.0063	3.60	$P < 0.005$
	R	599			–0.0047	0.0028		
Peduncle	RO	163	<0.005	0.95	0.036	0.0044	9.54	$P < 0.005$
	R	602			–0.0096	0.0022		
Caudal	RO	160	<0.005	0.94	0.020	0.0046	4.13	$P < 0.005$
	R	577			–0.0052	0.0029		
Pelvic	RO	163	<0.005	0.94	0.0061	0.0037	1.43	$P = 0.15$
	R	599			–0.0015	0.0026		
Pectoral	RO	163	<0.005	0.94	0.0113	0.0038	2.68	$P = 0.008$
	R	600			–0.0029	0.0026		

Table 4 Regression statistics from ln-transformed morphological trait length as a function of ln-transformed standard length, residuals and statistical comparisons using *t*-tests between brook trout residents from 2002 pooled migrant-resident (Édouard, Morin and Portage streams; R) and Saguenay River sea trout (Sea) for six morphological traits

Trait	Life-history form	*n*	Pooled regression		Mean	Residuals		*P*
			P	*R²*		SE	*t*	
Depth	Sea	192	<0.005	0.97	−0.028	0.0045	7.78	*P* < 0.005
	R	604			0.0090	0.0023		
Width	Sea	192	<0.005	0.97	−0.020	0.0047	4.69	*P* < 0.005
	R	601			0.0064	0.0028		
Peduncle	Sea	192	<0.005	0.97	−0.026	0.0034	7.83	*P* < 0.005
	R	604			0.0084	0.0023		
Caudal	Sea	184	<0.005	0.96	−0.044	0.0045	9.72	*P* < 0.005
	R	579			0.014	0.0030		
Pelvic	Sea	192	<0.005	0.94	−0.055	0.0035	13.4	*P* < 0.005
	R	601			0.018	0.0029		
Pectoral	Sea	192	<0.005	0.94	−0.060	0.0042	14.4	*P* < 0.005
	R	602			0.019	0.0028		

leading to an overall correct classification rate of 86.6% ($U = 0.42$, $F_{3,649} = 298.8$, $P < 0.001$).

The above function was employed to assess its validity for other sampling years, using the same canonical discriminant functions as above but using sample means and standard deviations specific to 2001 and 2003 samples (Table 5). In 2001, the function accurately classified 92.2% of migrants and 89.6% of residents, for an overall classification of 90.8%. Similarly in the year 2003, the function accurately classified 90.8% of migrants and 83.7% of residents, for an overall correct classification of 87.2%.

The same function was also applied to 2002 resident-only streams, using the function above, and the 2002 means and standard deviations. The function correctly predicted 96.3% of the 'pure' residents as being residents ($n = 160$). The function thus appears to work well across years and sites.

Discussion

Morphological differences between anadromous and resident brook trout

The present study compares morphological characteristics of anadromous (migrant) and resident brook trout of the Ste. Marguerite River system, Quebec, Canada in order to establish a link between morphology, habitat use, bioenergetics and life-history strategies. Migrant brook trout from Morin Stream, a migrant-resident stream, were found to be more streamlined than resident brook trout; they were both slimmer and less deeply-bodied indicating that migrants are better suited for swimming in fast waters than residents. Importantly, these differences persisted across years, suggesting that these characteristics may be selected for in mixed populations (i.e., those comprised of both migratory and resident individuals).

Morphological differences among brook trout using different habitats have been detected as early as age 0+ in resident populations (McLaughlin and Grant 1994). Young-of-the-year (YOY) brook trout using faster current velocities had shallower body depths compared to those using slower currents, giving support to the morphological differences observed in older trout (older than 0+) in this study. However, contrary to our findings, YOY utilizing fast currents in the wild (McLaughlin and Grant 1994) and YOY raised in fast waters (Imre et al. 2002) had larger caudal fin heights than those using slow currents. Moreover, such observations did not persist over time (Imre et al. 2001), suggesting the presence of other mechanisms. Other mechanisms could include differences in developmental rates (Martin 1949), physiology (such as standard metabolic rates) or behaviour, whereby certain
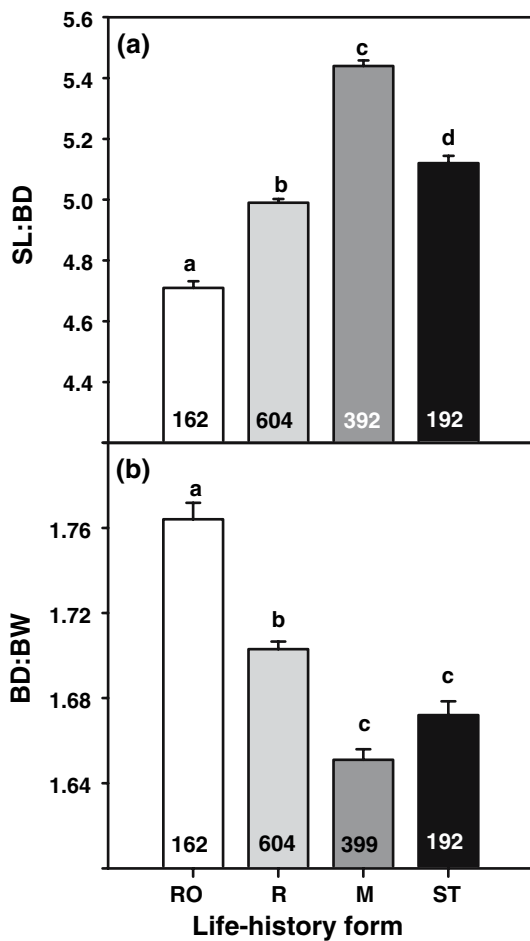
Fig. 3 Ratios of (a) standard length to maximum body depth (SL:BD; fineness ratio), and (b) maximum body depth to maximum body width (BD:BW; circular ratio) for 2002 resident brook trout from resident-only (RO) and migrant-resident streams (R), migrant brook trout (M) and sea trout (ST). Different letters above bars indicate significant differences at p < 0.001 between life-history forms. Numbers in bars indicate sample size

Table 5 Within year means, standard deviations and sample sizes for depth to standard length ratio (DEP_LTH), peduncle to caudal height ratio (PED_CAUD) and pectoral to standard length ratios (PECT_LTH) selected in field identification for Morin 2001 to 2003 brook trout

Ratio	Year	Mean	SD	N
DEP_LTH	2001	0.208	0.021	358
	2002	0.216	0.016	647
	2003	0.202	0.034	398
PED_CAUD	2001	0.312	0.031	358
	2002	0.323	0.036	647
	2003	0.343	0.053	398
PECT_LTH	2001	0.156	0.011	358
	2002	0.386	0.012	647
	2003	0.156	0.018	398

adaptations may be important at small sizes but not necessarily so at large sizes. In addition, provided there is a genetic basis to the differences, selection mechanisms in resident populations may differ from mixed populations such that the same morphological characteristics are not selected for or that the traits are present but selection is weak.

In addition to possessing a streamlined morphology that is better adapted for swimming, migrants were found to have shorter pectoral fins and shorter pelvic fins compared to residents. No

such differences were observed in YOY brook trout (lake strain) reared under slow and fast flow conditions (Imre et al. 2002). Slower growth of pelvic and pectoral fins may be selected for migrants in order to allow for immediate adaptation to pelagic swimming upon sea entry, since sea trout continue to exhibit short pelvic and pectoral fins throughout their ontogeny. Pectoral fins of lacustrine benthic-feeding brook trout were longer than those of pelagic-feeding ones (Bourke et al. 1997), the former facilitating slow and precise maneuvering (Webb 1984). Short pectoral fins, important for cruising, are required for searching efficiently for prey in open water habitats (Ehlinger 1990). Shorter pectoral fins also reduce drag (Drucker and Lauder 2003). Similarly, benthic feeding Arctic charr, characterized by stocky bodies, also possessed longer fins than streamlined piscivorous–planktivorous feeders (Skúlason et al. 1989, and references therein).

Sea trout also continued to be more streamlined in shape than residents, possessing slimmer and shallower body depths, as well as shallower peduncle depths. Similar differences were observed in a Nova Scotia population of migrant and resident brook trout where newly returning sea trout to freshwater had more cylindrical bodies and shorter fins than freshwater trout (Wilder 1952). This same pattern was observed even though the trout were larger (average size of 170 mm) and older than SMR fish (80% of migrants were at age 3+ compared to SMR system where almost 100% migrate before the age of 3+). The adaptations leading to anadromy

thus seem consistent across populations, regardless of the age or size at migration.

Efficient prolonged swimming requires a streamlined body shape of about equal depth and width, and a length/depth ratio around 5 to minimize drag (Sibbing and Nagelkerke 2001). Thus brook trout exhibiting all life-history forms have hydrodynamically efficient body forms, although trout captured during outmigration and at sea had the highest fineness ratio (ratio of standard length to maximum body depth), in addition to having the most circular body shape compared to residents from migrant-resident and resident-only streams. The morphology of migrants and sea trout thus produces the lowest drag. Thus overall, the variations in body shape reported here are consistent with previously reported studies regarding morphology and habitat use.

It should be noted that differential sampling periods may have contributed to the observed differences in body condition (body depth and width) because migrants were sampled in early spring following winter, a period associated with low feeding and growth. However, our results showed that residents from migrant-resident streams were also more streamlined than residents from resident-only streams, possessing narrower and shallower bodies, and thereby supporting initial predictions. The observation that the morphological differences among residents become less apparent at large sizes, which results in a steeper relationship between trait length and size, is logical as the older and larger brook trout of migrant-resident streams are most likely 'true' residents, because the majority of trout that migrate leave by the age of 2+. In addition, differences in body condition were not likely due to smoltification because brook trout do not experience physiological transformations prior to migration (Hoar 1976; McCormick et al. 1985; Beeman et al. 1995).

Linear discriminant function analysis revealed significant discernable and predictable morphological differences between migrants and residents from both migrant-resident and resident-only streams. The model accurately classified over 90% of migrants as migrants, whereas residents from migrant-resident and resident-only streams were correctly classified at 65% and 74%, respectively. The misclassification was mostly the result of residents from migrant-resident streams being misclassified as residents from resident-only streams, and vice-versa. Only 1.9% of resident-only residents were misclassified as migrants while 11.6% of residents were misclassified as migrants. Given the high correct classification rate, and the presence of future migrants within the brook trout population of migrant-resident streams we interpret this to mean that the migrant-resident residents that were misclassified as migrants, were probably fish that would migrate in future years (i.e., future migrants). Larger fish, older than >3+ (the oldest age of migration), would be expected to be true residents, while many of the smaller fish, younger than 2+, could likely be future migrants. Interestingly, the migrant-resident stream residents misclassified as migrants were smaller (82.6 mm ± 16.4 SD) than those misclassified as resident-only stream residents (106.8 mm ± 30.9 mm SD). Even so, the misclassification hypothesis remains to be confirmed.

Given the measurable differences between migrants and residents, a function with a high classification rate using three size-free ratios including depth to standard length ratio (DEP_LTH), peduncle to caudal height ratio (PED_CAUD) and pectoral to standard length ratio (PECT_LTH) could be derived from 2002 Morin Stream brook trout. Only five morphological trait measurements were required for accurate classification of migrants and residents. Cross-validation further also indicated that the function could be employed to accurately classify fish from other sampling years, and that misclassified residents were possibly future migrants. Although this function remains to be applied as a predictive tool in the field and confirmed, it indicates a potentially useful tool for distinguishing between migrants and residents in mixed populations. This tool would be very beneficial for fishery managers needing to estimate the yearly sea trout population in order to estimate and set fishing quotas.

Importantly, the observed morphological variations concurred with inferred anadromous and resident brook trout habitat use and bioenergetics

(Morinville and Rasmussen 2003, 2006), such that migrants, by possessing a more streamlined morphology, are more efficient swimmers (lower energetic costs) in fast waters than residents (Sagnes et al. 2000; Boily & Magnan 2002). Taylor and McPhail (1986) also found that anadromous three spine sticklebacks, *Gasterosteus aculeatus*, had less robust bodies (narrower bodies and heads, and shorter caudal peduncle depths) and fatigued less quickly than resident ones, coinciding with their habitat use.

Early morphological development
and the adoption of anadromy

Overall, this study demonstrates that morphological differences can be detected within a species exhibiting two life-history strategies, residency and anadromy. Importantly, these differences are powerful enough to develop predictive models for discriminating trout as either migrant or resident by measuring only a few morphological traits. Furthermore, the results agree with the expected habitat use of anadromous and resident brook trout, where the former exploits faster habitats and is more morphologically adapted for doing so than the latter.

Although morphological variations related to habitat use have been observed in the wild, uncertainties remain as to how these arise. In particular, it is still not fully understood whether fish that are morphologically pre-adapted for swimming in fast water prefer and select faster habitats or whether fish modify (phenotypic plasticity) their shape according to the habitat in which they experience. In addition, it has not been established whether early differences in physiological traits (such as higher aerobic metabolism) contribute to initial habitat preference and selection, although morphological variations between morphs have been found to be both heritable and related to physiological performance (Proulx and Magnan 2002, 2004). Early variations in metabolism and morphology thus suggest the presence of mechanisms involving both environmental and genetic factors.

Perry et al. (2004) found that maternal genetic effects were high for embryonic length, but quickly decreased for post-resorption length in brook trout bred from anadromous and resident parents. They in turn detected low but significant heritability for brook trout length at the alevin (after yolk sac resorption) stage. In addition, it was also found that maternal genetic differentiation between embryonic anadromous and resident brook trout was high ($Qst > 0.5$) and was greater than neutral genetic divergence in their study for specific embryonic traits including length and growth rate for length (Perry et al. 2005). Maternal Qst for post-resorption morphological traits was almost zero (Perry et al. 2005). This work suggests that post-emergence stages are more susceptible to developmental changes induced by early variations in environmental conditions, because maternal effects are greatly weakened. It is thus possible that immediately after emergence, size segregations occur in streams according to habitat. The larger post-hatch individuals (specifically those with an intrinsically high metabolic scope), possessing the competitive advantage for obtaining better feeding territories (Johnsson et al. 1999), could exploit the faster velocities characterized by high food delivery rates sooner, leading to subsequent morphological adaptations.

Such predictions are likely because body shape may be altered under different current regimes (Pakkasmaa and Piironen 2001; Imre et al. 2002; Peres-Neto and Magnan 2004). Sagnes et al. (2000) demonstrated a shift in body shape and swimming potential during grayling, *Thymallus thymallus*, ontogenesis in relation with habitat use. Grayling, over their ontogeny, developed towards a more hydrodynamically efficient shape for swimming at high velocities. Similarly, comparisons between older migrants and residents with pooled YOY revealed that YOY were intermediate both in maximum body depths and caudal fin heights, suggesting that the morphological differences observed between the two forms diverge with increasing size (data not shown).

Differential habitat use may thus influence fish morphology at young stages, leading to larger and more measurable changes over time. Such early size differences could result in the development of divergent body forms in parallel with the subsequent bioenergetic consequences of habitat use and ultimately to the presence of

migrant and resident phenotypes. However with the evidence at hand, it can only be concluded that brook trout adopting the migratory life-history strategy (prior to migration) have higher consumption rates, exhibit more elevated metabolic costs, utilize faster current velocities (Morinville and Rasmussen 2003, 2006) and are more streamlined in shape than those adopting the resident life-history. Further studies are needed to gain a better understanding of the link between early morphological development, habitat use and the adopted life-history strategy.

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