Phenotypic plasticity in brook charr: changes in caudal fin induced by water flow

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In the field, juvenile brook charr Salvelinus fontinalis inhabiting high-velocity water were found to have larger caudal fins and more slender bodies than those inhabiting low-velocity water. Young-of-the-year S. fontinalis were reared in either a high- or low-velocity treatment for 16 weeks and their morphology was measured bi-weekly. From the second to fourth weeks of the experiment onwards, fish reared in the high-velocity treatment had larger maximum caudal fin heights and deeper caudal peduncles than fish reared in the low-velocity treatment. This study demonstrated that the morphological variation in caudal area exhibited by wild juvenile brook charr from microhabitats differing in water velocity could be a consequence of phenotypic plasticity in response to hydrological conditions.

Key words: Salvelinus fontinalis; phenotypic plasticity; morphology; water velocity.

INTRODUCTION

Polymorphisms involve diversification of behavioural, morphological or life history traits in populations and are formed when species either invade new, species poor environments or radiate into new, under-utilized niches within an environment (Smith & Skúlason, 1996). Such polymorphisms are more common in vertebrate populations than originally thought (Robinson & Wilson, 1994; Wimberger, 1994; Skúlason & Smith, 1995). Further, they are attracting considerable interest because of the opportunity to understand the role of ecology in the divergence of populations and possible evolution of new species (Schluter, 1996).

Polymorphisms occur relatively frequently in lacustrine fishes (Wimberger, 1994) where benthic and limnetic morphs have been observed repeatedly (Robinson & Wilson, 1994). Few examples have been reported for stream fishes (Wimberger, 1994). As streams show less temporal stability than lakes, polymorphisms are considered less likely to occur in streams (Wimberger, 1994). McLaughlin & Grant (1994), however, documented that individual young-of-the-year (YOY) brook charr Salvelinus fontinalis (Mitchill) inhabiting high-velocity water had more slender bodies, narrower caudal peduncles, and deeper caudal fins than individuals in low-velocity water. The mechanism producing this morphological variation is unclear. The pattern of variation, however,

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parallels relationships between hydraulic conditions and body morphology reported in earlier, inter-population comparisons of salmonids (Riddell & Leggett, 1981; Taylor & McPhail, 1985; Bisson et al., 1988). In these examples, the differences in morphology were attributed to genetic differences among populations (Riddell et al., 1981; Taylor & McPhail, 1985) without exploring explicitly the possibility of phenotypic plasticity.

Phenotypic plasticity is recognized as an important mechanism of phenotypic adaptation to varying conditions (Pigliucci & Schlichting, 1995). Recent studies have revealed that polymorphic lacustrine fishes exhibit considerable plasticity in morphology (Robinson & Wilson, 1994; Wimberger, 1994). Morphological plasticity can be of considerable importance in the evolution of polymorphisms, and both plasticity and polymorphisms may contribute to speciation (West-Eberhard, 1989).

The aim of the present study was to test whether the differences in body shape observed among wild YOY brook charr sampled from microhabitats differing in water velocity could be a consequence of phenotypic plasticity in response to differences in hydraulic conditions. This hypothesis was tested in a laboratory experiment: randomly chosen fish with varied genetic backgrounds were reared in low- and high-velocity treatments for 16 weeks. Based on the field findings of McLaughlin & Grant (1994), it was predicted that fish in the high-velocity treatment would have larger maximum caudal fin height and smaller maximum body depth and caudal peduncle depth than fish reared in the low-velocity treatment. Seventeen additional morphological traits were also compared among experimental groups because theoretical arguments and empirical evidence have indicated that these traits can be important for swimming performance (Riddell & Leggett, 1981; Carl & Healey, 1984; Webb, 1984a, b).

MATERIALS AND METHODS

EXPERIMENTAL SUBJECTS

The experiment was conducted using YOY S. fontinalis (Hills Lake strain) obtained from the Hills Lake Fish Culture Station (Englehart, Ontario, Canada). A random sample of 5000 embryos at the eyed stage was collected from a large pool of embryos obtained by pooling gametes from several males and females. Embryos were reared in Heath incubators supplied with recirculated groundwater (temperature=4°C, pH=8) in the Hagen Aqualab facility of the University of Guelph. After emergence, alevins were transferred to a common tank in the same room until exogenous feeding commenced. Fish were fed to satiation with Prestarter commercial trout food (Martin Mills Ltd, Elmira, Ontario, Canada) once a day. During the period between emergence and placement into experimental tanks (4 weeks) fish were held at a 11:6 L : 12:4 D photoperiod. Fish were fed three times a day during the first month of the experiment then five times a day thereafter. Food particle size was increased midway through the experiment (Starter, Martin Mills Ltd, Elmira, Ontario, Canada). Unconsumed food and other debris were siphoned daily from each tank. Once a week all the tanks were emptied for a short period and cleaned thoroughly.

EXPERIMENTAL DESIGN

The experiment consisted of a low- (current velocity=c. 1 cm s\(^{-1}\)) and a high-velocity (current velocity=c. 10 cm s\(^{-1}\)) treatment, with six replicate tanks in each treatment. Treatment conditions were similar to the mean water velocities encountered in sidepools and slow runs in the field (McLaughlin & Grant, 1994). The water velocity in the
high-velocity treatment (10 cm s$^{-1}$) was well below the critical water velocity (c. 17 cm s$^{-1}$) reported for *S. fontinalis* of this size (Heggenes & Traaen, 1988).

 Tanks were assigned randomly to treatments to control for position effects. The tanks were cylindrical aquaculture tanks with conical bottoms. A flat bottom with a central standpipe was installed in each tank to provide a circular experimental channel (depth=45 cm, width=19.5 cm). Each tank was supplied with untreated groundwater. Constant water flow was provided by a submersible water pump (G 500 ACS Beckett Corp., Dallas, Texas, U.S.A.), positioned under the flat bottom of the experimental channel. The water from the pump was delivered to the experimental channel by a PVC tube. In order to ensure uniform water flow in the water column, the water delivery tube was located in the middle of the channel in a vertical position and it had several rows of holes from subsurface down to the bottom of the channel. Tanks were covered with black mesh to provide cover for fish and prevent their escape. All tanks were individually aerated using aquarium air stones.

 Water velocity was measured by floating a plastic disc (diameter=11.9 mm, thickness=0.3 mm, mass=0.09 g) on the water surface and timing its progress over half of the circular channel. Water velocity was calculated using the following equation:

$$\text{Water velocity (cm s}^{-1}) = \pi \times r \times t^{-1},$$

where $r$ is the radius and $t$ is the time.

 The disc was floated at several different radii across the experimental channel. The mean of these measurements was used as a measure of water velocity for each tank. This approach was taken because mechanical water velocity meters are not sensitive enough to measure water velocities $<1$ cm s$^{-1}$, and electromagnetic meters are sensitive to the proximity of the channel walls. The plastic disc was calibrated with a Flo-Mate velocity meter (model 2000, Marsh–McBirney Inc., Frederick, Maryland, U.S.A.). Velocity measurements obtained with the plastic disc were similar to those made with the meter ($r^2=0.96$, $n=7$).

 Ten days prior to the start of the experiment the experimental subjects were randomly placed (in groups of 10) into each tank. This time period was included to allow the fish to acclimate to the 12 L : 12 D photoperiod and to the gradually increasing water velocity in the high-velocity treatment. The velocity of the water was c. 1 cm s$^{-1}$ in the low-velocity treatment (treatment mean $\pm$ s.d.$=1.1 \pm 0.1$ cm s$^{-1}$) and c. 5 cm s$^{-1}$ in the high-velocity treatment at the time experimental subjects were added. During the 10 day period the water velocity in the high-velocity treatment was increased gradually to c. 10 cm s$^{-1}$ (treatment mean $\pm$ s.d.$=10.2 \pm 0.2$ cm s$^{-1}$). There were no significant differences in the mean water velocity between tanks within a treatment (low-velocity treatment, $P=0.156$; high-velocity treatment, $P=0.993$).

**EXPERIMENTAL PROCEDURE**

 Mortalities in the treatment groups were monitored to ensure that differences in body shape appearing during ontogeny were not a consequence of differential mortality based on shaped related differences in swimming ability. Each replicate tank had 150 fish (900 individuals per treatment) at the beginning of the experiment. Ten fish per tank were sampled at the start of the experiment and every 2 weeks afterward. The experiment was conducted for 16 weeks. At the end of the experiment all remaining individuals were sampled ($n=699$). Fish were captured with a dipnet. Due to high starting densities, there was very little aggression between individuals within tanks. Alternate net sweeps were made in the upper and lower half of the water column to get an accurate representation of the tank population and avoid any bias caused by potential differences in the size or development of the individuals in different zones of the tank. Immediately after capture sampled fish were killed and preserved in 70% (first eight samples) or 100% ethanol (final sample). Fish were not fed for 24 h prior to sampling to minimize the confounding effects of changes in the size of the abdomen on certain morphometric measures.

 Water temperature, dissolved oxygen level and pH were monitored regularly. There were no differences between treatments in temperature (low-velocity mean $\pm$ s.d.$=12.2 \pm 1.3^\circ$C, high-velocity mean $\pm$ s.d.$=12.1 \pm 1.4^\circ$C) and pH (low-velocity mean $\pm$ s.d.$=8.2 \pm 0.2$, high-velocity mean $\pm$ s.d.$=8.2 \pm 0.2$). There were slight differences in the dissolved O$_2$ levels (low-velocity mean $\pm$ s.d.$=81.9 \pm 9.8$% saturation, high-velocity
mean ± s.d. = 89.4 ± 4.1% saturation) between treatments due to differences in water circulation. The dissolved O₂ level in the low-velocity treatment, however, was well within the tolerance range of brook charr (Power, 1980).

MORPHOMETRIC MEASUREMENTS

Morphometric measurements were made on the left side and dorsal surface of individuals with a Wild Heerbrugg dissecting microscope (Wild of Canada Ltd, Ottawa, Ontario, Canada) and a Fowler Ultra-cal. II digital caliper (Fred V. Fowler Co., Inc., Newton, MA, U.S.A.) (Fig. 1). Trautman (1981) and Hubbs & Lagler (1964) were followed for the definitions of measurements with the following exceptions: (1) head width was defined as the distance between the normally closed opercula at the level of the occiput; (2) caudal peduncle depth was defined as the distance between the dorsal and ventral midline of the caudal peduncle at the caudal fin base; (3) minimum caudal fin height was defined as the distance between the tip of the dorsal procurent rays to the tip of the ventral procurent rays at the level of the caudal fin base; (4) maximum caudal fin height was defined as the distance between the uppermost tip of the upper caudal fin lobe and the lowermost tip of the lower caudal fin lobe with the fin rays arranged close to each other (i.e. connecting membrane not overly extended). Dorsal height was not ultimately included in the analysis because the dorsal fin of some fish became damaged. Dead fish were not measured, because most of them were partly decomposed by the time they were found in the tanks. Consequently the body shape of dead and surviving fish could not be compared.

Within-observer reliability was tested (Martin & Bateson, 1993) on 18 randomly chosen fish (two fish from each time sample). Measurements were highly repeatable (r = 0.98–0.99, P < 0.0001).
STATISTICAL ANALYSES

Morphometric variables were corrected for size with the common within-groups slope method, which adjusts the two within treatment regression lines to a common slope (Thorpe, 1975; Reist, 1986). Because of the changing relationship between size and shape during ontogeny, this method was employed separately for each time sample. Standard length ($L_s$) was used as a measure of body size. A value adjusted for size represents the value of a morphometric variable (backtransformed to mm) expected if the individual’s $L_s$ was the mean length of all individuals within a certain sample. The size-adjusted morphometric variables were used for all further statistical analyses unless stated otherwise.

Nested multivariate analysis of variance (MANOVA) of the final sample, with tanks nested within treatments, was used to test for body shape differences at the end of the experiment between low- and high-velocity treatments. Treatment and tank were considered fixed and random effects, respectively. Type III sums of squares were used to calculate $F$ statistics and significance levels. Univariate nested analyses of variance (ANOVA) were also performed to identify those variables for which the treatments differed significantly. The critical level of significance for these tests was adjusted to 0.00278 with Bonferroni’s multiple comparison adjustment.

Developmental reaction norm graphs were generated for each morphometric variable and inspected visually for evidence of consistent divergence between treatments. Repeated measures analysis of variance (ANOVAR) was used to detect differences between treatments and across sampling times for those morphometric variables that showed a consistent divergence of the developmental reaction norms. Tank means were used as replicates in the ANOVAR. Contrast analyses were performed to locate the time when the developmental reaction norms first diverged significantly.

Statistica 5.0 (StatSoft, 1995) was used to perform all statistical tests, with the exception of the nested MANOVA that was performed using the Statistical Analysis System package (SAS, 1988). The level of significance was 0.05 for all statistical tests unless specified otherwise.

RESULTS

SHAPE DIFFERENCES AT THE END OF THE EXPERIMENT

Fish were of the same $L_s$, on average, in both treatments (univariate nested ANOVA: $P=0.136$). The body shape of fish, however, was significantly different between treatments (nested MANOVA Wilks’ $\Lambda_{18,670}=0.60, \ P=0.0001, \ n=699$). Fish reared in the high-velocity treatment had maximum caudal fin heights that were 7.8% larger, on average, (univariate ANOVA $F_{1,10}=17.76, \ P=0.0018$) than fish reared in the low-velocity treatment, but did not differ significantly in other aspects of body shape (Table I).

The caudal fin rays (at the end of the caudal fin) were also counted for 120 fish (59–61 per treatment) in order to see if they contributed to the noted difference in maximum caudal fin height. The number of caudal fin rays increased with increasing $L_s$ (univariate nested ANCOVA: $F_{1,107}=22.87, \ P<0.001$), but it did not differ significantly (univariate nested ANCOVA: $P=0.615$) between the high-velocity (adjusted least squares mean ± s.e. = 52.7 ± 0.73) and the low-velocity treatment (adjusted least squares mean ± s.e. = 51.9 ± 0.75).

DEVELOPMENTAL REACTION NORMS

Caudal peduncle depth (ANOVAR time effect: $F_{8,80}=2359.41, \ P<0.0001$) and maximum caudal fin height (ANOVAR time effect: $F_{8,80}=2542.27, \ P<0.0001$) increased over the course of the experiment. There were significant differences
between treatments both in caudal peduncle depth (ANOVAR treatment effect: $F_{1,10}=23.35$, $P=0.0007$) and maximum caudal fin height (ANOVAR treatment effect: $F_{1,10}=60.2$, $P<0.0001$). Overall, fish reared in the high-velocity treatment developed a larger maximum caudal fin height and a deeper caudal peduncle than conspecifics reared in the low-velocity treatment (Fig. 2).

The caudal peduncle (ANOVAR time × treatment interaction: $F_{8,80}=2.54$, $P=0.0164$) and caudal fin (ANOVAR time × treatment interaction: $F_{8,80}=3.46$, $P=0.0018$) of fish reared in the high-velocity treatment exhibited faster development than that of fish reared in the low-velocity treatment. Differences arose within the first 2 and the first 4 weeks of the experiment in the case of the maximum caudal fin height (contrast analysis, second week, $F_{1,10}=82.92$, $P<0.0001$) and caudal peduncle depth (contrast analysis, fourth week, $F_{1,10}=15.68$, $P<0.0269$), respectively, and remained significant afterward (contrast analysis: maximum caudal fin height, fourth–16th week, $F_{1,10}=57.08$, $P<0.0001$; caudal peduncle depth, sixth–16th week, $F_{1,10}=25.34$, $P=0.0005$).

MORTALITY

Overall mortality was very low (141 individuals or 7.8%). Known causes of mortality included cannibalism (43 individuals or 2.4%) and tank cleaning accidents (15 individuals or 0.8%). Approximately twice as many fish died of unknown causes in the low-velocity (56) than in the high-velocity environment (27).

### Table I. Treatment means ± s.e. for all morphometrical variables (adjusted for $L_S$) for the final time sample ($n=6$ tank means). Per cent difference between low-velocity ($\bar{x}_L$) and high-velocity ($\bar{x}_H$) means was calculated from 100$(\bar{x}_L-\bar{x}_H)/\bar{x}_H$.

<table>
<thead>
<tr>
<th>Variables (mm)</th>
<th>Low-velocity</th>
<th>High-velocity</th>
<th>% difference between means</th>
</tr>
</thead>
<tbody>
<tr>
<td>$L_S$</td>
<td>93.09 ± 0.96</td>
<td>91.11 ± 0.73</td>
<td>2.2</td>
</tr>
<tr>
<td>Head depth</td>
<td>17.36 ± 0.07</td>
<td>17.04 ± 0.15</td>
<td>1.9</td>
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<tr>
<td>Body depth</td>
<td>23.44 ± 0.13</td>
<td>23.60 ± 0.14</td>
<td>-0.7</td>
</tr>
<tr>
<td>Peduncle depth</td>
<td>7.42 ± 0.09</td>
<td>7.65 ± 0.17</td>
<td>-3.0</td>
</tr>
<tr>
<td>Min. caudal height</td>
<td>12.46 ± 0.08</td>
<td>12.86 ± 0.21</td>
<td>-3.1</td>
</tr>
<tr>
<td>Head length</td>
<td>20.95 ± 0.10</td>
<td>20.96 ± 0.10</td>
<td>-0.0</td>
</tr>
<tr>
<td>Predorsal length</td>
<td>43.74 ± 0.06</td>
<td>44.03 ± 0.15</td>
<td>-0.7</td>
</tr>
<tr>
<td>Prepectoral length</td>
<td>19.47 ± 0.12</td>
<td>19.51 ± 0.09</td>
<td>-0.2</td>
</tr>
<tr>
<td>Prepelvic length</td>
<td>48.83 ± 0.07</td>
<td>48.96 ± 0.08</td>
<td>-0.3</td>
</tr>
<tr>
<td>Preanal length</td>
<td>67.51 ± 0.06</td>
<td>67.55 ± 0.10</td>
<td>-0.1</td>
</tr>
<tr>
<td>Anal fin height</td>
<td>15.83 ± 0.35</td>
<td>14.98 ± 0.39</td>
<td>5.7</td>
</tr>
<tr>
<td>Max. caudal height</td>
<td>18.08 ± 0.32</td>
<td>19.62 ± 0.17</td>
<td>-7.8</td>
</tr>
<tr>
<td>Pectoral fin length</td>
<td>16.50 ± 0.08</td>
<td>15.96 ± 0.23</td>
<td>3.4</td>
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<tr>
<td>Pelvic fin length</td>
<td>13.56 ± 0.09</td>
<td>13.41 ± 0.12</td>
<td>1.1</td>
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<tr>
<td>Caudal fin length</td>
<td>12.87 ± 0.06</td>
<td>12.71 ± 0.04</td>
<td>1.3</td>
</tr>
<tr>
<td>Peduncle length</td>
<td>17.63 ± 0.06</td>
<td>17.57 ± 0.15</td>
<td>0.3</td>
</tr>
<tr>
<td>Head width</td>
<td>15.02 ± 0.12</td>
<td>14.80 ± 0.22</td>
<td>1.5</td>
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<tr>
<td>Body width</td>
<td>16.55 ± 0.13</td>
<td>16.71 ± 0.20</td>
<td>-1.0</td>
</tr>
<tr>
<td>Peduncle width</td>
<td>6.36 ± 0.07</td>
<td>6.51 ± 0.05</td>
<td>-2.3</td>
</tr>
</tbody>
</table>
DISCUSSION

This study demonstrates that phenotypic plasticity could account for the morphological differences reported in wild YOY brook charr inhabiting microhabitats differing in water velocity in the field. Four lines of evidence support this conclusion. First, *S. fontinalis* reared in the high-velocity treatment developed significantly larger maximum caudal fin heights and deeper caudal peduncles than fish in the low-velocity treatment during the experiment. Second, the difference between treatments in maximum caudal fin height (−7.8%) at the end of the experiment was similar to the value (−9.1%) found by McLaughlin & Grant (1994) in the field. Third, these differences appeared from the first
2–4 weeks onward and were maintained throughout the experiment. Fourth, the differences observed in the experiment were probably not due to differential selection acting on shape related differences in swimming ability because overall mortality was very low and twice as many fish died in the low-velocity than in the high-velocity treatment.

Although the developmental differences between the treatments are small, it is reasonable to expect that they could be important ecologically. The direction of differences in the caudal fin height between the morphs is consistent with the expectations of hydrodynamic theory. The trailing edge of the tail is considered to be the most vital element in thrust generation (Webb, 1984a, b) thus fish swimming in high-velocity environments should have large caudal fin heights. Further, the relative morphological difference at the end of the experiment between the fish raised in the different treatments was −7.8% to 0% of a given measure, and it was comparable in magnitude to the variation found by Carl & Healey (1984) (0.8–12.5%), Meyer (1987) (0.5–18.7%), Wimberger (1992) (2–4%) and McLaughlin & Grant (1994) (−9.1–4.9%). In addition, morphological differences noted in this study are comparable in magnitude to morphological differences noted between salmonid populations, which are thought to be due to genetic differences (Taylor & McPhail, 1985, −18.2–4.7%). Although the functional significance of the morphological differences induced by this experiment was not assessed, it is worth noting that the differences are of comparable relative magnitude to trophic differences in other fish species for which functional significance was demonstrated (Liem, 1980; Ehlinger & Wilson, 1988; Meyer, 1989).

Previous studies of the body shape-water velocity relationship have traditionally focused on morphological differences between salmonid populations inhabiting environments differing in water velocity (Riddell & Leggett, 1981; Taylor & McPhail, 1985) where the authors demonstrated that the morphological differences were due to genetic differences between populations (Riddell et al., 1981; Taylor & McPhail, 1985). The present study is one of few (McLaughlin & Grant, 1994; Pakkasmaa & Piironen, 2001) to examine shape differences due to water velocity in a stream environment, and it is the first to conclusively show that changes in the caudal area of juvenile brook charr can be induced by water velocity. Another recent experimental study (Pakkasmaa & Piironen, 2001) found morphological differentiation in juvenile Atlantic salmon Salmo salar L. and juvenile brown trout Salmo trutta L. swimming at different water velocities. These examples indicate that plastic changes in the morphology of juvenile salmonids in response to water velocity are more widespread than previously thought. Two further studies, using guppies Poecilia reticulata Peters (Nicoletto, 1996) and blackfly Simulium lundstromi (Enderlein) larvae (Zhang & Malmqvist, 1997), suggested that water velocity in a stream environment could promote plastic responses in body shape. These studies raise the possibility that water velocity could have important developmental effects on a wide variety of stream organisms.

The number of caudal fin rays was not significantly different between treatments, providing indirect evidence for the hypothesis that the developmental difference in maximum caudal fin height is the result of the extension of the membrane connecting the fin rays. In fact, most cases of morphological
plasticity can be explained as being caused by plastical tissue response to biomechanical loading stimuli (Wimberger, 1994). Similarly, the deeper caudal peduncle in the high-velocity treatment was most probably caused by an increase in caudal muscle mass, as a result of higher levels of physical exercise.

There was perfect correspondence between this experimental study and McLaughlin & Grant’s (1994) field study for maximum caudal fin height, the trait for which both studies observed the greatest difference across water flows. Unlike in the laboratory, however, brook charr swimming in high-velocity water in the field had more slender bodies, shallower caudal peduncles than the individuals in low-velocity water. The discrepancies highlight the added complexities of the field where differences in habitat use also correspond with differences in diet (McLaughlin & Grant, 1994), where water flow may be more unsteady than in the laboratory (McLaughlin & Noakes, 1998), and where developmental responses by individuals in response to local environmental cues may be occurring along with population level responses to different selection pressures across habitats. In spite of these differences between the laboratory and field findings, these experimental results are sufficient to demonstrate that phenotypic plasticity could account, in part, for the morphological variation observed by McLaughlin & Grant (1994) in the field. Further, when considered in the light of recent evidence of phenotypic plasticity in lake fishes, these findings suggest that phenotypic plasticity could be an important mechanism facilitating morphological divergence within and among populations of fishes.

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