Repeatability and phenotypic plasticity of fish swimming performance across a gradient of urbanization

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Abstract How phenotypic plasticity of locomotor performance varies among populations in nature is poorly known. Swimming ability of blacknose dace (*Rhinichthys atratulus*) from eight different watersheds had previously been shown to depend upon watershed impervious surface cover (ISC) and stream base-flow. Keeping these populations of stream fish under low flow conditions produced changes in locomotor capacity suggestive of phenotypic plasticity varying among the populations. The present experiments were conducted to better understand the plasticity of swimming performance in dace and how urbanization affects dace biology. Two experimental approaches were used: 1) laboratory training of dace populations at two levels of flow for 6 weeks; and, 2) exploring in situ training by capturing fish from relatively fast and slow reaches of three different streams and comparing their swimming abilities at three different scales. Individual sprint and endurance (modified U_{crit}) swimming were significantly repeatable across a laboratory training regimen; sprint performance had previously been shown to not be repeatable when dace were held in static water. Both of our approaches suggested that sprint and endurance swimming ability significantly respond to changes in environmental flow. Although there was no evidence for a different magnitude of phenotypic plasticity among populations, urban populations that experience more stochastic flow regimes had more consistent plasticity. Phenotypic plasticity of locomotor performance in response to variable flow appears to be an important characteristic of blacknose dace biology, yet we did not uncover sufficient evidence to suggest that it is under selection in fish adjusting to urban stream habitats.

Keywords Blacknose dace · Exercise training · Locomotor performance · Swimming performance

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Introduction

One of the least appreciated impacts of humans on natural landscapes is how urbanization has altered the character and biota of urban streams. Although highly publicized point-source pollution problems have been minimized through environmental activism, massive hydrological and habitat changes wrought by water flowing over impervious surfaces of urban watersheds, coupled with unmodified stormwater runoff, remain the reality for many urban streams (Vitousek et al. 1997; Paul and Meyer 2001). Increased impervious surface cover (ISC) decreases the fraction of precipitation that enters groundwater. Thus surface run-off is much

greater in cities following rainfall or melting events and urban stream flow rises dramatically (Hirsch et al. 1990). The loss of water entering the groundwater also produces lower flows between periods of precipitation or melt in urban streams (Klein 1979). Thus, the % ISC of a watershed is a predictor of flow stochasticity and hydrologic degradation.

In these degraded waterways, fish diversity decreases drastically and fish assemblages become dominated by tolerant species (Schueler and Galli 1992). These tolerant species are then potential targets for anthropogenically-driven population diversification or even evolution (Vitousek et al. 1997; Atwell et al. 2012). The fragmentation of habitat in urban streams can also reduce gene flow within populations of these tolerant species (Sofia et al. 2006; Marcangeli 2013), possibly accelerating the rates of population diversification and evolution.

The blacknose dace (*Rhinichthys atratulus*) is one of those urbanization-tolerant species that exists in some of the most degraded streams around Baltimore, MD, USA, often to the point of being the only fish species left in a stream. However, blacknose dace are also abdundant in nearby, rural stream communities with a diverse fauna and they are also found in streams of all intermediate levels of urbanization. This gradient of urbanized streams at similar latitude, altitude and stream order, sets up an intraspecific comparative experiment from which one can test hypotheses concerning how human activities influence the biology of a species that is not extirpated from urban streams (Nelson et al. 2008).

Nelson et al. (2003, 2008) had previously shown phenotypic plasticity of a modified U_{crit} performance in blacknose dace. This performance was a significant function of stream baseflow in fish from rural and suburban streams (Nelson et al. 2003); fish from stream regions with greater baseflow had better swimming performance than those from slower reaches. Interestingly, fish from the site with the most variable current flow had the greatest variation in individual U_{crit} (Nelson et al. 2003). When urban fish were analyzed, the percentage of ISC was the most important environmental variable influencing U_{crit} (Nelson et al. 2008). Regardless of whether a group of fish was from a fast reach of a rural stream or from a city stream, holding them in static water (de-training) for 6 months caused their exceptional swimming ability to become ordinary (Nelson et al. 2008). In contrast, individuals that orginally had an average or below-average U_{crit} had significantly repeatable (unchanged) performance after 6 months in static laboratory water. Collectively, these results implied that phenotypic plasticity of endurance swimming ability might vary at the population level and motivated the present experiments.

Sprinting performance may be a more relevant gauge of a stream fish's ability to survive mortality selection (Nelson et al. 2002) and has been shown to be significantly repeatable on a daily and weekly basis in adult blacknose dace (Nelson et al. 2008). Sprint performance of individual blacknose dace correlates strongly with the %ISC of their watershed (Nelson et al. 2008). Urban fish are better sprinters than rural fish, suggesting that the increased "flashiness" of the urban flow environment is either sprint training fish (phenotypic plasticity), or directional selection is leaving only the better sprinting fish in the streams to be collected by scientists. Detraining of blacknose dace homogenized their sprint swimming performances (Nelson et al. 2008); fish that were top sprinters upon arriving from the field invariably lost ability by being held in static laboratory water whereas poor-sprinting fish tended to maintain or even gain ability in the laboratory. While the parsimonious explanation for these results was entirely speculative (Nelson et al. 2008), the changes in sprint performance in the laboratory were also suggestive of population-level differences in phenotypic plasticity.

Although research into the role of phenotypic plasticity and reaction norms in organic evolution and environmental adaptation has expanded exponentially in recent years (Hutchings 2011), many of the details remain controversial (Ghalambor et al. 2007). Whether phenotypic plasticity retards rates of evolution, is of itself a trait subject to natural selection or is even an evolutionary process are all under debate (De Jong 2005; Ghalambor et al. 2007). These debates notwithstanding, results from diverse taxa suggest that animals from more variable environments are more phenotypically plastic in traits as far-ranging as life history characters (Seigel and Ford 2001; Baker and Foster 2002), morphology (Peres-Neto and Magnan 2004; Svanbäck and Schluter 2012), thermoregulation (Cooper et al. 2012) and osmoregulation (Nelson et al. 1996). Thus, increases in phenotypic plasticity can be proposed as a biomarker of sorts for increased environmental variability and understanding plasticity has taken on some urgency as it may influence a species' ability to cope with climate change (Chevin et al. 2010).

The purpose of this study was to investigate whether the anthropogenic alteration of stream flow over the past 150 years has affected the phenotypic plasticity of locomotor performance in blacknose dace and to determine whether this plasticity varies at the population level as a function flow stochasticity. Specifically, we tested whether sprint and endurance swimming performance could be trained in the laboratory by forcing fish from different populations to swim continuously against two levels of flow. We also examined intrapopulation plasticity of three types of locomotor performance by testing fish from relatively fast and relatively slow reaches of the same stream. These populations were chosen across a gradient of urbanization so that, if population differences in plasticity were detected, they could be related to the changes in stream flow character brought on by urbanization.

Materials and methods

Field sites

Blacknose dace were collected in two separate years from five different watersheds. Table 1 summarizes the base-flow current velocity and percentage of impervious surface cover (%ISC) information for each of the field sites. Base flow velocity ($m•s^{-1}$) information for these sites was taken from Nelson et al. (2003) and Nelson et al. (2008). Information on the variability of base flow for some of the sites is presented in Nelson et al. (2003). Briefly, for every five meters of a 100 m reach, a perpendicular transect was sampled at five even intervals over the width of the stream using a Marsh-McBirney Model 2000 flowmeter placed at mid-depth of the stream while recording depth measurements at each interval. The %ISC for a watershed was calculated according to Nelson et al. (2008). Briefly, %ISC was determined by interpreting watershed boundaries from digital line graphs of topographic contours. Then, the 2001 impervious surface cover map of the National Land Cover database (U.S. Department of the Interior and US Geological Survey, Multi-Resolution Land Characteristics Consortium, http://www.mrlc.gov) was used to calculate the percentage of each watershed covered by impervious surfaces. These streams were classified as urban, suburban or rural based upon impervious surface cover of >20, 10–20 and <2 %, respectively (Nelson et al. 2008).

Fish capture and handling

Two separate studies are reported on here: 1) laboratory training of individuals from one reach of each of four separate streams, two urban, one suburban and one rural and, 2) assessment of intra-population natural training by collecting individuals from two separate reaches, differing in flow, from within each of three different streams varying in degree of urbanization. In addition, this second study included a few individuals that were fortuitously hatched in the laboratory and never exposed to any substantial flow.

Fish were collected using a Smith-Root Inc. back-pack Electro fisher from stream reaches of known base-flow and %ISC (Nelson et al. 2003, 2008). Because populations were experimented on sequentially, stream sampling order and thus experimental order, was determined randomly. In an attempt to minimize size effects, fish for each experiment were selected on site to be of similar size (Table 2). No attempt was made to separate sexes because blacknose dace are not sexually dimorphic except when breeding. Selected fish were placed into an aerated 94 L cooler with water from their home stream and transferred back to Towson University where they were kept with the gradual addition of de-chlorinated Baltimore city tap water until the water temperature reached 20 °C (laboratory training experiment) or 15 °C (natural training experiment). The rate of temperature change during this acclimation to the laboratory was kept below 2 °C per day.

Laboratory training experiment

Seven days after reaching the target temperature, fish ($n=32$ from each population; Table 2) were anesthetized with MS-222 [100 $mg•L^{-1}$; buffered with $Na^+;HCO_3^-$], weighed (g), and uniquely marked with a sub-dermal injection of fluorescent dye mixed with the antibiotic Maracyn® [5 $g•L^{-1}$]. This procedure has been shown not to affect fish swimming performance (Sutphin et al. 2007). Fish were then transferred to 20 L holding aquaria without flow, surrounded by black plastic with frosted covers to minimize visual disturbance and habituation to humans. Pre-training swim tests began on randomly selected individuals after 1 week in these holding tanks; the order of swimming was conserved throughout the experimental period to allow for equal recovery time between sprint and endurance tests and approximately equal training periods. Each fish

Table 1 Summary of sample sites including designation, watershed percentage impervious surface cover (%ISC) and mean baseflow (m s^{-1})

Site	Designation	%ISC	Mean baseflow (m·s^{-1})
Aspen Run	Rural	0.21	0.22
Beaver Run (slow)	Rural	1.0	0.092
Beaver Run (fast)	Rural	1.0	0.226
Gwynn's Falls (slow)	Suburban	15.2	0.065
Gwynn's Falls (fast)	Suburban	15.2	0.151
Herring Run (slow)	Urban	23.3	0.07
Herring Run (fast)	Urban	23.3	0.3
Red House run	Urban	26.8	0.03

See Nelson et al. (2003; 2008) for more information on the sites

underwent, in order: 1) a series of sprint performance tests within a period of 1–2 h (see below), 2) followed by 5 days of recovery, 3) a modified U$_{crit}$ test (see below), before 4) being transferred without air exposure to one of the training aquaria (Fig. 1). Thus the first fish in a group started training 21 days after being captured and the last at 27 days.

After completion of the two baseline swimming performance tests, fish were trained by randomly placing them into a lane of a "training tank" for 40–50 days at one of two randomly assigned current velocities. The order of populations, their designation and the chief month of training were: 1) Aspen Run, rural (August), 2) Herring Run, urban (September), 3) Gwynn's Falls, suburban (October) and 4) Red House Run, urban (November). Each of the four training tanks was a modified 380 L aquarium where flow was delivered via pumps and PVC piping to each of four training compartments (60×13×6 cm;

16 total; Fig. 1). Two training tanks were designated as high flow (average current velocity of 16 cm•s^{-1}) and two tanks were designated as low flow (average current velocity of 7 cm•s^{-1}). The average current velocities were determined empirically by averaging 60 mid-depth measurements across the training sections of each tank (240 total) using a Marsh-McBirney Model 2000 flow meter. The training compartments within a tank were partitioned with black plexiglass so that a fish could only see the other fish in its compartment and black plastic was placed on the sides and the top was frosted plexiglass to minimize habituation to humans. Fish were fed to satiation once daily with commercial flake fish food (Aquarian® or Tetramin®; flow discontinued during feeding), and kept on a 15:9 light:dark cycle. Water temperature was monitored daily whereas ammonia, nitrite, nitrate, pH, and DO$_2$ were monitored bi-weekly and a 25 % water change made weekly.

Table 2 Fish origin, sample size and fish size for both experimental approaches

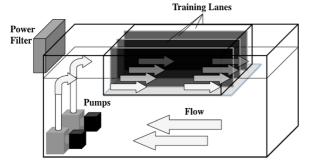| Fish origin	Experiment	Number	Mean total length ± SE (cm)	Mean mass ± SE (g)
Aspen Run	Laboratory training	32	6.6±1.3	2.76±0.15
Gwynn's Falls	Laboratory training	32	6.6±0.8	2.65±0.10
Herring Run	Laboratory training	32	6.6±0.4	2.84±0.06
Red house Run	Laboratory training	27	6.4±0.6	2.39±0.07
Herring Run-upstream	Natural conditioning	12	4.5±0.3	0.83±0.12
Herring Run-downstream	Natural conditioning	9	5.4±0.2	1.48±0.14
Herring Run-lab-reared	Natural conditioning	3	4.6±0.2	0.66±0.13
Beaver Run upstream	Natural conditioning	12	3.9±0.2	0.45±0.06
Beaver Run downstream	Natural conditioning	11	4.1±0.1	0.62±0.06
Beaver Run lab-reared	Natural conditioning	7	3.9±0.2	0.53±0.08
Gwynn's Falls upstream	Natural conditioning	11	5.1±0.1	1.57±0.05
Gwynn's Falls downstream	Natural conditioning	13	4.8±0.4	1.36±0.33

Fig. 1 Schematic diagram of the training tank design. All training tanks were constructed identically, with each having four unidirectionally flowing training lanes with swimming areas measuring 60×13×6 cm. Different current velocities were created by using different-sized pumps. Special nozzles spread the flow of water out at the entrance to the training lanes in order to help create a uniform water velocity profile across each lane

Natural training

To examine intra-population phenotypic plasticity in swimming performance, fish were collected from relatively fast or slow reaches of three streams spanning a rural to urban gradient: Herring Run (HR) urban, Gwynn's Falls (GF) suburban and Beaver Run (BR) rural (Table 1). The intra-stream sites were separated by an average of 9.7 km (range 6.4–15.3 km). The size and number of fish examined from each site are shown in Table 2. Sites were selected where base flow was known (Nelson et al. 2003, 2008) and so that fast/slow reach did not completely correlate with upstream/downstream (e.g., for the GF population, the slow site was downstream). Following the acclimation described above, fish were anesthetized, weighed and measured as above and immediately transferred to one of eight individual compartments within 60 L aquaria inside a temperature-controlled room and acclimated for another week before swimming commenced. Aquaria were covered with black plastic to minimize visual disturbance and habituation. Water temperature was monitored daily whereas ammonia, nitrite and nitrate were monitored biweekly and a 25 % water change made weekly. Fish were fed daily with flake fish food (Aquarian® or Tetramin®).

Sprint and acceleration performance

Sprint performance was measured as described in Nelson et al. (2002, 2008). Briefly, 30 min prior to the initiation of a sprint trial, a fish was herded into a submerged container and transferred to a sprint performance chamber (SPC) without air exposure. The dimensions of the chamber were 1.5 m (length) × 15 cm (width) × 15 cm (height). Light-emitting laser diodes (OnPoint Laser Inc. 6780 Vermar Terrace, Eden Prairie, MN 55346 USA) of approximately 5 mW power output, 645–670 nm wavelength, and 1.1 mm beam width were placed at 0, 1, 3, 7, 15, 23, 31, and 39 cm from the point at which a fish would begin its sprint. The lasers were mounted in front of clear glass windows on one side of the raceway. A 5 mm glass rod was attached transversely to the front of the laser lens. This rod refracted the beam to project a vertical plane or "curtain of light" across the raceway. The laser light was detected on the opposite side of the chamber by eight arrays of photo Darlington detectors (Honeywell® SDP, 18 sensors per array; 144 sensors total) of detection wavelength 580–720 nm. Individual sensors in an array were positioned vertically 0.5 cm from the bottom and then every 0.5 cm apart to a height of 8.5 cm (0.5 cm below the "fill" line at 9 cm). When activated by light, the photo Darlington detector arrays put out a 5 V signal to one of eight digital inputs on an AD Instruments Powerlab® 4 s interfaced to an Apple Macintosh I-Mac® computer running Chart® software. Fish were motivated to sprint by an attempted prod with a plastic pipette, but usually the fish would accelerate before contact with the pipette tip. Breakage of the first laser beam acted as a trigger and the time of subsequent laser beam breakage was recorded to 0.0001 s accuracy. Only intervals of 4 cm or greater were used to calculate sprint speed (intervals 3–7). A minimum of 5 min elapsed between the time of last human contact with a fish and initiation of a subsequent sprint trial. Fish were sprinted a minimum of four times and until the investigator was satisfied that three quality trials (straight path, motivated fish) had been obtained. All trials were run at the experimental temperature. Sprint speed was calculated by dividing the distance between the intervals by the time corresponding to beam breakages:

$$V = \Delta x / \Delta t$$

where V is sprint speed (m•s^{-1}) t is the elapsed time (s) and x the distance (m) between detector arrays. The animal's top speed recorded in an interval >4 cm and the mean maximum speed from an animal's top three trials were both analyzed. False detections were usually apparent during data analysis; suspect recordings were not

used and were identified as velocities that were more than 0.25 m•s^{-1} faster than any other recorded for that fish.

Acceleration performance was determined in the natural training experiment by taking the difference in speed of a subsequent interval divided by the time elapsed between intervals.

$$A = \Delta v / \Delta t$$

where A is acceleration (m•s^{-2}), t is the elapsed time (s) and v speed (m•s^{-1}). Acceleration values were only calculated from velocities that were within 0.25 m•s^{-1} of a value from a separate trial for that animal. Likewise, an acceleration value was only considered valid if there was another value from the same fish from a separate trial within 50 % of that value. Because the velocity of a fish is unknown as it breaks the first laser in the SPC, the investigator is faced with uncertainty in calculating an animal's maximal acceleration. Taking the fish's initial velocity as 0 will artificially inflate acceleration values since the fish had to be moving to break the 1st laser beam. However, not using the first interval will fail to incorporate the animal's initial "fast-start" and thus be unlikely to capture its maximal acceleration. Even though trials were only initiated when the fish was oriented with the tip of its head pointed down the chamber, there is no assurance that the initial phases of a "fast-start" are being captured with the SPC. In this paper, we have opted for the more conservative approach of not using the first 1 cm interval of the SPC in our maximal acceleration analysis (see Vandamm et al. 2012 for a more thorough discussion of this issue).

Endurance performance

Swimming endurance was measured in a swim tunnel described by Nelson (1989) using a modification of the U$_{crit}$ procedure (Brett 1967; Nelson et al. 2002). The swim tunnels were calibrated before and after each experiment using a Marsh-Mc Birney 2000 flow meter measured at 18 points in the swimming section of the tunnel region at each of 12 variable transformer settings spanning the velocity range of the tunnel (216 total measurements). The critical swimming speeds of the fish were calculated using an average of the before and after calibrations. Each fish was transferred to the swim tunnel without air exposure, acclimated for 1 h at a water velocity of 0.10 m•s^{-1} and then subjected to incremental

increases in water velocity of 0.5 m•s^{-1} (U$_{ii}$) every 5 min (T$_{ii}$) until the fish exhausted (Nelson et al. 2002). Exhaustion was defined as the point at which a fish impinged on the back screen of the swim tunnel no longer responded to prodding with a blunt plastic probe. Modified critical swimming speed was calculated as:

$$_5^5 U_{crit} = U_i + \left(^{T_i}/_{T_{ii}} * U_{ii} \right)$$

where U$_i$ is the highest water velocity at which a fish could swim for a full 5-min time interval and T$_i$ is the time it took to exhaust the fish in the final interval.

Statistical analyses

The laboratory training experiment was analyzed by repeated measures analysis of variance (ANOVA) with the main effects being flow regime, population, and training. The natural training experiment was analyzed by (ANCOVA) with size as the covariate and population and reach as the independent variables. A Tukey's HSD multiple comparison test was used along with interaction plots in order to analyze population differences in response to training. Least squares regression analysis and Pearson's correlation analysis was used when predictors and trends were tested. Repeatability of performance measures was tested with Spearman's rank-order correlation. A Shapiro-Wilks procedure was used to test the assumption of normality and observation of the scatterplot of the residuals showed whether these data have met the assumptions of linearity and homoscedasticity and were further tested with Levene's test. Appropriate transformations of the raw data were made if these assumptions were not met or non-parametric procedures were used (e.g., Kruskal-Wallis ANOVA). The fiducial level of significance was $\alpha=0.05$ for all statistical tests. All statistical analyses were performed with either Sigma Plot™, Statsoft™; Statistica™ 5.0 or JMP™ version 5.1.

Results

Laboratory training experiment

Endurance swimming performance (modified U$_{crit}$)

Blacknose dace populations differed significantly in their initial U$_{crit}$ ($F=7.47$, df (3, 80), $P<0.01$; Fig. 2).
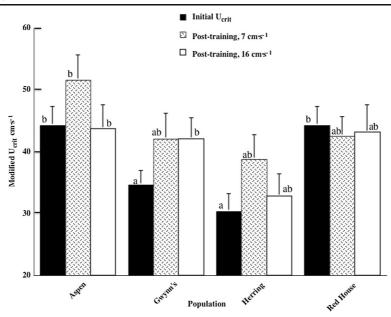
Fig. 2 Effect of laboratory training at two velocities on a modified critical swimming speed (U_{crit}) performance of fish from four populations. Fish were swum within 2–3 weeks of arriving at the laboratory (solid bars) or after 40–50 days of continuous swimming at either 7 cm•s^{-1}(stippled bars) or 16 cm•s^{-1}(solid bars). Means and standard errors are reported. Initial sample sizes were 27 for urban Red House Run (RH) and 32 for the other three populations. Final sample sizes were $n=26$, 20, 22, and 20 for rural Aspen Run (AR), suburban Gwynn's Falls (GF), urban Herring Run (HR), and urban Red House Run (RH) respectively. Bars sharing a letter were not significantly different (Tukey's HSD; $P<0.05$)

Fish from rural Aspen Run and urban Red House Run had significantly higher initial U_{crit} before training than did fish from suburban Gwynn's Falls and urban Herring Run (Fig. 2; $P<0.05$). These initial differences in U_{crit} were lost after training.

Forty to fifty days of training produced significant increases in U_{crit} across all four populations of blacknose dace (Fig. 2; $F=10.2$, df (1,80), $P=0.002$). Some fish died or escaped over the course of the training period causing the design to be unbalanced. Although Fig. 2 might suggest an interaction between population and training, this term was not significant ($P=0.227$). The different levels of flow did not produce significantly different U_{crit} performances ($P=0.075$), although, had there been a significant difference, the 7 cm•s^{-1} was actually the training velocity that produced better swimming (Fig. 2).

Sprint swimming performance

Swimming against flow for 40–50 days induced significant increases in the sprint swimming ability across all populations (Fig. 3; $F=24.3$, df (3, 81), $P<0.001$). Sprinting ability was also dependent on population

($F=7.7$, df (3, 81), $P<0.001$), but there was no significant interaction between population and training ($P=0.089$) despite the appearance of Fig. 3. The two different flow levels did not induce differences in post-training sprinting ability (Fig. 3; $P=0.330$), and similar to endurance swimming, the 7 cm•s^{-1} treatment would have been the better training velocity had there been a difference between training flow levels (Fig. 3). None of the other interaction terms were significant with regards to sprinting ability.

Repeatability of swimming performances

Each surviving individual performed both swimming tests before and after the training protocol, thus we could test for repeatability of rank order across the training regimen (i.e. did all fish train equally?). When all fish were examined, both the rank order of mean sprinting performance ($R_{90}=0.395$; $P<0.001$) and the modified U_{crit} procedure ($R_{72}=0.353$; $P=0.002$) were significantly repeatable. Interestingly, analyzing repeatability by population found significant repeatability only in the two urban populations; Red House Run fish for sprint
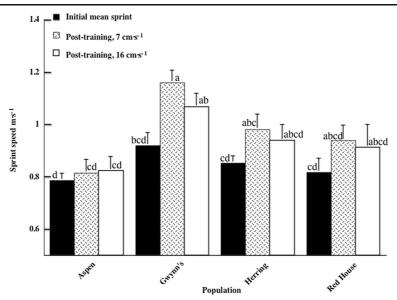
Fig. 3 Effect of laboratory training at two velocities on sprint speed of fish from four populations. Fish were swum within 2–3 weeks of arriving at the laboratory (*solid bars*) or after 40–50 days of continuous swimming at either 7 cm•s^{-1} (*stippled bars*) or 16 cm•s^{-1} (*solid bars*). The average of an animal's top sprint speed from each of its top three sprint trials was analyzed; population means and standard errors are shown. Initial sample sizes were 27 for Red House Run (RH) and 32 for the other three populations. Final sample sizes were n=26, 20, 22, and 20 for Aspen Run (AR), Gwynn's Falls (GF), Herring Run (HR), and Red House Run (RH) respectively. Bars sharing a letter were not significantly different (Tukey's HSD; $P<0.05$)

performance (R_{20}=0.498; P=0.026) and Herring Run fish for modified U_{crit} (R_{14}=0.700; P=0.005).

Size, growth and body condition

Training of blacknose dace for 40–50 days at 7 and 16 cm•s^{-1} while feeding to satiation once daily produced significant gains in mass (F=14.992, df (1, 80), $P<0.001$), however, a significant interaction between population and training (F=2.996, df (3, 80), P=0.036) indicated that weight gain during training was dependent on population. Rural Aspen Run and suburban Gwynn's Falls fish gained ~0.2 g, whereas fish from the urban populations of Red House Run and Herring Run gained ~0.1 and ~0.0 g, respectively. No significant differences in mass were found across blacknose dace populations either before or after training (P=0.11) and there was no effect of the two different flow velocities on mass growth (P=0.398) over the 40–50 day training period. All other interactions were also insignificant including those between population and flow level (P=0.897), training and flow

(P=0.925) and training, population origin and flow (P=0.683).

Modified U_{crit} was not related to total length (P=0.215) or mass (P=0.235) over the narrow size range of fish used in this experiment (Table 2). Sprint swimming performance was also not significantly related to either total length (P=0.362) or mass (P=0.275). Fulton's condition factor, K, where W is the whole body wet weight (g) and L is

$$K = \left(W \Big/ L^3 \right) * 100$$

fish length (cm), was found to be significantly correlated between trained and untrained fish (i.e. a fish of good condition before training tended to be in good condition after training; r=0.360, df=86, P <0.001). Condition homogenized slightly over the 40–50 day training period, but did not change significantly (P=0.855). There was a slightly significant positive relationship between trained body condition and trained U_{crit} (r=0.215, df=86, P=0.044), but no other relationship between condition factor and performance was significant. Growth rate during the training period had

negligible effects on both post-training U_{crit} ($P=0.243$) and sprint performance ($P=0.685$).

Natural training experiment

In this part of the study, we investigated whether three types of swimming performance were dependent upon the base-flow characteristics of the stream reach from which the fish were captured. Fish were swum within 2 weeks of being captured from a relatively fast or a relatively slow reach from each of three streams differing primarily in the amount of impervious surface in their watershed (Tables 1 and 2).

Endurance swimming performance (modified U_{crit})

Modified U_{crit} performance was determined by an interaction between the population origin (stream) and the base-flow current speed of the site it was captured from (Fig. 4; ANCOVA; $F=19.0$, df (2, 50), $P<0.001$). For the fish from the urban and suburban populations, fish from the faster reaches had greater U_{crit}, significantly so for the urban Herring Run population (Fig. 4; $P<0.05$). For these two populations, a 10 cm•s^{-1} increase in base-flow translated into an approximate 10 cm•s^{-1} increase in U_{crit}. The rural Beaver Run population actually exhibited the reverse phenomenon so that the animals from the high flow site had lower endurance swimming ability (Fig. 4). The laboratory-reared dace (from Beaver Run and Herring Run parents) had an average U_{crit} consistent

with coming from a low current stream (Fig. 4). There was no effect of size on U_{crit} across the entire experiment ($P=0.629$; mass), yet because of differential size effects within populations, size was retained as a co-variate in the general model.

Sprint performance

Sprint swimming performance was determined by both the population (stream) that the fish came from (Fig. 5; $F=10.3$, df (2, 49), $P<0.001$) and the base-flow current of the reach they were captured from ($F=7.3$, df (2, 49), $P<0.01$) but there was no interaction between these two independent variables ($P=0.48$). For each stream, the sprint performance of the average fish from the fast reach was about 20 cm•s^{-1} greater than that of the average slow-reach fish, and across streams, sprinting performance was linearly related to base-flow (Fig. 5). From the relationship seen in Fig. 5, fish that were reared in the laboratory, never having been exposed to substantial currents, had an appropriate mean sprinting performance. There was a significant effect of size on sprint swimming performance across the entire experiment ($F=19.6$, df (1, 49), $P<0.001$; mass), with larger fish tending to sprint faster than smaller fish. Sprint performance was not related to an individual's U_{crit} ($P=0.107$).

Acceleration performance

Acceleration performance largely mirrored the sprint swimming performance results but with larger variances

Fig. 4 Modified critical swimming speed (U_{crit}) performance of fish from three populations collected from two reaches of their stream that differed substantially in base-flow as a function of base-flow. Fish were swum within 2 weeks of arriving at the laboratory. A group of animals that were hatched and had spent their entire life in laboratory tanks with negligible flow are included for comparison. Means and standard errors are shown; sample sizes are reported in Table 2
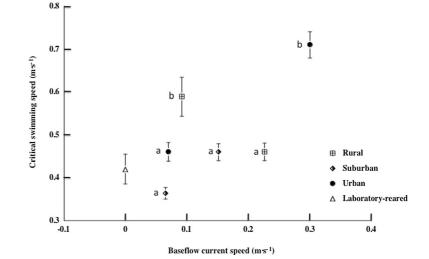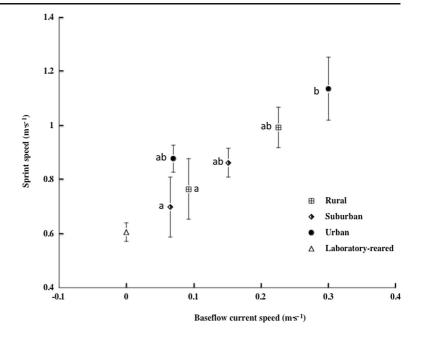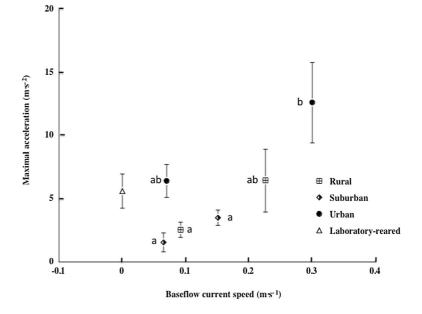
Fig. 5 Sprint swimming speed of fish from three populations collected from two reaches of their stream that differed substantially in base-flow as a function of base-flow. Fish were swum within 2 weeks of arriving at the laboratory. A group of animals that were hatched and had spent their entire life in laboratory tanks with negligible flow are included for comparison. Means of their top sprint performance and standard errors are shown; sample sizes are reported in Table 2

in several of the groups. Acceleration performance was determined independently by both the population (stream) that the fish came from (Fig. 6; $F=17.9$, df (2, 49), $P<0.001$; Kruskal-Wallis: H (2, $N=56$) $=20.22$ $P<0.001$) and somewhat by the base-flow current of the reach they were captured from ($F=5.5$, df (2, 49), $P=0.023$; Kruskal-Wallis: H (2, $N=56$) $=3.68$ $P=0.055$) but there was no interaction between these two independent variables ($P=0.15$). For each stream, the acceleration performance of the average fish from the fast reach was about twice that of the average slow-reach fish. Acceleration performance was approximately linearly related to base-flow current speed with the low-speed urban population (Herring Run) being the primary exception to this relationship. Interestingly, from the relationship seen in Fig. 6, fish that were reared

Fig. 6 Acceleration performance of fish from three populations collected from two reaches of their stream that differed substantially in base-flow as a function of base-flow. Fish were swum within 2 weeks of arriving at the laboratory. A group of animals that were hatched and had spent their entire life in laboratory tanks with negligible flow are included for comparison. Means of their top acceleration performance and standard errors are shown; sample sizes are reported in Table 2

in the laboratory had much higher acceleration performance than would be expected for fish from a no-flow environment (Fig. 6). There was no effect of size on acceleration performance across the entire experiment ($P=0.869$; mass).

Discussion

Phenotypic plasticity of locomotor performance

The purpose of the present work was to further explore the phenotypic plasticity of locomotor performance in dace populations occupying streams of variant urbanization using both field and laboratory approaches. Both sprint and U_{crit} performance of blacknose dace were plastic according to both empirical tests employed here. Endurance performance (modified U_{crit}) significantly improved with laboratory training (Fig. 2; $P=0.002$) and was determined by a significant interaction between stream current velocity and population in dace collected from stream reaches varying in base-flow current (Fig. 4; $P<0.001$); in the urban and suburban streams, fish captured from the faster stream reach had the expected greater endurance performance, significantly so for the urban fish (Fig. 4; $P<0.05$). Sprint swimming performance was also significantly improved by laboratory training of blacknose dace (Fig. 3; $P<0.001$), and was significantly greater in fish captured from the faster of two reaches within a stream (Fig. 5; $P<0.001$). In addition, fish that were raised in the laboratory and thus had never experienced substantial flow, had very low U_{crit} performance and the lowest sprinting performance measured (Figs. 4 and 5). Acceleration performance, although extremely variable when measured in a sprint performance chamber, was also significantly better in fish collected from the faster of two reaches within a

stream (Fig. 6; $P<0.05$). Together with the earlier detraining study (Nelson et al. 2008), these results provide evidence that locomotor performance of blacknose dace is plastic and is responding to in situ differences in the flow they experience. Dividing the magnitude of all swimming performance difference between fish from fast and slow current sites by the magnitude of the baseflow difference between the sites suggested that the populations were similarly plastic (Table 3).

Interestingly, training fish at 16 cm•s^{-1} in the laboratory did not produce significantly better swimming in either performance test than did training at 7 cm•s^{-1}. Since some of the fish came from stream reaches where the base-flow current velocity was at, or exceeded, these training velocities, this result implies that the training effect accrues from being forced to swim constantly, regardless of velocity, and that these fish are probably not swimming constantly in nature, as field observations have shown (Cunjack and Power 1986). This result contrasts with Young and Cech (1994) who showed endurance swimming capacity in striped bass (*Morone saxatilis*) to be directly proportional to several different training velocities.

Further support for the idea that swimming performance differences in blacknose dace result from flow differences in their home stream can be drawn from comparisons of the present data with Nelson et al. (2003) and Nelson et al. (2008) (Table 4). Fish for the present laboratory training study were collected in the late summer and early fall when stream discharges are generally at their lowest annual level, particularly in urban streams where impervious surfaces prevent groundwater recharging. Indeed, when these fish were collected, United States Geological Survey (USGS) gauging stations show approximately a ten-fold lower discharge volume in the urban Herring Run stream, a two-fold lower discharge volume in the suburban

Table 3 Magnitude of natural, within stream training effect for Baltimore, Maryland area streams of three different levels of urbanization

	Stream type		
Performance test	Rural (Beaver Run)	Suburban (Gwynn's Falls)	Urban (Herring Run)
Critical swimming speed (U_{crit})	−0.96	1.13	1.09
Sprint swimming speed	1.17	1.29	0.78
Acceleration (s^{-1})	28.9	22.8	27.0

The difference between the mean performance of fish collected from the faster current site minus the mean performance from that same test of fish collected from the slower current site divided by the difference in mean base-flow current speed between the two sites. This produced dimensionless numbers for the first two tests

Table 4 Comparison of population mean values for several sites with fish collected years earlier at the same site

Performance test	Critical swimming speed (U_{crit}) cm•s^{-1}		Sprint swimming speed cm•s^{-1}	
Stream	Previous studies	Present study	Previous studies	Present study
Rural (Aspen Run)	40.0 late winter-early summer	44.3 late summer	106.2 late winter-early summer	93.2 late summer
Suburban (Gwynn's Falls)	36.6 late winter -early summer	34.6 early fall	116.0 late winter -early summer	105.6 early fall
Urban (Herring Run)	47.9 late winter -early summer	30.3 early fall	140.6 late winter -early summer	96.9 early fall
Urban (Red House Run)	51.5 late winter -early summer	44.3 fall	112.4 late winter -early summer	97.2 fall

Data from the previous studies are from Nelson et al. (2003) and (2008)

Gwynn's Falls stream and about the same discharge in the rural Beaver Run stream relative to the times of fish collection for the earlier studies [Nelson et al. 2003, 2008 (there are no USGS gauging stations on either Aspen Run or Red House Run)]. Because the rural Aspen Run fish actually had a slightly higher U_{crit} than in previous studies (Table 4), we can discount systematic investigator bias (different humans guaging fish exhaustion) and suggest that the substantially lower U_{crit}s of the urban fish in the present study were because these fish were being detrained in the sluggish flows of their home streams at this time of year (Table 4). Alternatively, pathogen or parasite loads could be worse as a result of the sluggish flows, producing average poorer population swimming performance (e.g., Barker and Cone 2000). A similar result was seen for the top sprinting performance of fish. Although all populations had lower levels of this performance metric in the present study, the greatest deficits were seen for the urban populations (Table 4).

Finding plasticity of locomotor performance is supported by a multitude of laboratory studies on the trainability of fish swimming performance, primarily endurance or U_{crit} performance of salmonids (reviewed by Davison 1989, 1997). Generally, a period of exercise training of at least 1 month has been shown to cause improvements in U_{crit} values (e.g., Farrell et al. 1989). Cyprinids have been used infrequently in training studies, but common carp (*Cyprinus carpio*) (He et al. 2013), qingbo (*Spinibarbus sinensis*) (Zhao et al. 2012), and zebra danio (*Danio rerio*) (McClelland et al. 2006) have all been shown to have significantly improved U_{crit} performances after a period of exercise training. In addition, domesticated roach (*Rutilus rutilus*) held in a current, had biochemical responses to exercise more indicative of enhanced endurance capacity than conspecifics held in still water (Broughton et al. 1978).

Few studies have specifically trained sprint swimming performance or even examined how conventional training impacts sprint performance. Glycolytic enzyme activities of white muscle, which might be indicative of metabolic support of sprinting, have been shown to increase with conventional training in some cyprinids (Hinterleitner et al. 1992) but not in others (He et al. 2013). Actual laboratory training of sprint performance has been shown to somewhat improve acceleration and sprint performance in salmonids (Gamperl et al. 1991; McFarlane and McDonald 2002), and to improve metabolic support of high muscle power output (Pearson et al. 1990; McFarlane and McDonald 2002), but there is insufficient information to draw general conclusions about how sprint training modifies fish physiology. However, coupling the limited fish data with results from other ectothermic vertebrates (e.g., Adolph and Pickering 2008), would suggest that laboratory sprint training generally causes minimal gains in locomotor performance.

Comparisons of fish that are raised with minimal swimming with wild conspecifics or comparison of conspecifics that face variable swimming demands also support the result of swimming performance capacity being a function of swimming history reported here. In salmonids, populations with longer migrations tend to outperform populations with less challenging migrations (Taylor and McPhail 1985; Taylor and Foote 1991). Three-spined sticklebacks (*Gasterosteus aculeatus*) exist as sympatric anadromous and non-migratory forms in both North American and European rivers. In both settings, the anadromous form has been shown to have better swimming performance (Taylor and McPhail 1986; Tudorache et al. 2007). In Guppies (*Poecilia reticulata*), there is a positive correlation between current strength and swimming performance among populations from four different rivers in Trinidad (Nicoletto and Kodric-Brown 1999), and guppies

removed to the laboratory suffer diminished acceleration performance when compared with wild animals from the same populations (Walker et al. 2005). Similarly, damselfish *Acanthochromis polyacanthus* collected from a heavy surf zone had better swimming performance than conspecifics collected from calmer waters (Binning et al. 2013).

Numerous investigators report diminished swimming performance in cultured fish when compared with wild conspecifics. For example, Gibson and Johnston (1995) show a reduced escape response of farmed juvenile turbot (*Scophthalmus maximus*) when compared with wild juveniles, but only if the wild fish were freshly captured, suggestive of very rapid laboratory de-training (Nelson et al. 2008). However, Vincent (1960) found that swimming performance differences between wild and hatchery brook charr (*Salvelinus fontinalis*) remained after the wild strains were reared for one generation in the hatchery and Thomas and Donahoo (1977) found an inverse correlation between domestication time and swimming endurance for three strains of rainbow trout (*Oncorhyncus mykiss*). These latter studies attest not only to substantial phenotypic plasticity of locomotor performance in fish in response to swimming demand, but also to a rapid response of locomotor performance to selection.

Repeatability of swimming performance

Although scientists have been swimming fish for much of the 20th century (Beamish 1978), and repeatability of experimental results is one of the earliest foundations of the scientific method (Boyle 1661), demonstrating the repeatability of fish locomotor performances before extrapolating upon their applicability first arose in the last two decades of the 20th century (Reviewed by Kolok 1999; Nelson et al. 2002; and Oufiero and Garland 2009). In addition to being a foundation of the scientific method, establishing repeatability is important for mechanistic physiological and evolutionary studies of locomotion (reviewed by Oufiero and Garland 2009). The repeatability of the U_{crit} procedure is now well established over fairly long time spans and in a number of species. Nelson et al. (1994) showed 3-month repeatability of U_{crit} in Atlantic cod (*Gadus morhua*), Claireaux et al. (2007) demonstrated 6-month repeatability of a modified U_{crit} procedure in European Sea Bass (*Dicentrarchus labrax*) in mesocosms and Oufiero and Garland (2009) determined

U_{crit} to be repeatable in guppies (*Poecilia reticulata*) over 3–4 weeks, but not a year. We had previously shown the modified U_{crit} procedure used here to be repeatable in blacknose dace for a period of 1 month (Nelson et al. 2002) and 6 months in some populations (Nelson et al. 2008). The present study adds to this growing list by establishing significant individual repeatability of a modified U_{crit} procedure in blacknose dace across 40–50 days of a laboratory training regimen.

The short-term repeatability of laboratory measures of sprint swimming performance or acceleration has also been reported for a number of fish species (Reviewed by Oufiero and Garland 2009; Marras et al. 2011). However, demonstrating longer-term repeatability has remained elusive with just a few exceptions. Reidy et al. (2000) and Martinez et al. (2002) found stable sprint performances of Atlantic cod (*Gadus morhua*) over 1.5–3 months. Claireaux et al. (2007) found sprint swimming performance of European Sea Bass to be repeatable over 4 weeks and across a temperature change, but not after 6 months of mesocosm residence. Oufiero and Garland (2009) discovered that some components of the fast-start response were repeatable in guppies (*Poecilia reticulata*) over 3–4 weeks, but none were repeatable a year later. They did, however, find significant annual repeatability of a constant acceleration test (CAT; their U_{max}). Marras et al. (2011) found all seven components of a fast-start response to be significantly repeatable on a daily basis in European Sea Bass, but after 4 weeks of laboratory residence, only five of the components were significantly repeatable. Experimenting with this same species, Vandamm et al. (2012) reported significant daily repeatability of acceleration measured with a sprint performance chamber, but not after 6 months of mesocosm residence. Sprint performance of blacknose dace had previously been shown to be repeatable over a period of 7 days (Nelson et al. 2002), but not after 10 weeks of keeping this stream fish under static flow conditions (Nelson et al. 2008). The present study substantially adds to this literature by establishing the individual repeatability of sprint performance in blacknose dace that were forced to swim for 40–50 days. Nelson et al. (2008) proposed that the lack of 10-week repeatability in dace under static flow conditions was likely due to differential swimming activity elicited by social interactions. The present result of significant rank-order repeatability across 6–7 weeks of forced swimming support that contention because swimming activity should have

been more uniform under the latter conditions. It is perhaps not surprising, but nonetheless interesting and a new finding, that holding stream fish under static flow conditions resulted in loss of repeatable sprint swimming performance, whereas holding them in a current maintained individual differences in sprinting ability.

Population-level differences in phenotypic plasticity

A major impetus for the work described here was to further investigate the variance in phenotypic plasticity at the population-level found in an earlier detraining experiment (Nelson et al. 2008). The results provide a mixed assessment of whether phenotypic plasticity of locomotor performance varies among populations of blacknose dace. There were non-significant interaction terms for both laboratory training of U_{crit} performance (Fig. 2; $P=0.227$) and sprint performance (Fig. 3; $P=0.089$) and similar non-significant interactions between population and reach current speed for sprint performance (Fig. 5; $P=0.48$) and acceleration (Fig. 6; $P=0.15$), yet the idea that these populations vary in their degree of plasticity should not be entirely dismissed. Endurance performance was determined by a significant interaction between population and current velocity in the natural training experiment (Fig. 3; $P<0.001$); both the suburban and the urban population showed the intuitive result of individuals from the faster stream reach having better average endurance performance, whereas the fish from the rural population showed the reverse trend. Furthermore, the fact that the only two populations to show significant repeatability of performance across 40–50 days of a laboratory training regimen, when analyzed in isolation, were the urban ones, implies that consistent plasticity of locomotor performance may be part of the suite of characters that allow blacknose dace to persist in hostile urban environments.

Size, growth and behavior

Although size was deliberately restricted in this study, lack of fish availability resulted in some size differences between groups in the natural training experiment (Table 2), but size only significantly influenced sprint swimming performance, not U_{crit} or acceleration. A similar significant effect of size on sprint but not U_{crit} was reported previously (Nelson et al. 2008). All groups were statistically homogenous for size in the laboratory training experiment.

Growth over the 40–50 day laboratory training period was determined by a significant interaction between population and training. The rural and suburban populations both gained around 0.2 g on average whereas fish from one urban population gained around 0.1 g and the other gained nothing. This may be due to the different life-history trajectories of the urban populations (Fraker et al. 2002) wherein the urban fish invest more in growth during their first year and thereafter invest more acquired energy into reproduction; the fish used in this portion of the study were of sizes suggesting they were at least 1 year old (Table 2; Fraker et al. 2002). There was no consistent pattern between these differential growth rates and either absolute swimming performance or the increment in swimming performance achieved through training (Figs. 2 and 3). This result conflicts with several studies. For instance, faster growing Atlantic silversides (*Menidia menidia*) had lower endurance and sprint swimming performance when compared to slower growing populations of conspecifics (Billerbeck et al. 2001). Alvarez and Metcalfe (2007) also found a decrease in endurance swimming performance of threespine sticklebacks (*Gasterosteus aculeatus*) during periods of increased growth. European sea bass (*Dicentrarchus labrax*) in mesocosms had an inverse relationship between growth rate and both sprint swimming performance Handelsman et al. (2010) and acceleration Vandamm et al. (2012). In contrast, Royle et al. (2006) found no effect of treatment-induced differential growth on the fast-start performance of green swordtails (*Xiphophorous helleri*). Similarly, Alvarez and Metcalfe (2007) induced differential growth rates in a number of three-spined stickleback populations, and found no effect on fast-start swimming velocity in one entire segment of their populations (those from ponds). Finally, in probably the most relevant comparison to the present study, Oufiero et al. (2011) found that natural differences in growth rate induced by differences in community composition had no effect on either sprint or endurance performance capacity in a rivuline

(*Rivulus hartii*). Thus, current best evidence suggests that environmentally-induced differences in growth rate do not necessarily incur a locomotor capacity tradeoff in wild stream fishes.

Caveats

A number of confounding factors should be considered when interpreting the results presented here. We analyzed mean values of populations from specific sites, yet individual dace collected from any site can show dramatically different flow selection behaviour in the laboratory (Williamson et al. 2012). The field sites were selected by their differences in mean baseflow, but within any site there is a mosaic of current choices available to a fish. There is no guarantee that the fish we collected at a site were not over-representative of a relatively fast or slow region of flow within their reach. Likewise, although the average flow velocity was the same across the various training lanes in the laboratory, the fish had access to a range of flows within each lane, and since flow selection is a significantly repeatable behaviour in dace (Williamson et al. 2012), there is no guarantee that all fish in a given training treatment were being equally trained.

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