

Environmental Correlates, Plasticity, and Repeatability of Differences in Performance among Blacknose Dace (*Rhinichthys atratulus*) Populations across a Gradient of Urbanization

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ABSTRACT

Urbanization alters stream and watershed hydrology so that fish from urban stream systems are confronted with extreme flows during storms and runoff events. To test whether residence in urban streams is associated with altered swimming ability, we compared sprint and endurance swimming performances of eight populations of blacknose dace (*Rhinichthys atratulus*) from different watersheds along an urban/rural gradient. Watershed impervious surface cover, a measure of urbanization, was significantly correlated with sprint performance in dace from all stream types and endurance swimming performance (U_{crit}) when only fish from urban streams were analyzed. Three estimators of water flow in a stream system, watershed area, mean annual discharge, and base-flow current speed, were all related to U_{crit} in fish from nonurban streams. The U_{crit} was significantly repeatable after 6 mo in the laboratory, but dace populations with exceptional U_{crit} values lost ability under no-flow, “detraining” conditions. Sprint performance changed substantially in individual dace after 10 wk under no-flow conditions and was a significant function of the animal’s original performance. Animals with high sprint performance tended to lose ability, whereas those with poor performance gained ability. Interpopulation differences in both sprint and endurance swimming were robust over multiple years of collection from the same sites.

Introduction

Urbanization is a significant anthropogenic stressor of streams, affecting more than 130,000 km of streams in the United States alone (USEPA 2000). The increase in impervious surface cover (ISC) in a watershed (paved surfaces, buildings, etc.) that results from urbanization alters the hydrological and geological integrity of streams (Paul and Meyer 2001). Increased ISC decreases the amount of water that percolates through the soil, producing an increase in surface runoff. Thus, urban stream flow rises dramatically following rainfall or melting events (Espey et al. 1965; Hirsch et al. 1990). The loss of water percolating through the soil also causes decreased groundwater recharge, resulting in reductions in flow between periods of precipitation or melt in urban streams (Klein 1979; Barringer et al. 1994). Thus, the amount of ISC in a watershed is a good estimator of the amount of water that will enter a stream as surface run-off and is a reliable predictor of hydrologic degradation as a consequence of urbanization (McMahon and Cuffine 2000).

Hydrologic changes to urban streams are likely to be some of the stressors that limit the diversity of fish communities in this environment. Schueler and Galli (1992) found that fish diversity in Maryland streams decreased dramatically above 10%–12% ISC, and Klein (1979) found that fish were absent from streams in Maryland when ISC exceeded 30%–50%. Undoubtedly, other factors linked to urbanization, such as toxic metals, xenobiotics, eutrophication, and habitat degradation, contribute to the loss of fish diversity in urban streams (Yoder et al. 1999), yet how a species responds to altered flow regimes may be a key factor in predicting their tolerance of urbanization.

Blacknose dace (*Rhinichthys atratulus* Hermann) were chosen for this experiment because they are widely distributed throughout the east-central portion of the North American continent and are abundant in most Maryland streams, including some of the most urbanized streams. Thus, this species can be exploited for an intraspecific, comparative experimental design wherein the biology of fish populations from urban streams is compared with that of conspecifics from nearby rural streams. From these comparisons, we may be able to infer character states that either facilitated persistence in the streams as urbanization developed or emerged in response to urbanization. This approach may also offer mechanistic explanations as to why other species are unable to persist in urban environments. Toward that end, this study compared swimming

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Table 1: Present-day names of the streams used, percentage of impervious surface cover (ISC) in their watershed, mean current speed at base flow for the study site, (averaged over a calendar year [2005–2006] across the entire stream channel), stream annual discharge, and the area of the streams' watersheds

Site	% ISC	Designation	Current Speed (m s ⁻¹)	Annual Discharge (m ³ s ⁻¹)	Watershed Area (ha)
Aspen Run	.21	Rural	.22	NA	15,626
Beaver Run	1.01	Rural	.23	.328	28,872
Honeygo Run	11.69	Suburban	.06	.057	7,279
Gwynn's Falls	15.18	Suburban	.15	.114	14,931
Herring Run	23.32	Urban	.07	.049	10,177
Red House Run	26.81	Urban	.03	NA	11,342
White Marsh Run	31.18	Urban	.11	.089	12,330
Herbert Run	35.72	Urban	NA	.070	13,876

Note. NA = not available.

abilities of populations of urban, suburban, and rural blacknose dace in the greater Baltimore (Maryland) region.

Locomotor performance has frequently been used as an indicator of Darwinian fitness in animals *sensu* Arnold (1983). These studies have primarily used herpetofauna as model organisms and have advanced our knowledge of phenotypic selection considerably (Kingsolver and Huey 2003). The few studies that have used performance differences in fish as indicators of fitness in natural populations of fishes (e.g., Billerbeck et al. 2001; Ghalambor et al. 2003) have returned important results. Here we use two laboratory swimming performance tests as fitness indicators in blacknose dace. We first explore the utility of these two performance tests in this role by comparing interindividual variance in performance with intraindividual variance in repeat tests (i.e., establishing the repeatability of the tests). We then examine whether interindividual differences in performance correlate with environmental variables associated with urbanization.

Our initial study (watershed) was designed to test the hypothesis that urbanization and the ensuing stream habitat changes will structure the performance capacity of blacknose dace. This was accomplished by comparing endurance (U_{crit}) and sprint swimming abilities with a suite of watershed and stream characteristics between individuals from replicate urban, suburban, and rural populations of blacknose dace. Nelson et al. (2003) previously found that blacknose dace from rural and suburban streams had swimming performances that mirrored differences in base-flow current speed at the site of their collection. However, because the percentage of ISC (%ISC) may be the main determinant of flow in urban systems, we also tested the hypothesis that the relationship between stream flow and U_{crit} will be different in urban streams. A second experiment (U_{crit} plasticity) was designed to test whether interpopulation differences in endurance performance were phenotypically plastic. This was accomplished by measuring U_{crit} in dace from seven populations along a rural/urban gradient and then exposing the animals to identical no-flow conditions in the lab-

oratory for 6 mo and reassessing their performance after 3 mo and 6 mo. A final experiment (sprint plasticity) tested whether interpopulation differences in sprint performance were phenotypically plastic, by exposing individuals of known sprint performance to no-flow conditions in the laboratory for 10 wk and then reassessing their sprint performance. Finally, because fish for all of these experiments were collected from the same locations and we had swimming performance data from previous studies (Nelson et al. 2003), we were able to analyze the site-specific stability of mean population performance over 3.5 yr.

Material and Methods

Field Sites

Blacknose dace were collected from streams in eight different watersheds (one site per watershed) across a rural-urban gradient around the city of Baltimore. Sites were of similar latitude and stream order and were chosen based on %ISC of the watershed, proximity of a United States Geological Survey (USGS) gauging station on the stream, and population independence (i.e., unlikely faunal interchange between the streams). Table 1 presents some characteristics of the study streams and the collection sites.

ISC Determination

The ISC for each watershed was determined by interpreting watershed boundaries from digital line graphs of topographic contours. Then, the 2001 ISC of the National Land Cover database (U.S. Department of the Interior and USGS Multi-Resolution Land Characteristics Consortium; <http://www.mrlc.gov/>) was used to calculate the percent of impervious cover for each watershed. We defined urban, suburban, and rural sites as those that had >20%, 10%–20%, and <2% impervious surface cover in their watersheds, respectively.

Flow Determination

We characterized base-flow current speed at each site at two times of the year using methods similar to those reported by Nelson et al. (2003). Briefly, current speed was measured after at least five precipitation-free days at four evenly spaced points across 11 transects spaced at 5-m intervals along the stream. At each sample point, we measured current speed at middepth using a Marsh-McBirney Model 2000 flowmeter. One urban site (Herbert Run [HB]) was located close to a magnetic field created by an adjacent railroad, which prevented use of the flowmeter. Thus, for any data analyses that include flow, fish from the HB site are omitted. Similarly, two streams (Aspen Run [AR] and Red House Run [RHR]) were without USGS gauging stations; thus, we report no discharge analyses for these sites.

Fish Capture and Holding

Fish were collected three times: February 2004 for the watershed study, June–July 2003 for the U_{crit} plasticity study, and January 2005 for the sprint plasticity study (Table 2). Fish were captured with a beach seine, selected streamside for a common size range (50–70 mm total length), and returned to the lab in water from their native stream. Fish were brought to the experimental temperature of 20°C at a maximum rate of 2°C d⁻¹, transferred to 400-L tanks of dechlorinated tap water with a current speed of 1–3 cm s⁻¹, and held for 2 wk before any performance tests were conducted. Holding tanks were calibrated with a Marsh-McBirney Model 2000 flowmeter by averaging readings from 18 stations in the approximately 42-L holding section of the tanks. Animals used in the plasticity studies were moved to different tanks after their initial performance tests. After approximately 1 wk in the laboratory, fish were anesthetized with buffered MS-222 (water concentration 100 mg L⁻¹), weighed (wet blotted weight) to the nearest milligram, and measured for standard length to the nearest millimeter. Fish were individually marked with a subdermal injection of sterilized acrylic

paint and swabbed with an antibiotic mixture. Animals were fed daily with flake fish food and supplemented biweekly with live brine shrimp, but they were fasted 24 h before performance tests.

Fish and populations subject to no-flow conditions in the laboratory (detraining) were randomly assigned to 10-gal aquaria with under-gravel filtration as the only water movement. At least two tanks were set up for each population to control for tank effects. Each tank housed a maximum of eight individuals from a population. Fish-handling protocols were approved by the Towson University Institutional Animal Care and Use Committee (F01102RPR.27).

Endurance Swimming

Critical swimming performance was determined as described by Nelson et al. (2002). Briefly, the procedure, first described by Brett (1964), was modified to use 5-cm-s⁻¹ increases in water velocity at 5-min intervals to account for the size and ecological demands placed on blacknose dace (Nelson et al. 2002). Performance was measured in swim flumes that were originally described by Nelson (1989) and that followed the design specifications of Vogel (1981). Swim flumes were calibrated with a Marsh-McBirney Model 2000 flowmeter by averaging readings from 27 stations in the 32 × 10 × 10-cm swimming section of the tunnel for each of 10 settings of the motor controller.

To minimize the stress of capture and transfer, fish to be swum were captured with a dip net and immediately placed in an anesthetic bath containing 50 mg L⁻¹ MS-222 until they reached phase 1 of anesthesia (loss of equilibrium; Iwama et al. 1989). Fish were then randomly assigned and transferred to one of two swim flumes; fish were acclimated to the flume for 1 h at 20°C and a current of 5 cm s⁻¹ before graded velocity increments began. A light was used to deter fish from the rear of the swim tunnel, and fish that attempted to rest there were gently prodded with a blunt probe. Exhaustion was defined as the time point at which a fish no longer responded to prodding,

Table 2: Experiment name, sample sizes (n) and fish sizes (mean \pm SD) by collection site for three separate fish collections that are reported on here

Study Site	Watershed (February 2004)		U_{crit} Plasticity (June–July 2003)		Sprint Plasticity (January 2005)	
	n	Mass (g)	n	Mass (g)	n	Mass (g)
Aspen Run	9	1.71 \pm .65 ^A	10	1.38 \pm .33 ^A	11	2.89 \pm .71 ^{BC}
Beaver Run	11	1.80 \pm .35 ^{AB}	10	1.82 \pm .44 ^{ABC}		
Honeygo Run	8	1.82 \pm .62 ^{AB}	14	1.70 \pm .36 ^{AB}	10	2.02 \pm .56 ^A
Gwynn's Falls	7	2.56 \pm 1.15 ^{AB}	11	1.44 \pm .28 ^A		
Herring Run	10	2.99 \pm 1.28 ^{AB}	10	2.21 \pm .34 ^{BC}	10	3.50 \pm .44 ^C
Red House Run	8	3.06 \pm .48 ^B	12	2.15 \pm .38 ^{BC}		
White Marsh Run	8	1.86 \pm .43 ^{AB}	12	2.07 \pm .44 ^B		
Herbert Run	8	2.79 \pm .87 ^B			10	2.51 \pm .30 ^{AB}

Note. Means followed by different letters differed significantly ($P < 0.050$) based on Tukey's post hoc comparisons.

and critical swimming speed (U_{crit}) was calculated with the following equation (Brett 1964):

$${}^5U_{\text{crit}} = U_i + \left(\frac{T_i}{T_{ii}} \times U_{ii} \right),$$

where U_{crit} = critical swimming speed, U_i = highest speed maintained for a full 5-min interval, T_i = time of fatigue at last current velocity (min), T_{ii} = interval length (5 min), and U_{ii} = velocity increment (5 cm s⁻¹). This modified U_{crit} protocol had been shown to be repeatable over a period of 1 mo in blacknose dace held at a constant current (Nelson et al. 2002).

Sprint Performance

Sprint performance was tested as described by Nelson et al. (2002) and Reidy et al. (2000) in a sprint chamber modified for blacknose dace and utilizing commercial analog/digital recording equipment. Briefly, 30 min before the initiation of a sprint trial, a fish was captured by dip net, herded into a beaker, and then transferred to the sprint chamber while submerged, to minimize air exposure. The dimensions of the chamber were 1.5 m (length) × 0.15 m (width) × 0.15 m (height). Light-emitting laser diodes (OnPoint Laser, Eden Prairie, MN) 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 Darlington photodetectors (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 to a height of 8.5 cm (0.5 cm below the “fill” line at 9 cm). When activated by light, the Darlington photodetector arrays put out a 5-V signal to one of eight digital inputs on an ADInstruments Powerlab 4s, which was interfaced to an Apple Macintosh i-Book computer running Chart software. Breakage of the first laser beam acted as a trigger, and the time of subsequent laser beam breakage was recorded to 0.1 ms accuracy. Sprint swimming speed and acceleration were calculated from the times of laser beam breakage and the distance between detector arrays. Intervals of 2 cm or greater were used to calculate sprint speed. 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 20°C. Only the maximum speed from each of an animal’s top three trials was analyzed. Re-

peatability of the test was investigated by sprinting a group of 10 fish held in the laboratory under a current of 1–3 cm s⁻¹ for one additional week after their initial sprint trial. The second sprint test was analyzed without knowledge of the fishes’ performance in the first sprint test. This method has been shown to be repeatable in two other fish species (Reidy et al. 2000; Nelson and Claireaux 2005).

Statistical Analyses

We investigated potential differences in the size of fish and the relationship between size and swimming performance among populations by using ANOVA and ANCOVA models, respectively. Repeatability of swimming performance was examined by using Spearman rank correlation coefficients or Kendall concordance tests. Relationships among sprint speed, U_{crit} , and watershed variables were analyzed using least squares regression analysis. The general model for analyzing variance among populations was an ANCOVA or a repeated-measures ANCOVA with population as a main effect, time under a flow regime as a repeated measure (for the two plasticity experiments), and size (standard length) or mass as a covariate. Tukey’s HSD tests were used to make multiple comparisons among populations, time periods, or both when ANCOVA models were significant ($P < 0.050$). The PROC MIXED procedure of SAS with an unconstrained covariance matrix was used to implement repeated-measures models. Stability of mean population endurance performances over time was also tested with Friedman ANOVA, a nonparametric tests of mean rank. Where applicable, assumptions of normality and homogeneity of variance were assessed with Kolmogorov-Smirnov and F_{max} tests, respectively. Data that did not meet these assumptions were log transformed before analysis. Unless otherwise stated, results are given as means ± 1 standard error. All statistical analyses were performed with either SAS (SAS, Cary, NC) or Statistica (Statsoft, Tulsa, OK).

Results

General

Although attempts were made to restrict the size range of fish used, the lack of fish in the targeted size class in some collections resulted in various size differences among collections for the three studies (Table 2). Among dace from the watershed study, there was a significant effect of mass on sprint performance (ANCOVA; $P = 0.015$) but not on U_{crit} ($P = 0.544$), although the interaction between U_{crit} and mass was nearly significant ($P = 0.087$). Critical swimming performances of fish from the watershed study met the assumptions of normality (Kolmogorov-Smirnov test, $P > 0.050$ for all collections) and equal variances (F_{max} test, $P = 0.067$, watershed). Likewise, sprint performance data from the watershed study and the plasticity study met the assumptions of normality (Kolmogorov-Smirnov test, $P > 0.050$) and equal variances (F_{max} test: $P = 0.092$, watershed; $P = 0.189$, plasticity).

Watershed Study

Critical Swimming Speed. No watershed parameter (%ISC, watershed area, stream discharge rate, or base-flow current speed) significantly influenced endurance swimming performance in blacknose dace when all populations were analyzed together ($P > 0.05$). Although this might suggest that watershed dynamics do not influence endurance swimming of resident fish, grouping populations by degree of watershed urbanization suggests that environmental factors do control swimming performance but that their influence changes across the urban/rural gradient. If only suburban and urban populations (those with $>10\%$ ISC) are considered together, endurance performance of blacknose dace was significantly related to the %ISC of the watershed (Fig. 1: $r^2 = 0.14$; $P = 0.007$). In contrast, if only rural and suburban populations (those with $<20\%$ ISC) are considered, all measured watershed variables correlate significantly with endurance swimming performance (Fig. 2). Only two variables (watershed area and base-flow current speed) are presented in Figure 2; however, stream discharge and %ISC also correlated significantly with endurance swimming performance in nonurban fish ($r^2 = 0.41$, $P < 0.001$ and $r^2 = 0.12$, $P = 0.035$, respectively). Interestingly, the base-flow current speed (CS) and U_{crit} values in nonurban fish (Fig. 2B) were very similar to those reported for fish from several rural and suburban streams investigated in 2000: $\log U_{crit(2004)} = 1.544 + 0.004 \text{ CS}$ compared with $\log U_{crit(2000)} = 1.486 + 0.007$

CS (in cm s^{-1} and logged to facilitate comparison with Nelson et al. 2003).

An ANCOVA with population as the treatment, U_{crit} as the response variable, and size as a covariate showed significant differences between the critical swimming speeds of dace populations ($P = 0.014$) that were independent of size and not due to an interaction between size and population. Fish from RHR and HB had the highest mean U_{crit} and were significantly greater than the mean U_{crit} of fish from AR, Honeygo Run (HON), Gwynn's Falls (GF), and White Marsh Run (WM; Tukey's HSD, $P < 0.050$; Fig. 3). Fish from Beaver Run (BR) had intermediate endurance performances that were significantly greater than those for WM and HON (Tukey's HSD, $P < 0.050$; Fig. 3).

Sprint Swimming Performance. Interindividual differences in blacknose dace sprint performance exceeded intraindividual variance in replicate trials run on the same day. Correlation between first- and second-fastest and second- and third-fastest sprint speeds for individual fish were significant ($P < 0.001$) and strong (Spearman rank correlation coefficient, $r = 0.90$ and 0.98 , respectively; Kendall concordance coefficient of 0.98 , $P < 0.001$, for all three trials considered together). Additionally, sprint speeds in a group of 10 fish measured 1 wk after their initial sprint trial were highly correlated with their initial sprint speeds (Spearman rank correlation of the top velocity with the top velocity measured a week later, $r = 0.88$, $P < 0.001$).

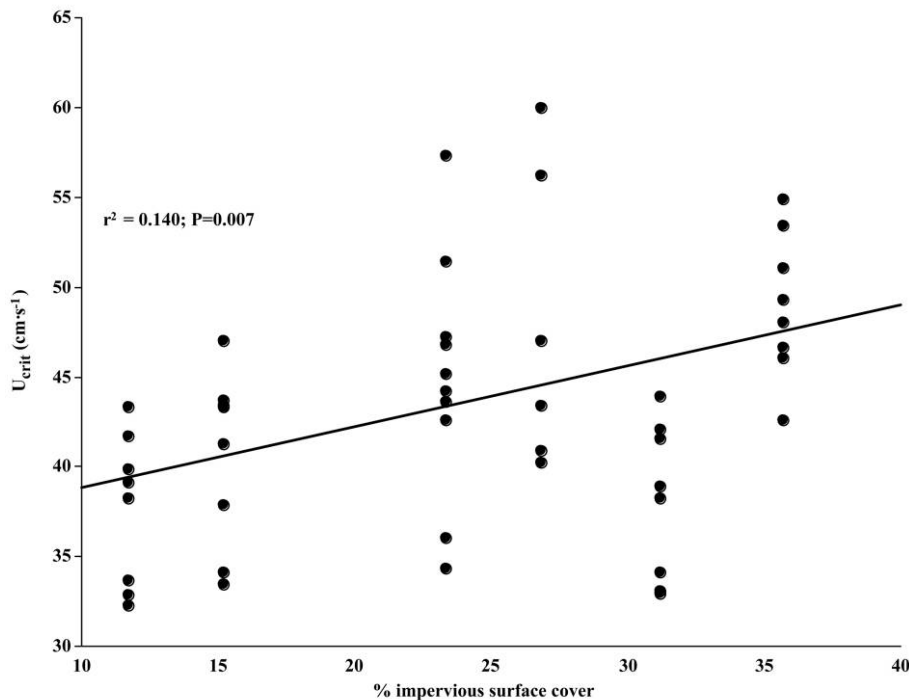


Figure 1. Critical swimming speed of individual blacknose dace from urban and suburban streams as a function of the percentage of impervious surface in the watershed the fish came from during the watershed study (February 2004). The coefficient of determination and the significance level (F -test) of the regression are included. See the text for details concerning determination of the independent and dependent variables.

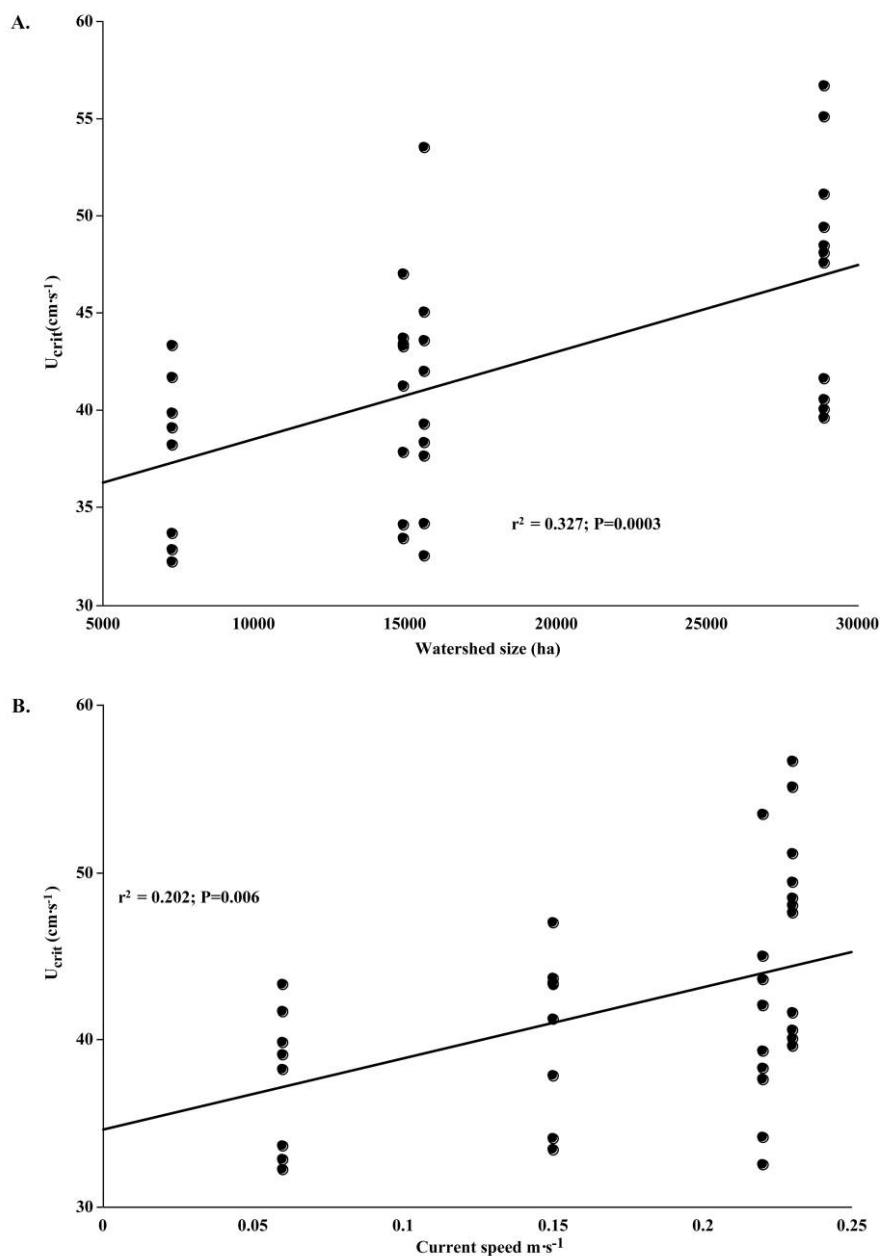


Figure 2. Critical swimming speed of individual blacknose dace taken from rural and suburban streams during the watershed study (February 2004) and plotted as a function of two watershed parameters, watershed size (A) and mean base-flow current speed (B). The coefficient of determination and the significance level (F -test) of the regression are included. See the text for details concerning determination of the independent and dependent variables and the results from the other watershed variables.

Sprint performance was significantly dependent on mass ($P = 0.015$); thus, comparative analyses of sprint performance were based on size-adjusted sprint speeds. These differed significantly among populations ($P < 0.001$; Fig. 4A); fish from two of the most urbanized sites had sprint speeds that were significantly greater than sprint speeds of fish from the most rural sites and one of the suburban sites ($P < 0.050$; Fig. 4A). Sprint speed correlated significantly with %ISC for all fish

($r^2 = 0.25$; $P < 0.001$) and among fish from urban and suburban sites only ($r^2 = 0.27$; $P < 0.001$; Fig. 4B). The only other significant relationship between watershed characteristics and sprint performance was a weak one with annual discharge ($r^2 = -0.10$; $P = 0.020$; not shown).

Relationship between Critical Swimming and Sprint Swimming Performance. There was no relationship between critical swim-

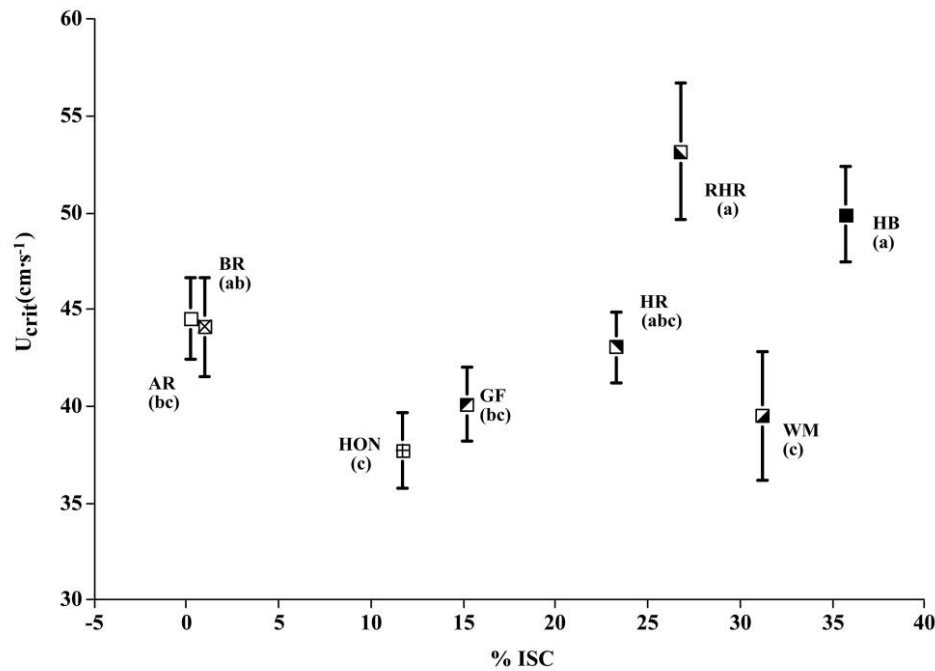


Figure 3. Mean population critical swimming speed ± 1 SE of eight blacknose dace populations from the watershed study (February 2004), plotted as a function of the percentage of impervious surface in the watershed to emphasize the potential role of that variable in causing population differences in urban and suburban fish. Least squares means from the ANCOVA model, with mass as a covariate, are plotted. AR = Aspen Run; BR = Beaver Run; HON = Honeygo Run; GF = Gwynns Falls; HR = Herring Run; RHR = Red House Run; WM = White Marsh Run; and HB = Herbert Run ($n = 69$). Lowercase letters in parentheses indicate significance levels; populations not bearing the same letter are significantly distinct (Tukey's HSD $P < 0.05$).

ming performance and sprint swimming performance of individual blacknose dace from the eight populations across a rural to urban gradient ($n = 70$; $r^2 < 0.01$, $P = 0.942$; Fig. 5). Furthermore, there was a strong tendency for the top-performing individuals in both tests to have average performance in the other test (Fig. 5). There was no clear trend for the two performance measures to be either positively or negatively correlated among populations, and there was no pattern related to urbanization (Fig. 5).

Plasticity of Critical Swimming Performance

Change in mean population endurance performance under no-flow conditions in the laboratory was dependent on the initial performance of the population. A repeated-measures ANOVA with an unstructured covariance matrix, with population and test time as the treatments and U_{crit} values as the response variable, was used to test for differences in U_{crit} . A significant interaction between population and time was found for the repeated measures of critical swimming performance over time ($P < 0.001$). Populations with an initial mean U_{crit} above 45 cm s^{-1} (HR, RHR, and BR) all had significantly higher mean U_{crit} values than the other four populations at time 0, except that HR and HON were not statistically distinct (Tukey's HSD, $P < 0.05$; Fig. 6A). These three populations with high initial

mean U_{crit} also showed a substantial decline in mean U_{crit} from the initial measurement to the 3-mo measurement, such that all three populations had statistically lower performance at 3 mo than at time 0 (Tukey's HSD, $P < 0.05$; Fig. 6A). These three populations then had little change in mean performance between the 3-mo and 6-mo U_{crit} measurements (Fig. 6). Populations with a mean U_{crit} below 45 cm s^{-1} (AR, HON, GF, and WM) showed no significant change between initial U_{crit} measurements and those at 3 or 6 mo (Fig. 6A). After 3–6 mo in no-flow conditions, all populations converged on a mean U_{crit} of between 33 and 43 cm s^{-1} ; the population with the highest mean U_{crit} (HON) at those two time points had significantly greater mean performances than fish from the AR, GF, HR, and RHR populations, whereas fish from the WM population had significantly greater U_{crit} values than fish from the AR, HR, and RHR populations at the 3- and 6-mo time points (Tukey's HSD, $P < 0.05$; Fig. 6A).

Because of the aforementioned large decline in U_{crit} performance in the three top-performing populations under no-flow conditions, the Spearman rank estimation of the repeatability of individual dace performances was less significant between the initial and the 3-mo U_{crit} trials ($r = 0.39$, $P < 0.001$) than it was between the 3-mo and the 6-mo swims (Spearman $r = 0.89$, $P < 0.001$; Fig. 6B). Initial, 3-mo, and 6-mo U_{crit} measurements were not significantly related to the covariates of

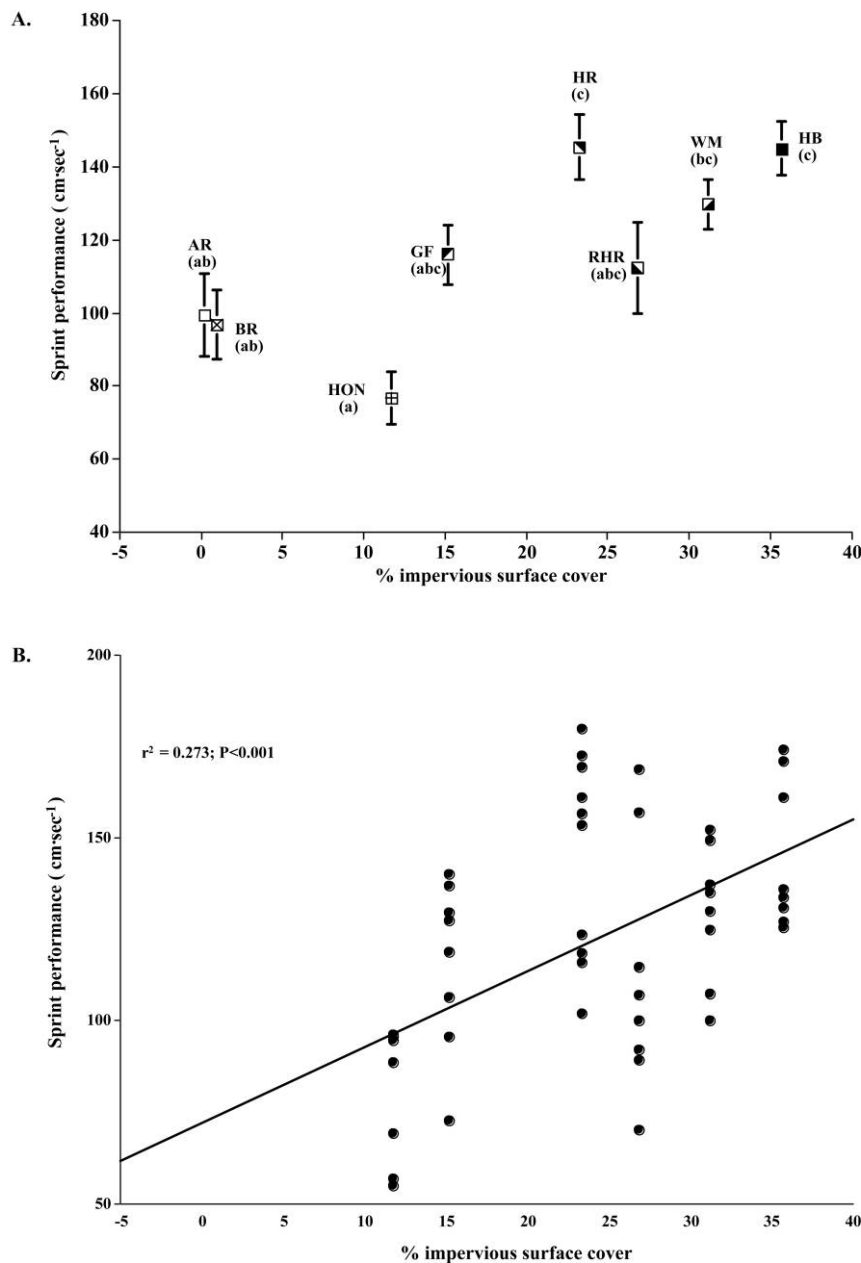


Figure 4. Sprint swimming performance of blacknose dace as a function of the percentage of impervious surface in the watershed from which the fish were removed for the watershed study (February 2004). *A*, Mean population maximal sprint swimming speed \pm 1 SE for all populations ($n = 69$). Least squares means from the ANCOVA model with mass as a covariate are plotted. Lowercase letters in parentheses indicate significance levels; populations not bearing the same letter are significantly distinct (Tukey's HSD $P < 0.05$). Population abbreviations are defined in the Figure 3 legend. *B*, Individual performances for urban and suburban populations only. The coefficient of determination and the significance level (F -test) of the regression are included

standard length or mass (ANCOVA, $P > 0.050$). The 3- and 6-mo U_{crit} measurements were also not significantly related to the change in standard length or to the change in mass that occurred during the period of laboratory residence under no-flow conditions (ANCOVA, $P > 0.050$).

Long-Term Repeatability of Critical Swimming Performance

Preexisting data on U_{crit} of dace from some of the same collection sites used in this study (Nelson et al. 2003), coupled with the two separate collections described here, allowed us to

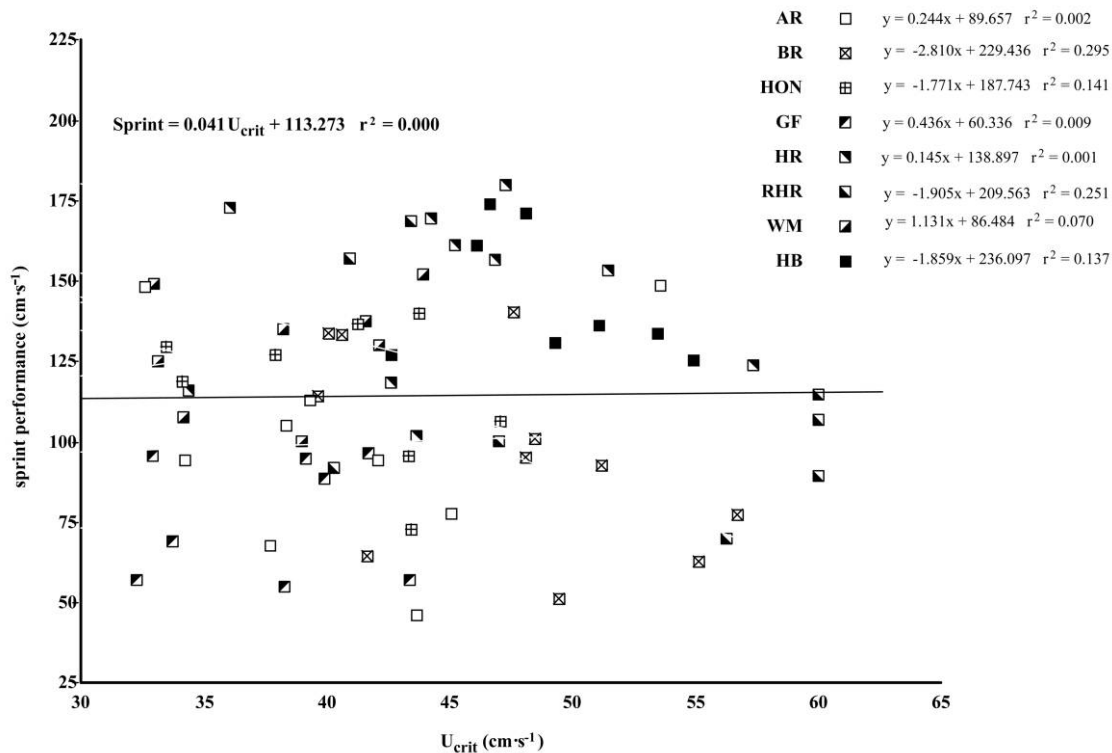


Figure 5. Relationship between critical swimming speed and maximal sprint performance for all individual blacknose dace from the watershed study (February 2004; $n = 69$), plotted by population (population abbreviations are defined in the Fig. 3 legend). The best-fit line for the entire sample as well as the equations and the coefficients of determination for the entire relationship and each individual population are included. Populations are listed in order of watershed percentage of impervious surface cover (smallest value at the top).

compare the stability of U_{crit} values in different dace, captured from the same sites, over a period of 3.5 yr (Fig. 7). Although there were insufficient data to test this hypothesis robustly, we compared U_{crit} values from fish collected in summer 2000, summer 2003, and February–March 2004 with an ANCOVA model with population as the treatment, log-transformed U_{crit} values as the response variable, and year as a covariate. This analysis showed that U_{crit} was statistically consistent for each population at that particular collection site over a span of up to 3.5 yr (Tukey’s HSD, $P > 0.05$; Fig. 7). No population mean U_{crit} was ever significantly different from a mean U_{crit} from that same population in a different year, using an average sample size of 9 individuals. Because there were not collections from each site for all 3 yr, collection year could not be used as a treatment variable in a repeated-measures model. However, Tukey’s HSD post hoc comparisons of population means after an ANCOVA with U_{crit} as the response variable and year as a covariate ($P > 0.05$) revealed that the BR, HR, and RHR populations had consistently higher endurance swimming performance than the other four populations ($P < 0.05$; Fig. 7). The hypothesized stability of mean population endurance performance over time was also supported by nonparametric tests of mean rank showing insignificant variance in rank among the seven populations (Friedman ANOVA, $\chi^2 = 9.857$, $P = 0.131$) and significant

rank concordance between years (Kendall coefficient of concordance = 0.821).

Plasticity of Sprint Swimming Performance

Fish from four populations were collected between November 2004 and February 2005 (called “January 2005”) to test hypotheses concerning the plasticity and temporal stability of sprint swimming performance. These fish were sprinted after 2 wk in the laboratory and then held under no-flow conditions for 10 wk before being sprinted again. The sprint performance test was not significantly repeatable over this time period (Spearman $r = 0.186$; $P > 0.05$; Fig. 8A) The change in sprint performance over time was not related to growth over that period or the population origin of the fish (ANOVA, $P > 0.05$), but it was a significant function of the animal’s original sprint performance ($n = 22$, $r^2 = 0.318$, $P = 0.006$; Fig. 8B). Animals with exceptional sprinting ability on entering the lab tended to lose performance capacity after 10 wk in a no-flow environment, whereas animals with relatively poor sprinting ability tended to improve with 10 wk in a no-flow environment (Fig. 8B).

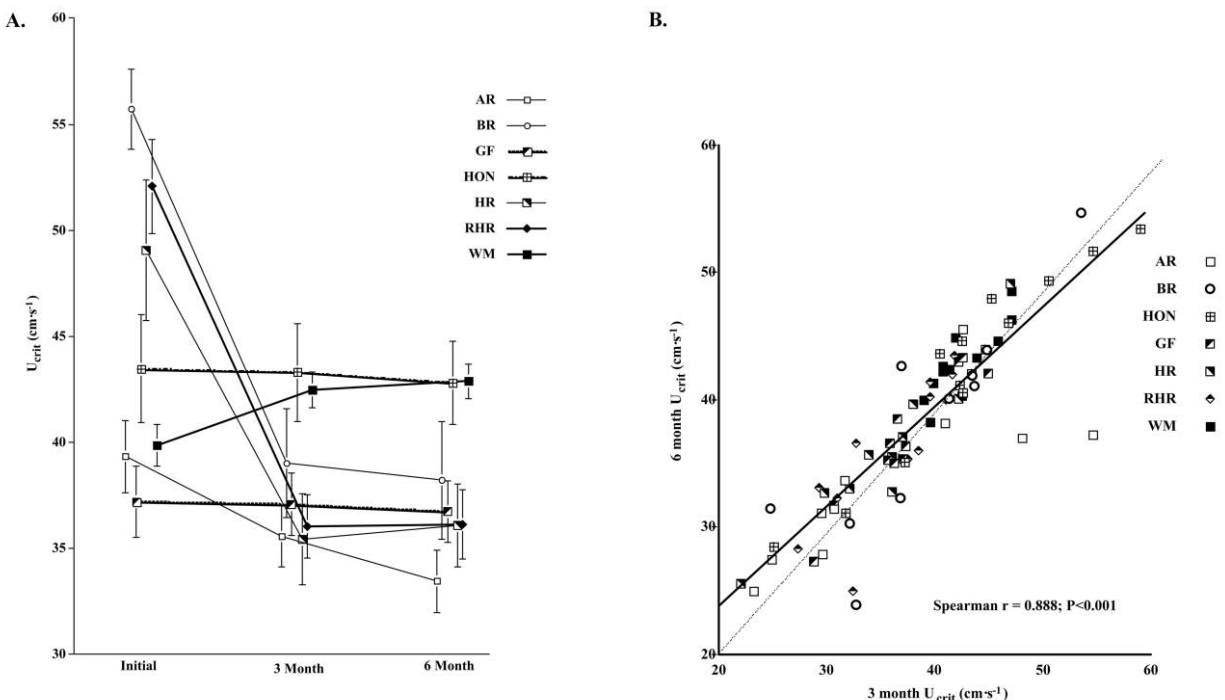


Figure 6. A, Mean population critical swimming speed ± 1 SE of blacknose dace as a function of laboratory residence time under no-flow conditions during the plasticity of U_{crit} study. Symbols are offset to facilitate clarity. Population abbreviations are defined in the Figure 3 legend ($n = 79$). B, Relationship between an individual blacknose dace's critical swimming performance after 3 mo of laboratory residence time under no-flow conditions and that same measure after 6 mo of laboratory residence time under static flow conditions. The best-fit line (solid) and the line of identity (broken) are included with the Spearman rank correlation coefficient and its significance level.

Long-Term Repeatability of Sprint Swimming Performance

Since fish from four sites were sprinted in both early 2004 and early 2005, we were able to compare the stability of sprint performance values in different dace from these sites over a period of 1 yr (Fig. 9). As for U_{crit} , there are insufficient data to evaluate the hypothesis of stable mean population sprinting ability over time, but we tentatively compared sprint performances with an ANCOVA with population and year as the treatment variables and body mass as a covariate. This analysis returned a significant population effect ($P < 0.001$), no effect of year or interaction with population, and a significant effect of mass ($P = 0.016$). Sprint performance was statistically consistent for each population at that particular collection site over a span of 1 yr ($P > 0.05$; Fig. 9). No population mean from 2004 was ever significantly different from a mean sprint performance from that same population in 2005, using an average sample size of 9.5 individuals. Tukey's HSD post hoc comparisons of population means after the ANCOVA revealed significant differences between the populations that were sustainable over time (Fig. 9). Although these results may arise from the tendency of the urban populations to be larger in this comparison (Table 2), the 2005 AR sample was the third-largest of the eight groups, and their collective sprint performances were virtually identical to those of the fish collected in 2004 from

the same location (Fig. 9). The hypothesized stability of mean population sprint performance over time was also supported by nonparametric tests of mean rank showing insignificant variance in rank among the four populations (Friedman ANOVA, $\chi^2 = 5.400$, $P = 0.145$) and significant rank concordance between years (Kendall coefficient of concordance = 0.900).

Discussion

Urbanization alters the hydrology and geomorphology of streams such that urban streams can have extremely rapid and dramatic increases in flow during precipitation or melting events (Hirsch et al. 1990). The blacknose dace is apparently resilient to these events and remains abundant in many urban streams that are devoid of most other fishes. One way that dace could persist in the urban environment, when most other small stream fishes do not, is through adjustments in swimming ability to match the change in demand produced by the altered hydrological regime. The endurance swimming performance of blacknose dace has already been shown to track natural gradients in stream flow resulting from differences in watershed morphology and discharge (Nelson et al. 2003). Could the torrential flows found in Baltimore area urban streams during precipitation events produce further modifications to the swimming ability of dace? This was a fundamental question of the

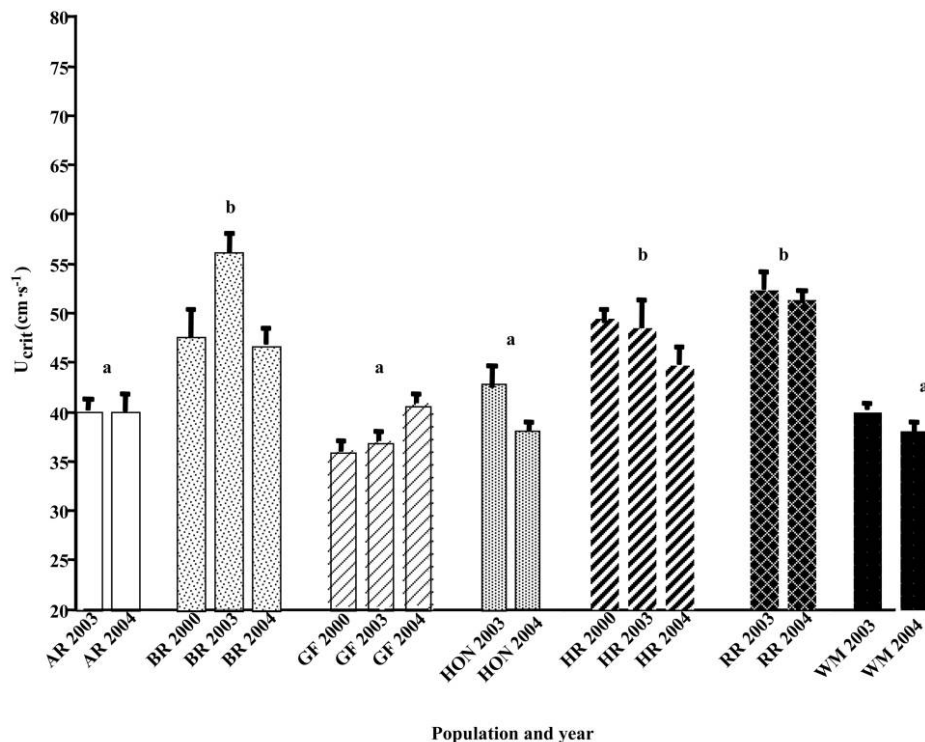


Figure 7. Mean population critical swimming speed ± 1 SE of separate blacknose dace captured from identical sites over a period of 3.5 yr. Population abbreviations are defined in the Figure 3 legend. Populations not bearing the same lowercase letter are statistically distinct (ANOVA $P < 0.05$).

study, initiated by us to better understand how the biology of blacknose dace is affected by coexistence with humans. The approach we used to address this question was an intraspecific, comparative one wherein the swimming ability of fish from four urban streams ($ISC > 20\%$) was compared with that of fish from two suburban streams ($10\% < ISC < 20\%$) and two rural streams ($ISC < 2\%$) from similar latitude.

To our knowledge, the influence of stream urbanization on the swimming ability of resident fish has not been studied. Most studies of urbanization's effects on fish have focused on long-term changes to fish assemblages (e.g., Siligato and Bohrer 2002) or the effects of pollutants (e.g., Gillies et al. 2003). Similarly, while numerous studies have addressed the influences of flow on fish ecology (e.g., Standen et al. 2004) and many of them involved stream cyprinids (e.g., Garner 1999), these studies have not specifically addressed altered flow regimes characteristic of urbanized streams. However, Booker (2003) compared published swimming performance data with results from a model of the hydrology of an urban system to suggest that swimming capacity may limit the ability of cyprinids from England to inhabit urban streams.

For our study, we use swimming performance as an integrated measure of animal morphology and physiology, that is, as a fitness parameter (sensu Arnold 1983). Although the idea is untested, we believe that swimming competence is likely to

be an important component of Darwinian fitness for blacknose dace because (1) foraging efficiency of blacknose dace declines with increasing current speed in the laboratory (Tyler 1993); (2) swimming ability is undoubtedly an important part of the flash flood resilience and recolonization capacity demonstrated by a congener, the speckled dace *Rhinichthys osculus* (Pearsons et al. 1992); (3) blacknose dace require swimming competence to move between habitat patches of varying quality in the stream environment (Nelson et al. 2003); and (4) blacknose dace are subject to a variety of avian and piscine predators in the mid-Atlantic region, escape from whom presumably entails some minimal level of locomotor capacity. Thus, studying factors that contribute to changes in swimming performance could be important in determining why dace are resilient to urbanization and why other species do not persist in urbanized systems.

Population-Level Endurance Swimming

A key finding of this study was that natural watershed dynamics influence the endurance swimming performance of resident fish, but this effect can be overshadowed by extensive urbanization. Because living in either a watershed with a large, heavy flow or an urbanized area can cause populations to have high U_{crit} values, analyzing equal numbers of urban and nonurban

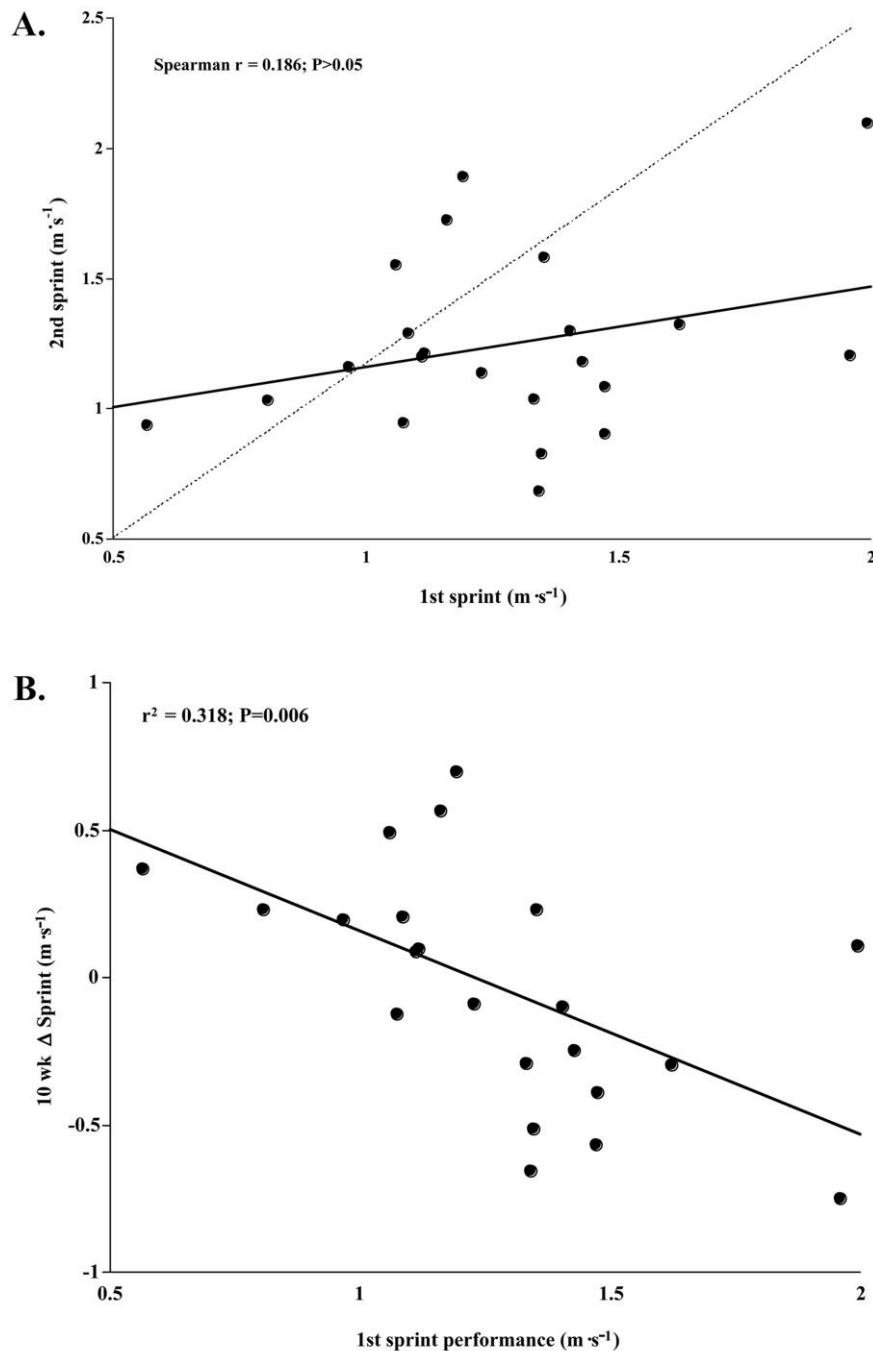


Figure 8. Relationship between sprint performances after 10 wk under static flow conditions in the plasticity of sprint performance study. *A*, Individual blacknose dace maximal sprint performance plotted against subsequent performance. The best-fit line (*solid*) and the line of identity (*broken*) are included as are the Spearman rank correlation coefficient and the significance level. *B*, Change in maximal sprint performance after 10 wk under static flow conditions plotted as a function of original maximal sprint performance. The coefficient of determination and the significance level (*F*-test) of the regression are included ($n = 22$).

fish together suggested that no watershed parameters influenced U_{crit} at the population level. However, evaluating only suburban and urban fish showed that endurance swimming performance was significantly related to the %ISC in these watersheds, albeit weakly because of the poor fit of the WM urban population

(31.2% ISC; Fig. 1; the coefficient of determination increases from 0.14 to 0.34 on removal of WM fish from the regression in Fig. 1). Why the WM population does not fit as well on this relationship as the other five urban and suburban populations is a matter of speculation, but it is possible that length of time

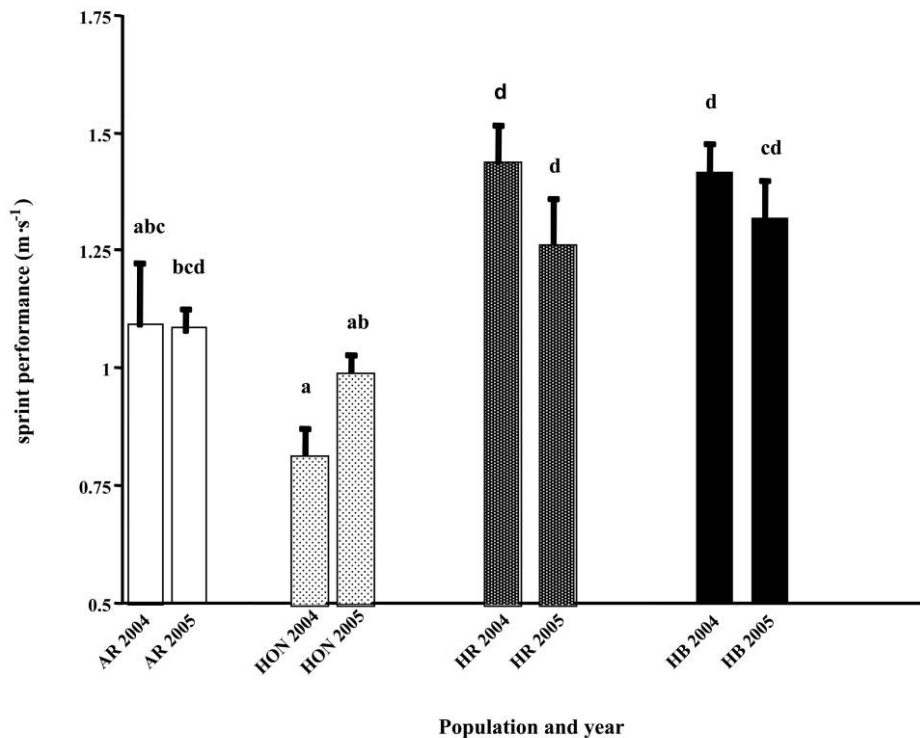


Figure 9. Mean population maximal sprint performance ± 1 SE of separate blacknose dace captured from identical sites over a period of 1 yr. Population abbreviations are defined in the Figure 3 legend. Populations and collections not bearing the same lowercase letter are statistically distinct (ANOVA $P < 0.05$).

as an urban site is involved. Despite having the second-highest %ISC in the study, this region has become urbanized only within the last 15 yr; the other sites have been urban for more than 50 yr.

Critical swimming performance of fish from nonurban streams correlated significantly and positively with all watershed parameters: area, mean annual discharge, and base-flow current speed (Fig. 2). Nelson et al. (2003) showed that base-flow current speed is significantly related to endurance swimming performance in blacknose dace. Here, we expand that finding to include watershed area, discharge rate, and %ISC in the watershed as environmental variables that are significantly related to endurance swimming ability of dace (Fig. 2). We also report a relationship between base-flow current speed and individual U_{crit} values that is almost identical to the one reported by Nelson et al. (2003), despite the fact that additional populations were included in the current study.

We interpret these results, taken together, to show that the amount of water flowing through the watershed helps to determine the mean endurance swimming performance of a population in unaffected stream systems. However, in urban systems, the key environmental determinant of swimming performance is the degree of urbanization; fish from systems with the most impervious surfaces have the greatest swimming

endurance, despite the nature of their stream or watershed. Figures 1 and 3 show that when ISC exceeds 10%, there is a fairly direct relationship between mean population endurance performance and %ISC. This mosaic of environmental influences on endurance swimming performance produces a number of significant differences between mean U_{crit} values in populations from different watersheds (Fig. 3).

Although there are alternative explanations, we believe that stream flow is responsible for these interpopulation differences in endurance swimming ability. As we pointed out in Nelson et al. (2003), a relationship between relative intraspecific swimming ability and water flow has been found in other systems and may become a general phenomenon. For example, McGuigan et al. (2003) found that rainbow fish (*Melanotaenia duboulayi*) populations inhabiting high-velocity habitats had higher U_{crit} values than conspecifics inhabiting low-velocity habitats. In addition, Nicoletto and Kodric-Brown (1999) found that the swimming performance of four guppy (*Poecilia reticulata*) populations correlated with the magnitude of the current they lived in. Fish in urban streams are exposed to further elevations of flow during precipitation events due to watershed changes that happened very quickly over evolutionary time. Jennings and Jarnagin (2002) reported a 323% increase in the number of days that a Fairfax County, Virginia,

stream was in their highest stream-flow category ($>14 \text{ m}^3 \text{ s}^{-1}$) and a 123% increase in the number of days it was in their second-highest stream flow category ($>9 \text{ m}^3 \text{ s}^{-1}$) as ISC rose from 3% to 33% with a 50-yr urbanization of the watershed. Presumably, fish remaining in urban streams have to swim against these stronger currents. Higher growth rates of urban blacknose dace (Fraker et al. 2002) suggests that these dace do not abandon foraging during high-flow conditions. Therefore, we conclude that dace from urban streams have greater endurance swimming performance because the altered flow regimes constrain the resources they must allocate to their propulsive systems. Since the general result is that pollutants associated with urban waters reduce the swimming performance of fish (e.g., Jain et al. 1998; Kolok et al. 1998), the performances of three of our four urban populations being better than predicted from the flow relationships (Fig. 2) appears to be a unique finding.

Another possible explanation for the enhanced endurance performance of urban populations is that the greater resource base in urban streams (Walsh et al. 2005) could simply allow fish to allocate more resources to structural and biochemical components of the swimming machinery without any selection or training. The populations of urban blacknose dace we worked with had faster growth compared with rural and suburban populations (Fraker et al. 2002), but studies generally show that increased growth rates actually reduce swimming ability (Kolok and Oris 1995; Farrell et al. 1997; Gregory and Wood 1998; Alvarez and Metcalfe 2005). Thus, the enhanced performance of urban dace most likely accrues from phenotypic plasticity of locomotor performance and the “stricter” training regimen they experience in urban streams.

Plasticity of Endurance Swimming Performance

Figure 6A demonstrates that regardless of the environment that produced significant elevations of endurance performance in blacknose dace, 3 mo of living without flow homogenized performance among the populations. Thus, these differences are phenotypically plastic. All three dace populations that had initial mean U_{crit} values greater than 45 cm s^{-1} , two from heavily urbanized sites (HR and RHR) and one from the largest but rural stream (BR), significantly lost endurance ability after 3 mo without flow. The other four populations that began with significantly lower U_{crit} values showed no change in mean swimming ability throughout the 6 mo without flow (Fig. 6). Individual repeatability of endurance performance from 3 mo to 6 mo under no-flow conditions was remarkable (Fig. 6B). We interpret these results to suggest that a U_{crit} of around 40 cm s^{-1} is characteristic of the species, whereas the elevations of mean performance found in the HR, RHR, and BR populations are the product of natural training induced by the flow regimen of their home stream. This elevated level of performance is rapidly lost when the training regimen is eliminated (detraining), at which time an individual’s endurance swimming performance becomes highly repeatable (Fig. 6B).

Multiple studies have shown that endurance swimming performance can be altered by exercise training (Davison 1997). However, most of this work has been performed on cultured fish and usually on fish that never experienced natural flows; very little information exists on whether natural variations in flow act as a training agent for feral fishes. Perhaps the most relevant support for our result comes from comparisons of endurance swimming performance in fishes that face variable migratory demands. Coho salmon (*Oncorhynchus kisutch*) populations with longer migrations outperformed populations with less challenging migrations (Taylor and McPhail 1985). Taylor and Foote (1991) further demonstrated that migratory juvenile sockeye salmon (*Oncorhynchus mykiss*) had greater endurance performance than a nonmigratory population of juvenile sockeye salmon. Finally, anadromous sticklebacks (*Gasterosteus aculeatus*) demonstrated a sevenfold increase in endurance capacity compared with nonmigratory conspecifics (Taylor and McPhail 1986).

There is also relatively little information on detraining of fish in the laboratory to compare with the information in our study. Young and Cech (1994) found that striped bass (*Morone saxatilis*) conditioned at varying water velocities for 60 d showed an increase in U_{crit} . This study also found that fish trained at only a moderate velocity level maintained improved swimming for 28 d of detraining, whereas fish trained at high velocity maintained the increased performance for 56 d post-conditioning. In our study, the three populations that detrained had a mean 29.5% ($\pm 1.6\%$ SD; $n = 32$) decline in endurance swimming performance that was complete by 3 mo under no-flow conditions. Most detraining studies use mammalian subjects but support our results nonetheless. For example, Andersen et al. (2005) found that 3 mo of detraining was sufficient to erase gains in concentric muscle contraction dynamics acquired through 3 mo of training in previously untrained humans.

Long-Term Site Stability in Endurance Swimming

Endurance swimming performances measured for wild populations from identical collection sites were relatively consistent over a period of 3+ yr (Fig. 7). This is a very interesting finding because long-term stability of population-level physiological measurements is rarely described. These repeated measures of U_{crit} were recorded not for the same individuals but rather on a sample of fish within a set size range that were collected at the same location. Thus, these site-specific differences in mean critical swimming speed of blacknose dace, first reported by Nelson et al. (2003), are relatively stable despite the yearly stochasticity of precipitation, aquatic community structure, and population genetics. Endurance locomotor performance has been shown to be significantly stable in the field for a number of other systems. For example, Huey et al. (1990) showed that endurance speeds of individual lizards (*Sceloporus merriami*) were repeatable for at least 1 yr. Jayne and Bennett (1990) demonstrated that the size-corrected endurance and sprint

speed of individual garter snakes (*Thamnophis sirtalis*) in the field were repeatable for a period of 1 yr but not 2 yr. Claireaux et al. 2007 found significant repeatability of U_{crit} in individual juvenile European sea bass (*Dicentrarchus labrax*) kept for 6 mo in mesocosms where they were exposed to natural environmental conditions and forage. Our inability to mark and recapture individual dace from our study streams precludes this type of study, but the stability of mean population performance coupled with significant laboratory repeatability over 6 mo hints at repeatability of endurance performance in wild blacknose dace.

Population Differences in Sprint Swimming

Studies of fish swimming performance have many goals. However, if the goal of a study is to use locomotor capacity as a potential indicator of fitness (Arnold 1983), a single incremental velocity (U_{crit}) test will probably prove insufficient. For many fishes, sprinting ability is likely a more relevant measure of performance for use in the morphology-performance-fitness paradigm of Arnold (1983; Nelson et al. 2002). Most predator-prey interactions take place at the scale of sprint performance (Wardle 1975), and movement within a stream during flood events is likely to tax an animal's sprinting ability as much as their endurance capacity. Unfortunately, intraspecific variance in sprinting ability and its significance have been infrequently studied in fishes. Most studies on sprint locomotion have focused on the first phase of sprinting, that is, the fast-start phase, defined as the first two contractions of the axial musculature (Domenici and Blake 1997). The evaluation of sprinting ability is therefore complementary to the evaluation of endurance and the fast-start phase and may be relevant to the Darwinian fitness of dace and other fishes.

Sprint swimming performance correlated with the amount of impervious surface in the watershed when we looked across all stream types (Fig. 4). This relationship was stronger when we analyzed only those systems that had some degree of urbanization (Fig. 4). Our favored explanations for why fish from urban streams sprint better is that they have been trained against higher flows or that natural selection has favored animals with better sprinting ability in urban systems.

Since predation intensity is most likely lower in the urban systems, selection for predator avoidance is probably not the cause of the better sprinting ability in urban fish. However, because of the increased density of dace in urban systems (J. W. Snodgrass, unpublished data), we cannot rule out intraspecific competitive interactions as the cause. Since species diversity is relatively poor in both aquatic (lower density of piscine predators; J. W. Snodgrass, unpublished data) and terrestrial urban environments (Schueler and Galli 1992; Clergeau et al. 1998), we would predict that predation intensity on blacknose dace would decline as the degree of urbanization increases. One of our measurements of fewer piscine predators (J. W. Snodgrass, unpublished data) at our urban collection sites supports that idea. If that prediction is true, then the better

sprint swimming performance of urban fish is opposite to the prediction from perceived differences in predation intensity (Ghalambor et al. 2003). As with endurance performance, the case could also be made that the enhanced sprint performance is merely a reflection of the greater nutrient abundance in the urban environment (Walsh et al. 2005). However, the increased growth rates of the urban dace populations (Fraker et al. 2002) and the negative trade-off between sprint performance and growth found in other fish species (Billerbeck et al. 2001; Claireaux et al. 2007) argue against it.

Plasticity of Sprint Swimming Performance

The sprint test was significantly repeatable in a group of 10 fish held for 1 wk in a current of 1–3 cm s⁻¹. However, sprint performance was not repeatable in fish from four populations held for 10 wk in no-flow conditions (Fig. 8A). There were no significant population-level trends to this change in performance under detraining conditions, and an almost equal number of fish gained in performance as lost (Fig. 8A). There was a significant tendency for animals with a high initial sprint speed to lose performance capacity and those with an initial low sprint speed to gain ability (Fig. 8B). Since as many animals gained performance ability as lost, this was not a strict detraining phenomenon, as observed for endurance performance (Fig. 6A). Because fish from the urban streams had higher initial sprint performances, they were more likely to lose capacity; however, the analysis of change in sprint performance by population was insignificant (ANCOVA, $P > 0.05$). Our interpretation of this experiment is that although not quantified, behavioral interactions were probably responsible for these results. The animals were held in replicate 20-gal tanks in groups of 5 individuals per tank where presumably the larger fish, which tended to be the better sprinters, were also the more dominant individuals. Garland et al. (1990) found a positive correlation between social dominance and sprinting ability in lizards. Thus, we speculate that dominant, better-sprinting fish were relatively inactive under these conditions and lost ability, whereas the subordinates were actually getting sprint-trained when being chased, and they improved their performance. Although sprint swimming performance appears to be fairly plastic in the laboratory, the question as to whether the population-level differences in sprint swimming performance are the result of phenotypic plasticity, selection, or some other factor must remain open.

Long-Term Site Stability in Sprint Swimming

Animals collected approximately 1 yr apart from the same site exhibited similar population-level differences in sprint performance (Fig. 9). Although temporal stability of individual sprint performance has been known for some time in reptiles (Huey et al. 1990; Jayne and Bennett 1990), to our knowledge, this is a unique finding for fishes. The extensive work on swimming in Trinidadian guppies from low- and high-predation habitats

(e.g., O'Steen et al. 2002; Walker et al. 2005) appears to rely on the consistency of swimming performance by habitat type, yet the temporal consistency of this appears to have not been tested. Again, while this is not a true field repeatability result (as defined by Bennett [1987]), the finding in this sprint test of statistically distinct population-level differences that are temporally stable (Fig. 9) bodes well for the test's use as a measure of animal performance that may come under selection.

Summary

Urbanization appears to be a potent environmental force, structuring the biology of fish that survive in city streams. Here we document how the urban environment changes the relationship between the endurance swimming ability of a dace and the watershed it inhabits. We also show that the degree of urbanization is a key environmental variable that determines sprint swimming performance. Population differences in endurance swimming ability are phenotypically plastic, whereas population differences in sprinting ability are of an indeterminate nature. Interpopulation differences in both sprint and endurance swimming were robust over multiple years of collection from the same sites. There was no significant relationship between sprint and endurance performance in individual blacknose dace, a finding reported previously for other fish species (e.g., Claireaux et al. 2007).

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