

# Swimming performance of blacknose dace (*Rhinichthys atratulus*) mirrors home-stream current velocity

Jay A. Nelson, Portia S. Gotwalt, and Joel W. Snodgrass

**Abstract:** Flowing waters may represent a force that structures the locomotor capacity of stream fishes. We used a modified critical swimming speed ( $U_{crit}$ ) procedure to investigate the relationship between base-flow conditions and locomotor performance of blacknose dace (*Rhinichthys atratulus*) from five sites within three watersheds of Baltimore County, Maryland. Our modified test used 5-min intervals between incremental increases of  $5 \text{ cm}\cdot\text{s}^{-1}$  in swim-tunnel current velocity. This time increment represented a realistic transit time across riffles found in the home streams of dace. To characterize current velocity conditions of the streams, we measured current velocity at 55 evenly spaced points per site during base-flow conditions. Swimming performance varied greatly among 32 individual fish from the five sites ( $\frac{2}{3}U_{crit}$  from  $26.33$  to  $69.00 \text{ cm}\cdot\text{s}^{-1}$ ) and was positively correlated ( $r^2 = 0.38$ ,  $p = 0.002$ ) with mean base-flow current velocities at the site of collection. Additionally, among fish from the site with the widest and most even distribution of current velocities (from  $0$  to  $54 \text{ cm}\cdot\text{s}^{-1}$ ), we observed the largest range of swimming performances. Our results suggest that variation in flow conditions among streams influences swimming ability of blacknose dace and can result in heretofore-unappreciated intraspecific variation in swimming performance.

**Résumé :** Les eaux courantes peuvent représenter une force qui structure la capacité locomotrice des poissons des cours d'eau. L'utilisation d'une procédure modifiée basée sur la vitesse de nage critique ( $U_{crit}$ ) nous a permis d'étudier la relation entre les conditions d'écoulement de base et la performance locomotrice du naseux noir (*Rhinichthys atratulus*) à cinq sites, dans trois bassins versants du comté de Baltimore, au Maryland. Notre test modifié comprenait des intervalles de 5 min entre les accroissements successifs de  $5 \text{ cm}\cdot\text{s}^{-1}$  de la vitesse du courant dans un tunnel de nage. Un tel intervalle de temps représente une période réaliste de passage d'une zone de rapides à une autre dans les cours d'eau d'origine du naseux. Pour déterminer les conditions de vitesse de courant dans les cours d'eau, nous avons mesuré la vitesse du courant à 55 points situés à égale distance l'un de l'autre à chacun des sites dans des conditions d'écoulement de base. La performance de nage variait considérablement chez les 32 poissons provenant des cinq sites ( $\frac{2}{3}U_{crit}$  de  $26,33$  à  $69,00 \text{ cm}\cdot\text{s}^{-1}$ ) et était en corrélation positive ( $r^2 = 0,38$ ,  $P = 0,002$ ) avec les vitesses de courant moyennes au site de récolte dans les conditions d'écoulement de base. De plus, c'est chez les poissons provenant du site qui présentait la répartition la plus grande et la plus uniforme des vitesses de courant (de  $0$  à  $54 \text{ cm}\cdot\text{s}^{-1}$ ) que nous avons observé la plus grande étendue de performances de nage. Nos résultats laissent croire que les variations des conditions d'écoulement d'un cours d'eau à un autre influencent la capacité de nage du naseux noir et que cela peut résulter en une variation intraspécifique de la performance de nage que l'on ne soupçonnait pas jusqu'ici.

[Traduit par la Rédaction]

## Introduction

Optimization theory holds that evolutionary processes will favor a close match between local environmental demands and animal performance either through maintenance of phenotypic plasticity or evolutionary adaptation (Diamond and Hammond 1992). Aquatic organisms in lotic environments experience forces unlike those associated with terrestrial or lentic habitats. In lotic environments, flowing water is an omnipresent force that threatens to displace the organism and may require behavioral and physiological adjustments to

successfully inhabit these waters. Because the physical properties of lotic systems vary immensely both across and within watersheds, the physiological requirements to survive and move in these diverse habitats may in turn vary and may be reflected in the performance of these animals.

The hypothesized link between locomotor capacity and fitness has generated abundant interest in demonstrating the ecological and evolutionary relevance of variance in animal performance (e.g., Feder et al. 2000). There has also been considerable interest in determining inter- and intra-specific variations in physiological and morphological variables that

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may constrain various locomotor capacities (e.g., Garland and Losos 1994; Nelson et al. 1996). Most of this work has advanced using terrestrial organisms as subjects but recently has included fish (Kolok 1999; Nelson et al. 2002). Interestingly, little of the fish work that has been done has utilized fishes taken directly from flowing waters, yet selection on locomotor capacity and the physiological mechanisms that support it is postulated to be more stringent in lotic environments than in terrestrial or lentic habitats. Thus, stream fishes could be an ideal system in which to examine factors affecting locomotor capacity and possible links to fitness.

Locomotor performance is generally cited as a potential fitness parameter because of its direct impact on foraging success and predator avoidance (Webb 1986). A less commonly stated, but potentially important, constraint on fitness is the ability to move between habitat patches of varying quality or among patches required for successful completion of different biological functions such as reproduction, sheltering, or foraging. Small streams are particularly patchy environments from the standpoint of water depth, current velocity, and substrate composition (Pringle et al. 1988). Fishes occupying small streams move between foraging patches of different quality (e.g., Petty and Grossman 1996) and often require patches of several types to complete their life cycle (Bart 1989). Because areas of higher current velocities in streams separate patches of lower current velocities, fish must cross these high current velocity areas to move among preferred patches. Therefore, individuals with a greater ability to cross high current velocity areas should be able to access more of the stream landscape and may experience higher fitness. Additionally or alternatively, when current velocities are high, fish may be "conditioned" (sensu Farrell et al. 1990) as they traverse higher current velocity areas or try to maintain position in the stream channel. Because of these potentialities, we formulated the null hypothesis that performance variation among conspecific populations of resident, lotic fishes should be independent of base-flow current. Blacknose dace (*Rhinichthys atratulus*) are small minnows that occur across a range of stream types in eastern North America, from sluggish headwater streams to moderately sized, faster-flowing rivers (Lee et al. 1980). Thus, they are an ideal species for testing this hypothesis.

## Materials and methods

During summer of 2000, we collected blacknose dace from five separate locations in three watersheds (Fig. 1) using a Smith-Root Inc. (14014 NE Salmon Creek Ave., Vancouver, Wash.) Model 15-D backpack electroshocker. Study sites were chosen to represent a range of stream sizes and three independent watersheds; watersheds are considered independent because each is separated by tidally influenced portions of the Chesapeake Bay, making genetic exchange among blacknose dace populations unlikely. Approximately 20 fish from a 50-m reach at each site (45–60 mm total length (TL)) were returned to the laboratory in water from their native stream. We attempted to collect fish of approximately the same size from each site to minimize the influence of variation in size on swimming performance. We characterized base-flow current velocities at each site within a week of collecting the fish. No rain was recorded within a

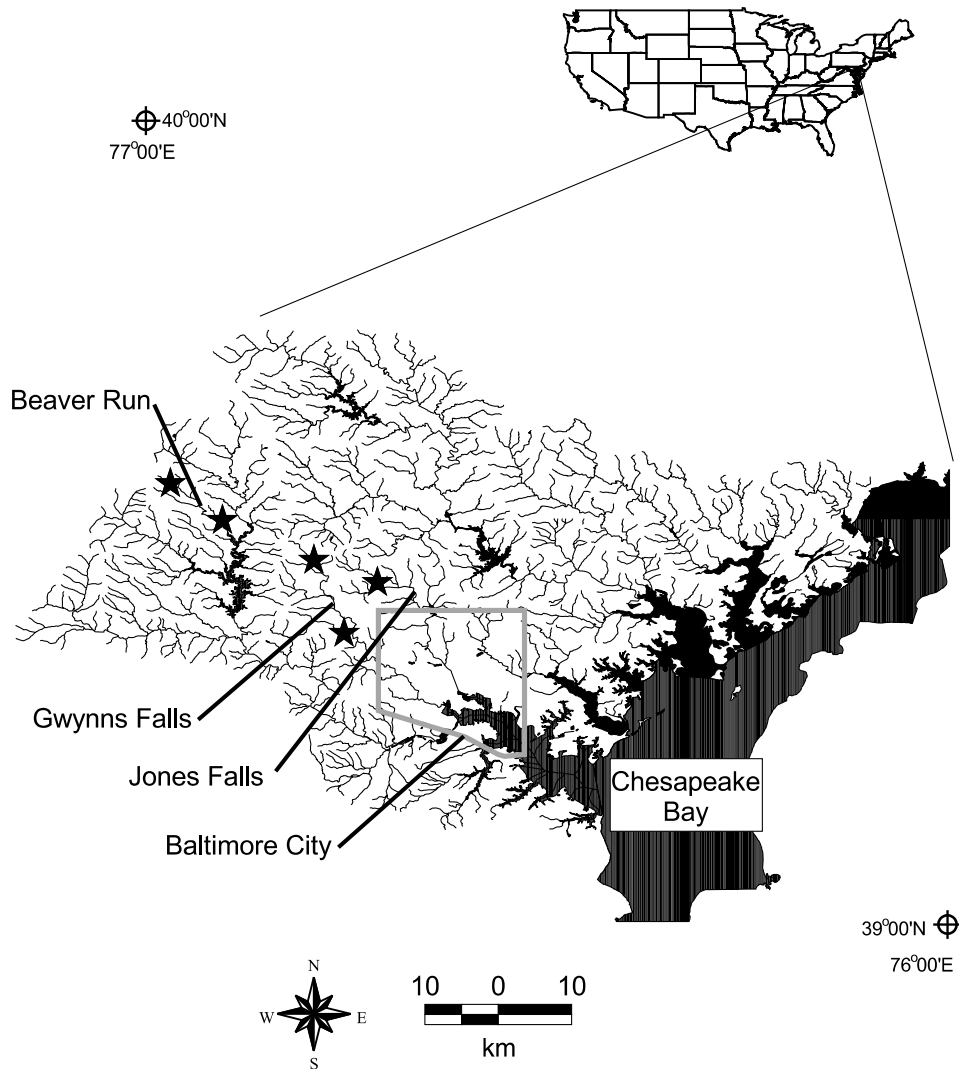
week prior to measuring mean base-flow current velocities at any site. Inspection of a plot of annual base-flow from three U.S. Geological Survey (USGS) gauging stations, one in each of three local watersheds (USGS stations 1586210, 1585200, and 1589197), indicated that base-flow discharge rates varied seasonally in the streams we studied, but that this variation was tightly correlated among watersheds (Fig. 2). Therefore, we may have obtained different values for mean base flow in different years or seasons, but the degree of differences among sites would be maintained. Current velocity was measured at four evenly spaced points across 11 transects spaced at 5-m intervals beginning at the downstream end of each 50-m reach. We measured current velocity at mid-depth using a Marsh-McBirney (4539 Metropolitan Court, Frederick, MD 21704-9452) Model 2000 flow meter. We chose to measure current velocity at mid-depth because there was little variation in current velocity with depth in the shallow (<1 m) streams from which we collected fish, and blacknose dace were often observed foraging for drifting prey in the water column.

We held fish in the laboratory for at least 2 weeks at a water temperature of 24°C (standard deviation (SD) = 1) and a current speed of 1–3 cm·s<sup>-1</sup> before testing their swimming ability using the laminar-flow swim chambers described by Nelson (1989). Two weeks was considered the minimum time required to assure that the animals had recovered from the stress of capture (e.g., Pickering et al. 1982; Haux et al. 1985). Stream water temperatures ranged from 19 to 26°C at the time of sampling, so our laboratory temperature value was intermediate to the field conditions at the time of sampling. Current speeds of the holding tanks (180 × 50 × 35 cm) were measured by establishing a vertical and horizontal grid of 108 stations throughout each tank and measuring current speeds at each station with a freshly calibrated Marsh-McBirney Model 2000 flow meter. To maintain swimming abilities, we restricted fish to those regions of the tank in which current speed was >1 and <3 cm·s<sup>-1</sup> (~ middle 1/3 of each tank). There were no refugia in the holding tanks, thus the fish were required to swim constantly, but at these current velocities, the fish did not fatigue. Animals were fed daily with live adult brine shrimp (*Artemia* spp.) but were fasted 24 h before having their swimming performance tested.

Swimming performance was tested with a modification of the critical swimming procedure first described by Brett (1964) using the swim flumes described by Nelson (1989). Briefly, the flumes are of the "Brett style", with the propeller in series with the fish. The design specifications of Vogel (1994) were followed in constructing the flumes. The swim flume was calibrated with the Marsh-McBirney Model 2000 flow meter by averaging readings from 27 stations in the 32 × 10 × 10 cm swimming section of the tunnel.

Fish to be tested were captured with a dip net and anaesthetized with MS-222 (water concentration of 50 mg·L<sup>-1</sup>) until they reached phase I of anesthesia (loss of equilibrium; Iwama et al. 1989). Anaesthetized fish were transferred to the swim tunnel wherein they immediately revived. The fish were further acclimated for 1 h under a current velocity of 5 cm·s<sup>-1</sup> and a water temperature of 24°C (SD = 1). Fish were then exposed to increasing velocity increments of 5 cm·s<sup>-1</sup> at 5-min intervals until exhausted. Five minutes was

**Fig. 1.** Location map of the study region in the U.S.A. and regional map of sampling sites in relationship to the Chesapeake Bay. From north to south, the three watersheds flowing into the Chesapeake Bay are Jones Falls, Gwynns Falls, and the mainstem of the Patapsco River. Beaver Run is a tributary of the Patapsco River.



chosen as an interval time because it was considered the time that a dace would take to traverse the average riffle in their home stream. The longest riffles near our sampling sites are in the order of 75 m, a distance that a fish swimming at  $25 \text{ cm}\cdot\text{s}^{-1}$  would traverse in 5 min.

Fish generally remained at the front third of the swim section to avoid the bright light that was placed at the rear of the swimming section. Fish that tried to rest on the rear retaining grid were gently prodded with a rubber pencil eraser. Exhaustion was defined as the point at which a fish impinged on the back screen of the swim tunnel no longer responded to prodding. Critical swimming velocity ( $U_{\text{crit}}$ ) was calculated according to Brett (1964) with the formula:

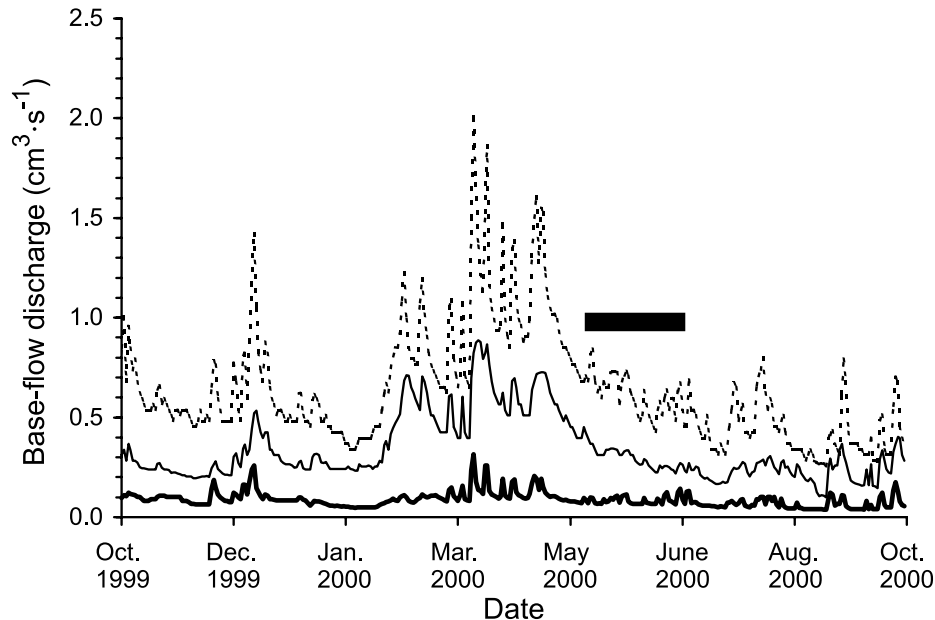
$$\sum_5 U_{\text{crit}} = U_i + [(T_i/T_{ii})U_{ii}]$$

where  $U_i$  represents the highest velocity maintained for a full 5-min interval,  $T_i$  represents the time of fatigue at the last current velocity (min),  $T_{ii}$  represents the interval length (5 min), and  $U_{ii}$  represents the velocity increment ( $5 \text{ cm}\cdot\text{s}^{-1}$ ). Upon exhaustion, fish were removed from the tunnel and reanaesthetized with  $100 \text{ mg}\cdot\text{L}^{-1}$  MS-222 until they entered

stage II anesthesia (loss of gross body movements, but still ventilating; Iwama et al. 1989). Fish were then weighed to the nearest milligram, measured for standard length (SL) to the nearest millimetre, and uniquely marked with a subdermal injection of sterilized acrylic paint and swabbed with antibiotic. A subset of these fish ( $n = 14$ ) was retested, without our knowledge of their previous performance, approximately 1 month from the date of initial swimming. This latter experiment tested the repeatability of the swimming test (Nelson et al. 2002).

To investigate differences among sites in mean base-flow current velocities, we used a Kruskal–Wallis test because of the left-truncated data structure for some sites. Post-hoc comparisons of individual means were conducted with a Tukey-type multiple comparison procedure applying a correction for tied ranks (Zar 1996). We used a multivariate analysis of variance (MANOVA) model to test for differences in fish size among sites with weight and SL as dependent variables. We used linear regression to investigate relationships between SL, weight, and  $U_{\text{crit}}$  values across all sites and within individual sites. We calculated a mean current velocity for

**Fig. 2.** Base-flow discharge rates at three U.S. Geological Survey gauging stations in watersheds (Beaver Run, thin solid line; Jones Falls, broken line; Gwynns Falls, heavy solid line) in which blacknose dace (*Rhinichthys atratulus*) were collected between October 1999 and October 2000. Base flow was determined following Nathan and McMahon (1991). The horizontal bar indicates the period during which we estimated mean base-flow current velocities.



each site as a representation of overall current conditions. To test for a relationship between mean base-flow current velocities and  $U_{crit}$  values, we used a group-data approach to linear regression as described by Williams (1959). We used this approach because we had six to eight measures of  $U_{crit}$  for each mean current velocity, and it allowed us to test for a deviation from a linear relationship. Normal probability plots and Hartley's test were used to examine the assumptions of normality and homogeneity of variance; to meet these assumptions  $\log_{10}$ -transformed  $U_{crit}$  values were used in all analyses.

## Results

Mean current velocities ranged from 2.1 to 22.6  $\text{cm}\cdot\text{s}^{-1}$  (Table 1) and differed significantly among sites ( $\chi^2 = 111.33$ ,  $p < 0.001$ ). Mean current velocities were lowest at the Jones Falls site where no values  $>10 \text{ cm}\cdot\text{s}^{-1}$  were observed (Fig. 3). At the other sites, maximum observed values were in the range of 45–50  $\text{cm}\cdot\text{s}^{-1}$ , but the distribution of values differed between the Gwynns Falls 2 and Beaver Run 1 sites and the Gwynns Falls 1 and Beaver Run 2 sites. At the former two sites, few current velocities  $>15 \text{ cm}\cdot\text{s}^{-1}$  were observed, whereas at the later two sites, most of the current velocity observations were  $>15 \text{ cm}\cdot\text{s}^{-1}$  (Fig. 3). Post-hoc comparisons indicated that mean current velocities were significantly higher at the Gwynns Falls 1 and Beaver Run 2 sites when compared with the other sites but did not differ between these sites. Mean current velocity at the Jones Falls site was significantly lower than at all other sites except Gwynns Falls 2.

A total of 32 dace (5–8 from each site) were tested for swimming performance.  $U_{crit}$  values ranged from a low of 26.33  $\text{cm}\cdot\text{s}^{-1}$  for a dace from the Jones Falls site to 69.00  $\text{cm}\cdot\text{s}^{-1}$  for a dace from the Beaver Run 2 site. Mean

$U_{crit}$  values for each site followed a similar trend to that of overall minimum and maximum values (Table 1); lowest mean  $U_{crit}$  values were found among dace from the Jones Falls site and highest mean  $U_{crit}$  values were among dace from the Beaver Run 2 site.

$U_{crit}$  values were not related to fish size but were positively related to mean base-flow current velocities at the site of their capture. Fish size did not vary significantly (Wilks'  $\lambda = 0.650$ ,  $p = 0.160$ ) among sites. Furthermore, there was no relationship between fish weight ( $r^2 = 0.002$ ,  $p = 0.816$ ) or SL ( $r^2 = 0.037$ ,  $p = 0.84$ ) and  $U_{crit}$  values for all fish tested or among fish from individual sites ( $-0.24 > r^2 < 0.35$ ,  $p > 0.416$  in all cases). In contrast,  $U_{crit}$  values showed a significant positive relationship with mean base-flow current velocities ( $F = 11.31$ ,  $p = 0.002$ ; Fig. 4). The regression analysis of the relationship between  $U_{crit}$  values and mean current velocity also suggested that a linear model was adequate to describe the relationship (nonsignificant deviation from the regression model;  $F = 1.67$ ,  $p = 0.198$ ) and that the regression model accounted for 38% of the variation in  $U_{crit}$  values among dace.

There was no difference between swimming performances of 14 dace measured by the modified  $U_{crit}$  procedure ~1 month apart (Nelson et al. 2002; Table 2). A nonparametric Kendall's  $\tau$  test of the repeatability of this method over 1 month was highly significant ( $R = 0.6$ ,  $P = 0.003$ ).

## Discussion

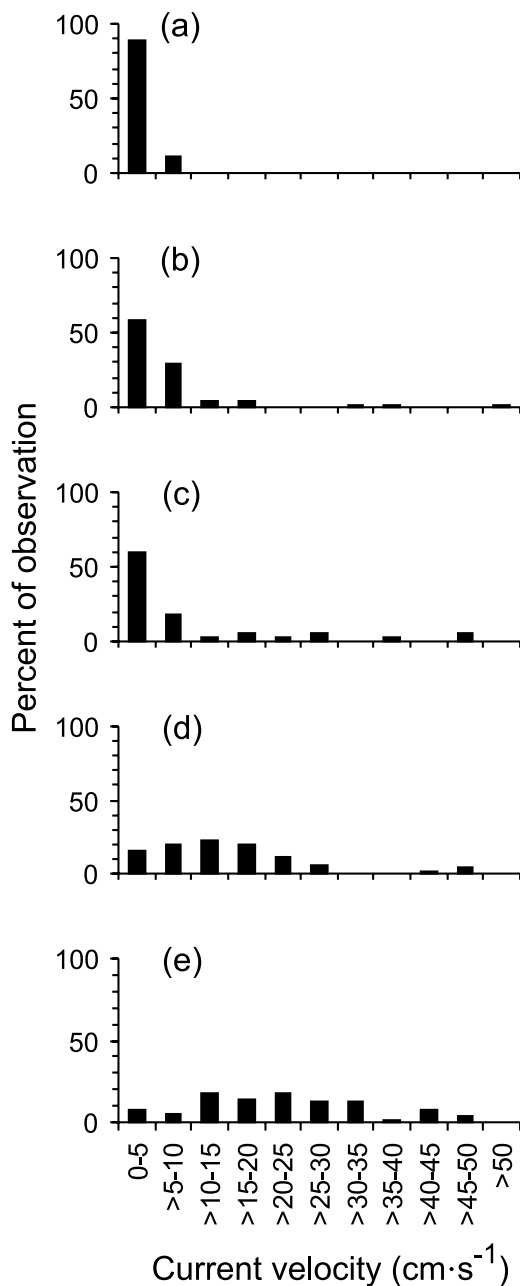
The original  $U_{crit}$  procedure with 30- to 60-min time intervals was designed by Brett (1964) to mimic the flow conditions that anadromous salmonids experience as they ascend lotic waters to spawn in British Columbia, Canada, primarily the large Fraser River. The modified  $U_{crit}$  procedure utilized

**Table 1.** Fish sample size (*n*), mean current velocities at each study site, and mean weight, standard length (SL), and  $U_{crit}$  of swim-tested fish.

Site	<i>n</i>	Mean current ( $\text{cm} \times \text{s}^{-1}$ )	Mean weight (g)	Mean SL (mm)	Mean $\frac{5}{5}U_{crit}$ ( $\text{cm} \times \text{s}^{-1}$ )
Beaver Run 1	5	9.2 (2.0)	0.9 (0.07)	42.38 (0.94)	35.58 (4.07)
Beaver Run 2	8	22.6 (1.6)	1.02 (0.08)	42.6 (1.75)	46.12 (12.63)
Gwynns Falls 1	7	15.1 (1.4)	1.12 (0.09)	44.14 (0.86)	39.6 (4.85)
Gwynns Falls 2	6	6.5 (1.4)	0.87 (0.07)	40.67 (0.76)	36.3 (6.52)
Jones Falls	6	2.1 (0.4)	1.09 (0.09)	42.8 (0.86)	30.87 (1.64)

**Note:** Standard errors are given in parentheses.

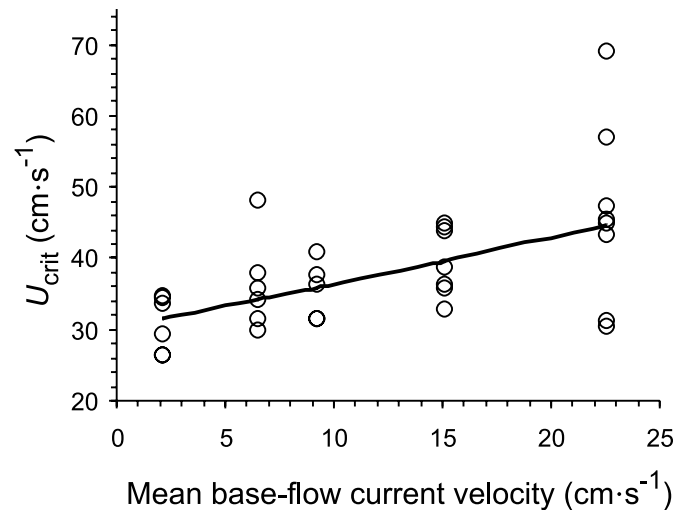
**Fig. 3.** Frequency histograms of current velocities at each of the sites from which blacknose dace (*Rhinichthys atratulus*) were collected for swim testing: (a) Jones Falls; (b) Gwynns Falls 2; (c) Beaver Run 1; (d) Gwynns Falls 1; and (e) Beaver Run 2.



**Table 2.** Descriptive statistics ( $U_{crit}$  ( $\text{cm} \cdot \text{s}^{-1}$ )) for 14 blacknose dace subjected to two swimming performance trials (initial swim at 2 weeks after capture and second swim at ~6 weeks after capture).

	$U_{crit}$ ( $\text{cm} \cdot \text{s}^{-1}$ ), initial swim	$U_{crit}$ ( $\text{cm} \cdot \text{s}^{-1}$ ), second swim
Mean	41.9	41.5
Standard error	3.10	2.2

**Fig. 4.** Relationship between  $U_{crit}$  values and mean base-flow current velocities across five stream sites from three watersheds in Maryland. The regression line is given by  $\log(U_{crit}) = 1.486 + 0.007(\text{current velocity})$ .



here was designed to more closely mimic the swimming environment that a dace might encounter as it moves about in the small streams of the Atlantic coastal plain. In the region in which these animals were captured, riffle length varies between 5 and 75 m, and thus, it should take animals a matter of minutes to traverse the average riffle, not a half hour. The repeatability of this test was verified by the almost identical performances of 14 fish swum ~1 month after their initial swim trial (Nelson et al. 2002). This result also shows that no laboratory-induced diminution of performance occurred between weeks 2 and 6 after capture; thus, by inference, these swimming performances can be taken to be indicative of feral fish. Importantly, this intraindividual variance of performance in consecutive tests was, on average, far smaller than the interindividual variance in performance among the 32

fish in the present study. The largest change in performance was a drop of  $11.4 \text{ cm}\cdot\text{s}^{-1}$  in  $U_{\text{crit}}$  for the best-performing dace among this group of 14 fish (Nelson et al. 2002).

The variation in swimming performance observed, as measured by  $\frac{5}{3}U_{\text{crit}}$ , was considered large. The maximum  $\frac{5}{3}U_{\text{crit}}$  value measured for 32 blacknose dace was 2.6 times the minimum value. The coefficient of variation of 23.5% for  $\frac{5}{3}U_{\text{crit}}$  of these blacknose dace was roughly double the average coefficient of variation of 12.5% reported by Nelson (1989) for  $\frac{30}{5}U_{\text{crit}}$  of another freshwater fish, the yellow perch, from three different lakes measured in the same swim flumes. Some comparison reports of coefficients of variation in swimming performance among conspecific stream fish are 11.7–20.8 for guppies (*Poecilia reticulata*) from four rivers in Trinidad (Nicoletto and Kodric-Brown 1999) and 9.5–16.6 for juvenile coho salmon (*Oncorhynchus kisutch*) from three rivers in British Columbia (Taylor and McPhail 1985) and confirm the large variance in performance among dace. This large variation in swimming performance among dace was partially accounted for by the environmental characteristics of stream reaches in which individuals were captured, specifically the mean base-flow current velocity. Our characterization of current conditions using mean base-flow current velocity is coarse and may not accurately reflect conditions experienced by individual blacknose dace, especially in more diverse stream reaches. In more diverse streams, individual dace may occupy smaller areas of more restricted current velocities. If this were the case, a wider range of swimming performances might be expected among dace from more diverse reaches. Although our study was not designed to test this hypothesis, our results do suggest that this may be the case and is worth further study. Specifically, at the Beaver Run 2 site, there was a more even distribution of current velocities across a broad range (i.e., a more diverse habitat), and we observed a much wider range in  $U_{\text{crit}}$  values among fish from this site. However, despite other potential sources of variation, we only found a positive correlation between swimming performance and mean base-flow current velocities, suggesting blacknose dace swimming performance is shaped by flow conditions within individual reaches, either through natural selection or conditioning (i.e., training). Furthermore, our findings agree with those of Nicoletto and Kodric-Brown (1999), who also found a positive correlation between current magnitude and guppy swimming performance among populations from four rivers in Trinidad.

Confirmation of this result can be inferred from studies comparing populations of conspecific fish with variable swimming demands throughout their lifetimes. For example, Taylor and colleagues have compared swimming performances among several Pacific coastal species with populations that either vary in the length of their anadromous migrations or have migratory and nonmigratory forms (Taylor and McPhail 1985, 1986; Taylor and Foote 1991). A consistent finding of this body of work is that the populations with greater migratory demands have significantly greater endurance swimming performance. Taylor and McPhail (1985) found that a population of coho salmon (*Oncorhynchus kisutch*) that must ascend deep into the interior of British Columbia had four- to five-fold greater endurance performance than two coho populations that had relatively modest migrations into coastal streams. Tsuyuki and Willisicroft

(1977) made an identical observation for two populations of migratory steelhead trout (*Oncorhynchus mykiss*). Similarly, juveniles of the anadromous form of sockeye salmon (*Oncorhynchus nerka*) had significantly greater endurance swimming performance than juveniles of a sympatric sockeye population that remains landlocked for its entire life cycle (Taylor and Foote 1991). This finding is not restricted to salmonids. The taxonomically distant stickleback (*Gasterosteus aculeatus*) exists as sympatric population pairs on the west coast of North America, only one of which undergoes an anadromous migration. In this species, the anadromous form averages seven times greater endurance swimming performance than its resident conspecific (Taylor and McPhail 1986).

Comparative studies of hatchery stock and wild populations of salmonids suggest relatively rapid evolution of swimming performance differences in this group and that natural selection could be responsible for shaping the swimming performance differences of the dace that we measured. Vincent (1960) found that wild strains of brook trout (*Salvelinus fontinalis*) had better swimming performance than domestic conspecifics; in Vincent's (1960) study, these differences persisted after the wild strains were subjected to one generation of hatchery rearing. Bams (1967) found that freshly emerged fry of wild sockeye salmon (*O. nerka*) had superior swimming performance compared with artificially propagated fry, although this difference might have been due to the large size differences at swim-up. McDonald et al. (1998) found that wild yearling Atlantic salmon (*Salmo salar*), but not fingerlings, had superior stamina in a fixed-velocity test compared with hatchery-raised individuals. Finally, Thomas and Donahoo (1977) found an inverse correlation between length of time under domestication and swimming endurance for three strains of hatchery rainbow trout (*O. mykiss*).

Although these salmonid studies suggest that selection can produce swimming performance differences among conspecifics relatively quickly, the intrawatershed, intersite differences in dace swimming performance that were as large as interwatershed comparisons argues against the dace swimming performance differences arising through natural selection. However, some recent studies render this explanation plausible. Carlsson et al. (1999) found genetic differentiation of brown trout populations (*Salmo trutta*) within the same stream over distances shorter than the same-stream collection sites of the present study. Hendry et al. (2000) described sympatric, intralacustrine differentiation of sockeye salmon (*O. nerka*) populations that took place over less than 30 generations. Thus, one possibility is that the swimming performance differences in dace that correlate with the base flow at the site of capture were a product of natural selection.

Although studies of wild populations with different migratory demands and comparisons between hatchery-raised and wild animals may indirectly suggest a role for natural selection in shaping blacknose dace swimming, other studies suggest that conditioning may be responsible. There is ample evidence for plasticity of endurance locomotor performance among fishes, primarily salmonids (reviewed by Beamish (1978) and Davison (1989)). Generally, a period of exercise training for at least 1 month has been shown to cause improvements in  $U_{\text{crit}}$  values (e.g., Farrell et al. 1990). By extension, one explanation for our results could be that dace

from regions of higher base flow are “better trained” than individuals from lower flow sites. Thus, the former fish were able to outperform their conspecifics in the  $U_{crit}$  test. Obviously, dace seek refugia to avoid high stream flows, and flow varies considerably with precipitation events, but the idea here is that individuals from higher base-flow sites would, on average, have to exercise more when moving between sites and capturing prey and than individuals from areas of lower base flow. No physiological measurements were made to support this explanation, but training of other fish species has been shown to alter muscle ultrastructure (e.g., Broughton et al. 1980), biochemistry (e.g., Johnston and Moon 1980), and the cardiovascular system (e.g., Farrell et al. 1991) in directions that should enhance swimming performance (reviewed by Davison (1989)). Cyprinids have not generally been used in training studies, but domesticated roach (*Rutilus rutilus*) held in flowing water were shown to have different biochemical responses to exercise than domesticated roach held in still water (Broughton and Goldspink 1978). These biochemical differences were suggestive of greater endurance swimming capacity in the animals from running water (Broughton and Goldspink 1978).

Finally, a possible explanation for our data that must be considered is that dace settle in stream reaches based on whatever swimming genotype they possess. Because this would involve substantial intrastream migrations of juvenile fish, we consider this alternative unlikely. However, because there are no data on movements of juvenile blacknose dace in mid-Atlantic, coastal plain streams, this must be considered a viable alternative.

Size accounted for less than 4% of the variation in performance from this group of 40 dace. Size is usually a significant factor in determining swimming capacity of fishes (e.g., Webb 1976). However, because we preselected fish to encompass a narrow size range and because of the overshadowing effect of current velocity, size was of little import in determining the  $\frac{5}{2}U_{crit}$  of this group of dace.

An interesting aside is that this data set represents a warning for investigators of both population-level physiological differentiation and environmental influences on animal physiology. Had we not collected fish from multiple sites of variant current velocity within two of the watersheds, a likely conclusion from this study would have been that performance physiology of these three populations of dace had diverged, which is obviously not the explanation for the large variance in dace swimming performance seen in this study.

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## References

Bams, R.A. 1967. Differences in performance of naturally and artificially propagated sockeye salmon migrant fry, as measured with swimming and predation tests. *J. Fish. Res. Board Can.* **26**: 1117–1153.

- Bart, H.A., Jr. 1989. Fish habitat association in an Ozark stream. *Environ. Biol. Fishes*, **24**: 173–186.
- Beamish, F.W.H. 1978. Swimming capacity. *In* *Fish physiology*. Vol. 7. Edited by W.S. Hoar and D.J. Randall. Academic Press, New York. pp.101–187.
- Brett, J.R. 1964. The respiratory metabolism and swimming performance of young sockeye salmon. *J. Fish. Res. Board Can.* **21**: 1183–1226.
- Broughton, N.M., and Goldspink, G. 1978. Biochemical changes in the lateral muscles of roach, *Rutilus rutilus*, from two habitats following exercise. *J. Fish Biol.* **13**: 613–618.
- Broughton, N.M., Goldspink, G., and Jones, N.V. 1980. The effect of training on the lateral musculature of 0-group roach, *Rutilus rutilus*, and their fatigue in subsequent exercise tests. *J. Fish Biol.* **17**: 209–217.
- Carlsson, J., Olsen, K.H., Nilsson, J., Overij, O., and Stabell, O.B. 1999. Microsatellites reveal fine-scale genetic structure in stream-living brown trout. *J. Fish Biol.* **55**: 1290–1303.
- Davison, W. 1989. Training and its effects on teleost fish. *Comp. Biochem. Physiol. A*, **94**: 1–10.
- Diamond, J., and Hammond, K. 1992. The matches achieved by natural selection between biological capacities and their natural loads. *Experientia (Basel)*, **48**: 551–557.
- Farrell, A.P., Johansen, J.A., Steffensen, J.F., Moyes, C.D., West, T.G., and Suarez, R.K. 1990. Effects of exercise training and coronary ablation on swimming performance, heart size, and cardiac enzymes in rainbow trout, *Oncorhynchus mykiss*. *Can. J. Zool.* **68**: 1174–1179.
- Farrell, A.P., Johansen, J.A., and Suarez, R.K. 1991. Effects of exercise training on cardiac performance and muscle enzymes in rainbow trout, *Oncorhynchus mykiss*. *Fish Physiol. Biochem.* **9**: 303–312.
- Feder, M.E., Bennett, A.F., and Huey, R.B. 2000. Evolutionary physiology. *Annu. Rev. Ecol. Syst.* **31**: 315–341.
- Garland, T.J., and Losos, J.B. 1994. Ecological morphology of locomotor performance in squamate reptiles. *In* *Ecological morphology: integrative organismal biology*. Edited by P.C. Wainwright and S.M. Reilly. University of Chicago Press, Chicago, Ill. pp. 240–302.
- Haux, C., Sjöbeck, M., and Larsson, Å. 1985. Physiological stress responses in a wild fish population of perch (*Perca fluviatilis*) after capture and during subsequent recovery. *Mar. Environ. Res.* **15**: 77–95.
- Hendry, A.P., Wenburg, J.K., Bentzen, P., Volk, E.C., and Quinn, T.P. 2000. Rapid evolution of reproductive isolation in the wild: evidence from introduced salmon. *Science (Wash., D.C.)*, **290**: 516–518.
- Iwama, G.K., McGeer, J.C., and Pawluk, M.P. 1989. The effects of five fish anaesthetics on acid–base balance, hematocrit, blood gases, cortisol and adrenaline in rainbow trout. *Can. J. Zool.* **67**: 2065–2073.
- Johnston, I.A., and Moon, T.W. 1980. Exercise training in skeletal muscle of brook trout (*Salvelinus fontinalis*). *J. Exp. Biol.* **87**: 177–194.
- Kolok, A.S. 1999. Interindividual variation in the prolonged locomotor performance of ectothermic vertebrates: a comparison of fish and herpetofaunal methodologies and a brief review of the recent fish literature. *Can. J. Fish. Aquat. Sci.* **56**: 700–710.
- Lee, D.S., Gilbert, C.R., Hocutt, C.H., Jenkins, R.E., McCallister, D.E., and Stauffer, J.R. 1980. Atlas of North American freshwater fishes. State Museum of Natural History, Raleigh, N.C.
- McDonald, D.G., Milligan, C.L., McFarlane, W.J., Croke, S., Currie, S., Hooke, B., Angus, R.B., Tufts, B.L., and Davidson, K. 1998. Condition and performance of juvenile Atlantic salmon

- (*Salmo salar*): effects of rearing practices on hatchery fish and comparison with wild fish. *Can. J. Fish. Aquat. Sci.* **55**: 1–12.
- Nathan, R.J., and McMahon, T.A. 1991. Evaluation of automated techniques for base flow and recession analyses. *Water Resour. Res.* **26**:1465–1473.
- Nelson, J.A. 1989. Critical swimming speeds of yellow perch *Perca flavescens*: comparison of populations from a naturally acidic lake and a circumneutral lake in acid and neutral water. *J. Exp. Biol.* **145**: 239–245.
- Nelson, J.A., Tang, Y., and Boutilier, R.G. 1996. The effects of salinity change on the exercise performance of two Atlantic cod (*Gadus morhua*) populations inhabiting different environments. *J. Exp. Biol.* **199**: 1295–1309.
- Nelson, J.A., Gotwalt, P.S., Reidy, S.P., and Webber, D.M. 2002. Beyond  $U_{crit}$ : matching swimming performance tests to the physiological ecology of the animal, including a new fish “drag strip”. *Comp. Biochem. Physiol.* **133**: 289–302.
- Nicoletto, P.F., and Kodric-Brown, A. 1999. The relationship among swimming performance, courtship behavior, and carotenoid pigmentation of guppies in four rivers of Trinidad. *Environ. Biol. Fishes*, **55**: 227–235.
- Petty, J.T., and Grossman, G.D. 1996. Patch selection by mottled sculpin (Pisces: Cottidae) in a southern Appalachian stream. *Freshw. Biol.* **35**: 261–276.
- Pickering, A.D., Pottinger, T.G., and Christie, P. 1982. Recovery of the brown trout, *Salmo trutta* L., from acute handling stress: a time-course study. *J. Fish Biol.* **20**: 229–244.
- Pringle, C.M., Naiman, R.J., Gretschko, G., Karr, J.R., Oswood, M.W., Webster, J.R., Welcomme, R.J., and Winterbourn, M.L. 1988. Patch dynamics in lotic systems: the stream as a mosaic. *J. North Am. Benthol. Soc.* **7**: 503–524.
- Taylor, E.B., and McPhail, J.D. 1985. Variation in burst and prolonged swimming performance among British Columbia populations of coho salmon, *Onchorhynchus kisutch*. *Can. J. Fish. Aquat. Sci.* **42**: 2029–2033.
- Taylor, E.B., and McPhail, J.D. 1986. Prolonged and burst swimming in anadromous and freshwater threespine stickleback, *Gasterosteus aculeatus*. *Can. J. Zool.* **64**: 416–420.
- Taylor, E.B., and Foote, C.J. 1991. Critical swimming velocities of juvenile sockeye salmon and kokanee, the anadromous and non-anadromous forms of *Onchorhynchus nerka* (Walbaum). *J. Fish Biol.* **38**: 407–419.
- Thomas, A.E., and Donahoo, M.J. 1977. Differences in swimming performance among strains of rainbow trout (*Salmo gairdneri*). *J. Fish. Res. Board Can.* **34**: 304–306.
- Tsuyuki, H., and Willisroft, S.N. 1977. Swimming stamina differences between genotypically distinct forms of rainbow trout (*Salmo gairdneri*) and steelhead trout. *J. Fish. Res. Board Can.* **34**: 996–1003.
- Vincent, R.E. 1960. Some influences of domestication upon three stocks of brook trout (*Salvelinus fontinalis* Mitchell). *Trans. Am. Fish. Soc.* **89**: 35–52.
- Vogel, S. 1994. *Life in moving fluids*. Princeton University Press, Princeton, N.J.
- Webb, P.W. 1976. The effect of size on the fast-start performance of rainbow trout *Salmo gairdneri* and a consideration of piscivorous predator–prey interactions. *J. Exp. Biol.* **65**: 157–177.
- Webb, P.W. 1986. Locomotion and predator–prey relationships. *In* *Predator–prey relationships*. Edited by M.E. Feder and G.V. Lauder. University of Chicago Press, Chicago, Ill. pp. 24–41.
- Williams, E.J. 1959. *Regression analysis*. John Wiley & Sons, New York.
- Zar, J.H. 1996. *Biostatistical analysis*. 3rd ed. Prentice Hall, Upper Saddle River, N.J.