Flow preferences of individual blacknose dace (*Rhinichthys atratulus*); influence of swimming ability and environmental history

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Abstract Fish from lotic environments generally have a variety of flow velocities available to them in their immediate environment. Other than prey availability or predator presence, little is known about what factors determine where in this mosaic of flows an individual fish will choose to locate. Since individuals of a species can have substantially different swimming abilities, and interspecific differences in flow velocity selection have been related to differential swimming abilities, one possibility is that an animal's physical condition constrains the flow environments it chooses to occupy. Additionally, since the flow in an animal's environment can contribute to swimming ability, there could also be environmental control over flow selection behavior. This study examined whether flow velocity selection by individual blacknose dace (*Rhinichthys atratulus*) is a repeatable trait in the laboratory, and whether it is a function of either the animal's swimming ability or the magnitude of flow in their home stream reach. Blacknose dace from two populations, collected from each of two separate reaches with substantially different flows from within their home streams, exhibited significantly repeatable flow velocity selection over the course of 1 day in the laboratory. The flow velocity selected by the fish varied significantly among individual dace. Some of this variance was accounted for by fish from the slower stream reaches choosing significantly faster flows than did those from faster reaches. There were no significant differences in flow selection behavior between populations. There was also no relationship between sprinting ability and the flow velocity selected by a fish.

Keywords Blacknose dace · Flow velocity selection · Swimming ability · Population differences · Intraspecific behavioral plasticity

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Introduction

Nearly three-fourths of the earth is covered with water, and only rarely is this water not in motion. In lotic aquatic habitats, where an animal positions itself in the flow has important consequences for its presumed fitness (Tyler and Gilliam 1995; Steingrímsson and Grant 2011). Where an aquatic animal positions itself in a flow field could determine many of the factors that potentially contribute to its Darwinian fitness such as foraging efficiency, success in predator–prey interactions, metabolic expenditure to maintain position etc. In the present study, we asked whether the preferred

water-velocity of a stream fish is a function of either its swimming ability or its past exposure to environmental flow. To address this question, an intraspecific comparative approach was used. Fish of the same species, blacknose dace (*Rhinichthys atratulus*), inhabiting stream reaches that differed substantially in flow, were analyzed for both their flow preference and sprinting ability. As a form of replication, animals from two separate populations were analyzed.

Swimming performance of individual blacknose dace correlates positively with the mean base-flow current velocity of their local habitat (Nelson et al. 2003). In addition, blacknose dace from urban streams, where flow is extremely strong after storms, generally have better swimming ability than those from rural environments where flow is more stable (Nelson et al. 2008). Most of this apparent flow-based performance differential is due to phenotypic plasticity (Nelson et al. 2008). Since there are a myriad of flow microhabitats within any given stream reach, questions of scale arise. The earlier studies reported (Nelson et al. 2003, 2008) uncovered broad correlations between the mean baseflow of a reach and mean swimming performance of fish captured in that reach, but could this finding be extended to individuals within a given reach? Since little is known about flow velocity selection (FVS) of individual fish within an environment or whether it is a function of performance ability or environment, the matching of swimming performance to environmental flow may be greater than previously reported (Nelson et al. 2003, 2008), or not. While interspecific comparisons have shown a relationship between swimming ability and the flow regime fish select in a stream (Schaefer et al. 1999; Leavy and Bonner 2009), little is known about the relationship between intraspecific variation in swimming performance and flow selection.

Our objective was to determine how the individual's position in the stream is linked to individual behavior and performance, using velocity-gradient and sprint-performance chambers. Do better-swimming fish choose faster currents (e.g., thereby increasing their access to food), or are the flow characteristics of their home-stream reach the main determinant of this behavior? Lastly, are there significant behavioral differences in fish collected from faster and slower reaches? The null hypothesis for this experiment was that FVS by fish is independent of swimming performance and the current velocity of their native stream reach.

Materials and methods

Environment

Fish were collected from two reaches with substantially different flows within each of two different streams in the greater Baltimore Metropolitan region (Table 1). The average base-flow current speeds of each of the four, 100-m reaches had previously been determined with a Marsh-McBirney Model 2000 flow meter (Table 1; see Nelson et al. (2003) for a description of the procedure). Blacknose dace were collected from the lower flow Beaver Run upstream site on February 27, 2009 at a reach temperature of 5.2°C and from the higher flow downstream site on March 6, 2009 at a temperature of 7.2°C, and from both of the Gwynn's Falls sites on March 4, 2009 at a temperature of 2.1°C. Three of the sites were very similar with a stream width of between 1 and 2 m and an abundance of medium size cobble and tree-fall wherein the dace could find refuge from flow. The "Beaver Run fast" was slightly larger 3–4 m and the substrate tended to be finer, on average, but interspersed with larger rocks that provided cover for the dace.

Fish collection

Dace were collected from each site with a Smith-Root Inc. Model 15-D backpack electro shocker. Approximately 20 fish of similar size (Table 2) were collected from each site and returned to the laboratory at Towson University in their native water where the temperature was raised to the experimental temperature of 20°C at a rate of 2°C/day and gradually switched over to Baltimore City tap water. Tap water was always aged a minimum of 24 h before usage to ensure evaporation of any chlorinated disinfectants added to the water supply. There was no significant difference in fish size by population or reach nor was there an interaction between the two (ANOVA $P>0.25$).

Table 1 Location and base flow current velocities of collection sites (Nelson et al. 2003)

Stream	USGS coordinates	Base flow slow site (cm • s^{-1})	Base flow fast site (cm • s^{-1})
Beaver Run	39.518, -76.941	9.2	22.6
Gwynn's Falls	39.277, -76.668	6.5	15.1

Table 2 Masses of the fish collected for the study ± 1 standard deviation.

| Stream	Slow site (g)	Fast site (g)
Beaver Run	1.98±0.41	1.95±0.60
Gwynn's Falls	1.81±0.43	2.09±0.72

After approximately 1 week, the fish from each site were transferred to two separate 265 L holding tanks (Fig. 1) filled with Baltimore City tap water at 20°C. Each holding tank had four separate lanes for holding fish (2 lanes per reach) that were calibrated to approximately match the current velocity of their respective collection site. Lanes were separated by black Plexiglas® so that fish could not be influenced by the swimming behavior of fish in the other lanes. Fish were maintained on a natural photoperiod via illumination from laboratory windows, but their tanks were partially covered with black plastic to limit visual contact and thus habituation to humans. The sides and top were covered with black plastic but light could enter from the front and back of the tank where experimenters rarely ventured. Approximately equal amounts of gravel, sticks, and larger rocks were placed in the lanes to more closely mimic stream conditions and to allow refugia from flow within the tank lanes. The pumps were turned off every night for 12 h to mimic the period when these diurnal fishes would be hiding in cobble interstices. Fish were fed Tetramin® goldfish flake food until they stopped feeding every morning before the pumps were turned back on. The temperature of the holding tanks was recorded and adjusted each day to keep the temperature at 20°C throughout the entire experiment (mean 19.76 ±1.71°C

SD). Fish were acclimated to the holding tanks for at least 1 week before any experimental test was performed.

Experimental velocity selection

A chamber modified from that described by Katzman et al. (2010) was used to analyze flow velocity selection (FVS). The flow selection chamber was 215 cm× 81 cm×20 cm and had three PVC water-inlet pipes with ball valves, three drains, two external water storage tanks, and a pump. The depth of the water in the flow selection chamber was maintained at 9.5 cm by balancing water inflow with outflow through the drains (Figs. 2, 3). Velocity gradients were made by setting inflow valves for relatively slow, medium, and fast velocities, respectively, across the width of the testing tank and adjusting the corresponding drain to match. Velocities were modified from those described by Katzman et al. (2010) due to differential size and swimming capacity of blacknose dace compared to the coho salmon (*Oncorhynchus kisutch*) used by Katzman et al. (2010). The velocity-preference chamber was nominally set to have unidirectional flow from front to back in all areas of the tank, although the slower-velocity portion of the tank included small eddying areas of "negative" flow. A 550L reservoir allowed the water to be chilled to the proper temperature before being pumped back into the selection chamber. Fish were restricted to a section of the selection chamber enclosed by a mesh fence across both the inlet and outlet ends (Fig. 2). Gridlines on the bottom of the testing tank delineated 25-cm^2 squares (Figs. 2, 3). Each square was characterized for current speed using a portable Marsh-McBirney Model 2000 flow

Fig. 1 Diagram of holding tanks showing water circulating uni-directionally through four separate velocity-maintenance lanes in the holding tanks
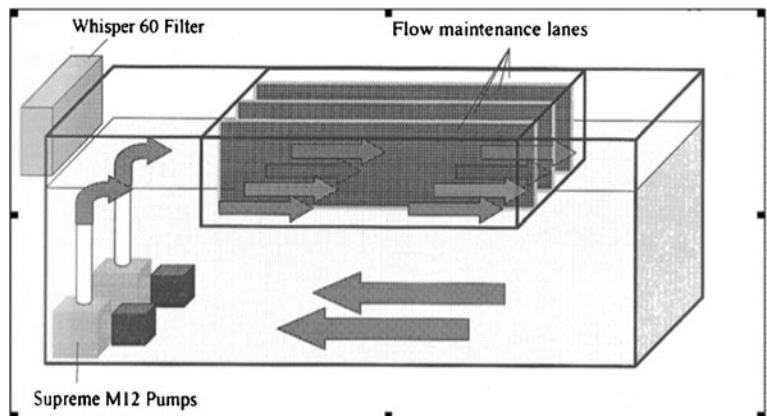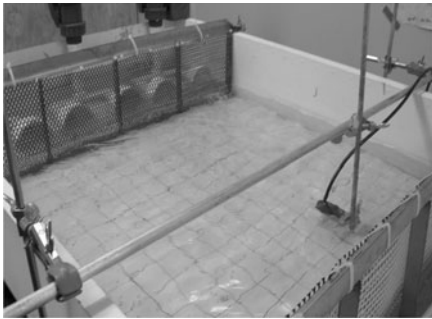
Fig. 2 Measuring the velocity of one of the 25-cm^2 squares in the testing tank, using the Marsh-McBirney Model 2000 flow meter. Higher velocity flow is towards the top of the picture and towards the right of the picture

meter by placing the sensor in the center of each square at mid-depth for 30 s and averaging the flow recorded (Fig. 2). Current speeds ranged from −1.5 cm·s^{-1} to 15 cm·s^{-1} with roughly equal availability of speeds <5 cm·s^{-1}, between 5 cm·s^{-1} and 10 cm·s^{-1} and > 10 cm·s^{-1}.

To test the velocity preference of an individual, one randomly selected fish per day was transferred without air exposure to the flow selection chamber. After an overnight acclimation, the fish was videotaped for 15 min every 2 h for 8 h, producing 1 h of total observation time. The flow selection chamber was elevated so that the fish could not see people in the room as potential predators or sources of food, thus eliminating this potential influence on their behavior (Dionne and Dodson 2002). In addition, people were never allowed in the same room as the chamber during the 15 min of videotaping. Each 15-min segment
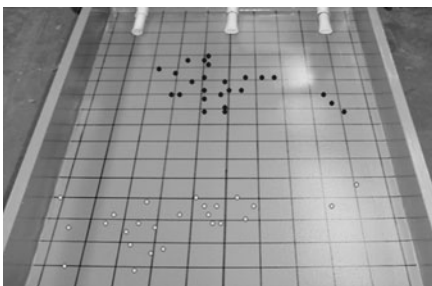

Fig. 3 Diagram of two extreme examples of FVS within the chamber. The closed circles represent areas where an individual fish with a preference for higher flow was found at randomly selected intervals during one trial. The mean FVS for this fish was 6.1 cm·s^{-1}. The open circles represent areas where an individual fish with a preference for lower flow was found at randomly selected intervals during one trial. The mean FVS for this latter fish was 1.6 cm·s^{-1}

constituted a trial. From each trial, 5 s of each minute were randomly selected for assessment of fish position using an internet-sourced random number generator. This sampling frequency was chosen based upon a preliminary study wherein a sampling frequency of 10 randomly chosen s per minute of tape (150 data points/trial; 600 data points total per fish) was compared with a more frugal method of 2 s per min (30 data points per trial; 120 data points total per fish). The results of this experiment suggested that there was little additional information to be obtained from sampling more frequently than 2 s out of each recorded minute, however, the sampling frequency of 5 randomly selected s out of each minute was chosen for this study as one that would adequately characterize an individual's flow preference without incurring excessive analysis time. This provided 75 data points per fish per trial, or 300 total data points per fish. All trials were run without food present. After a fish's 4 trials, the fish was then removed, weighed, and measured, and a 10 % water change performed for the next fish.

Sprint-swimming performance

Sprint performance was measured as described in Nelson et al. (2002, 2003, 2008). Briefly, 30 min prior to the initiation of a sprint trial, a fish was captured by dip net, herded into a submerged beaker and then transferred to the sprint chamber without air exposure. The dimensions of the chamber were 1.5 m (length) × 15 cm (width) × 15 cm (height). Light-emitting laser diodes (OnPoint Laser Inc. 6780 Vermar Terrace, Eden Prairie, MN 55346 USA) of approximately 5 milliwatt 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 8 arrays of photo Darlington detectors (Honeywell® SDP, 18 sensors per array; 144 sensors total) of detection wavelength 580–720 nm. Individual sensors in an array were positioned vertically 0.5 cm from the bottom and then every 0.5 cm apart to a height of 8.5 cm (0.5 cm below the "fill" line at 9 cm). When activated by light, the

photo Darlington detector arrays put out a 5 V signal to one of 8 digital inputs on an AD Instruments Power-lab® 4 s interfaced to an Apple Macintosh I-Mac® computer running Chart® software. Breakage of the first laser acted as a trigger and the time of subsequent laser beam breakage was recorded to 0.1 ms accuracy. Sprint swimming speed was calculated from the times of laser beam breakage and the distance between detector arrays. Intervals of 4 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.

Statistics

Differences among sprint swimming speed, flow selection velocity and size among groups of fish from different populations and reaches were assessed by 2-way ANOVA. For FVS, a repeated measure ANOVA was used with each of the four 15' trial periods (every 2 h) serving as a replicate for each fish. Repeatability of flow selection for individual fish and trials was assessed with Friedman's ANOVA by ranks and the Kendall Concordance Coefficient (KCC). Normality of distributions was tested with the Kolmogorov-Smirnov test. For sprint performance, the maximal velocity attained by the fish was used as the dependent variable and population and stream reach were the independent variables. The fiducial level of significance for all tests was $P<0.05$.

Results

Sixteen fish were successfully evaluated for both their FVS and sprint performance. The fish exhibited a wide range of behaviors in both the holding tanks and the experimental tanks. In the holding tanks, some fish consistently preferred to swim close to the pumps directly in the current, whereas others consistently spent most of their time hiding behind rocks.

In the flow-selection chamber, differences in fish behavior were also readily apparent. Even without food present, some fish swam directly into the

strongest currents, directly in front of the water-inlet. These fish would intermittently let the current take them to the rear of the tank only to quickly return to the front, thus completing "laps" of the flow-selection chamber (Fig. 3). In contrast, other fish swam far from the water-inlet pipes, periodically even "resting" on the downstream screen of the chamber (Fig. 3). These behavioral extremes were significantly different from one another ($P<0.01$; Friedman ANOVA of ranks across the four trials). Each fish exhibited a statistically significant similar choice in velocity among trials throughout the entire experiment (Fig. 4; Kendall coefficient of concordance = 0.562) that was not dependent upon the order of determination ($P>0.05$; Fig. 4) and was independent of time of day (Fig. 5).

Flow velocity selection (FVS) was normally distributed among the 16 fish (Kolmogorov-Smirnov test $P>0.2$) and was independent of animal size. The coefficient of variation for flow selection using the mean value for each fish (mean of 4 trials; 1 data point/fish; 16 total) was 50 % or using the mean value for each trial (4 data points/fish; 64 total) was 62 %.

Flow velocity selection (FVS) was a significant function of home reach current velocity ($P<0.01$ ANOVA; Fig. 6). Curiously, animals from the slower reaches of their home stream chose significantly higher currents in the velocity-preference chamber. Dace from the slow reach of Beaver Run chose an
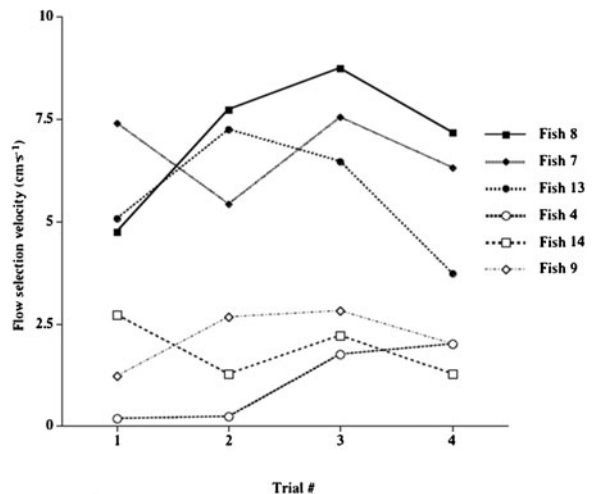

Fig. 4 Graph of the flow selection pattern of six individual fish, the three with the highest mean velocities chosen (closed symbols) and three with the lowest mean chosen velocities (open symbols), demonstrating the relative repeatability of flow selection across an 8-h period. Fish # was also the order of determination
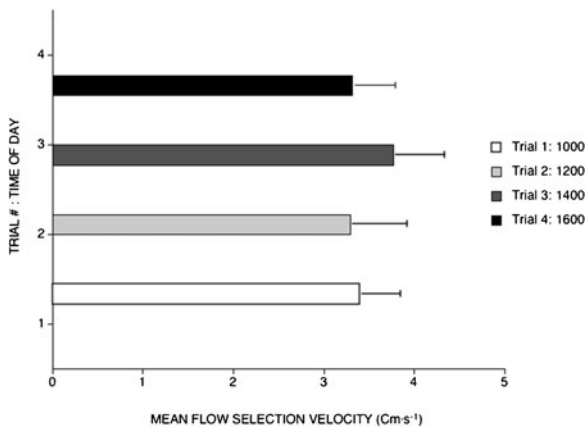
Fig. 5 Flow velocity selection (FVS) at different times of the day (Trial #). Means and standard errors for all 16 fish are plotted

average velocity of 4.54 cm·s^{-1}, while those from the fast reach chose a considerably slower average velocity of 2.27 cm·s^{-1} (Fig. 5). Fish from the slow reach of Gwynn's Falls chose an average velocity of 4.17 cm·s^{-1} whereas those from the fast reach chose an average velocity of 2.79 cm·s^{-1}. There was no significant population effect or interaction.

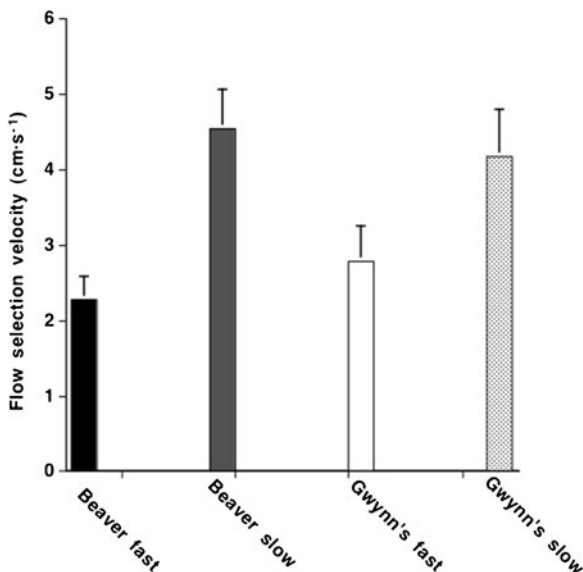Two-way ANOVA results returned a slightly significant difference between the sprinting ability of the

Fig. 6 Mean (± SE) velocities selected by individual blacknose dace from two separate streams in Maryland, originating from either a relatively fast or a relatively slow reach from within that stream. Animals from different reaches selected significantly different velocities ($p < 0.01$), but there was no effect of population or interaction between population and reach

two populations; Beaver Dam fish were slightly better sprinters than were the Gwynn's Falls fish, 146 cm·s^{-1} versus 131 cm·s^{-1}, respectively (not shown; $P = 0.046$). There was no significant difference in maximal sprint capacity between fish from the fast and slow reaches of the streams although the fish from the faster reach were better average sprinters (141 cm·s^{-1} versus 137 cm·s^{-1}). There was no significant relationship between the flow velocity selected by an individual dace and its top sprint velocity ($r^2 = 0.01$; $P = 0.5$). Similarly, but unlike earlier studies (Nelson et al. 2008), no relationship was found between fish size and sprinting ability. However these fish were pre-selected to be nearly uniform in size (Table 2).

Discussion

Blacknose dace are Nearctic cyprinids that are generally found oriented into the current of lotic systems where they feed on drift (Johnson and Johnson 1982; Tyler 1993). The purpose of this investigation was threefold: 1) to examine individual variance and repeatability of flow selection behavior in the laboratory; 2) to examine whether flow selection behavior was correlated with physical condition as assessed by sprint swimming performance; and 3) to test whether flow selection behavior correlated with differences in environmental flow, measured as the average base-flow current velocity from the precise reach of the stream where the fish was captured. To provide for replication but also to account for potential population differences (Nelson et al. 2008), we analyzed fish from two separate streams.

As has been reported for a multitude of behavioral and physiological characteristics, flow selection by blacknose dace in the chamber described by Katzman et al. (2010) was significantly variable among individuals of similar size and conformed to a normal distribution. Because this intraspecific variance exceeded the variability in repetitive flow selection by individuals (i.e. the test was significantly repeatable on a daily basis), we can assume that differences among individuals are reflecting some actual behavioral or physiological differences among them and are not an artifact of the test (Oufiero and Garland 2009). The variation in flow selected (FVS) by the various dace individuals in this experiment (coefficient of variation 50–62 %) was more than twice the variation in

swimming performance reported for the same species (Nelson et al. 2003). Although FVS in the laboratory may not reflect actual in situ flow selection by a fish, the repeatability of the test allows us to confidently test flow selection as a function of various intrinsic and extrinsic factors. In addition, because there was no trend in flow selection over the course of the day, we can feel confident that the fish were not fatiguing nor were they getting frustrated with the lack of forage and tending towards occupying the energetically least costly portions of the chamber.

Flow selection in situ is generally considered to be a complex function of animal size, age, available flows and microhabitats, community structure, predation risk, time of day and time of year (Heggenes et al. 1999). The FVS profiles reported here are devoid of most of these confounding variables and are considered to be indicative of intrinsic differences in flow preference among individual blacknose dace. While cognizant of the fact that flow selection will be multi-factorial in nature and most likely be the product of many genetic, ontogenetic, phenotypic and environmental factors, better understanding of the role of flow itself in stream fish ecology and physiology may help us better predict the outcomes of flow altering anthropogenic factors like climate change, flow alteration, and urbanization.

A major finding of this work was that FVS was strongly dependent upon the average base flow current velocity from the fish-collection site, but in a counterintuitive manner. Fish from the faster reaches chose significantly lower flow velocities than did those from the slower reaches (Fig. 6). While any explanation for this finding is conjecture, we think the best explanation is as follows: Blacknose dace are drift-feeding fishes whose primary prey consists of mayfly nymphs and chironomid larvae, among many other passing aquatic and terrestrial macroinvertebrates (Johnson and Johnson 1982). The fish collected from slow reaches may have selected faster currents because, in their native reach, more efficient foraging could be found in the faster sections of the reach. This idea is supported by Tyler's (1993) finding that the most efficient foraging for similar-sized blacknose dace came at around 20 cm·s^{-1}, and the general finding of an energetic tradeoff between cost of holding station and rate of food delivery as animals move towards faster current velocities (Tyler and Gilliam 1995; Asaeda et al. 2005). In contrast, the fish collected from

the faster reaches may have chosen slower currents to seek refuge from energetically costly swimming. Fish from the faster reaches had been held in a faster current in the laboratory and may have had energy savings as a greater behavioral motivation than seeking forage.

The other principle finding of this study was that there was no relationship between the sprinting ability of an individual and its FVS. Natural and artificial variations in flow can influence the swimming performance of fish (Nicoletto and Kodric-Brown 1999; Nelson et al. 2003; Young and Cech 1994) including sprinting performance (Nelson et al. 2008). However, the converse of swimming performance determining flow preference does not appear to hold true, at least for sprinting performance and blacknose dace. Fish with better swimming performance could possibly improve their feeding efficiency by positioning themselves in a stronger current (Tyler 1993; Asaeda et al. 2005), but under the no forage conditions of this study, sprinting ability was unrelated to FVS. However, that does not preclude a relationship between flow selection and other types of swimming such as endurance performance or a measure such as critical swimming speed that combines elements of aerobic endurance and burst swimming performance (Nelson et al. 2002). Several other studies have related interspecific differences in flow selection behavior to differences in swimming ability (e.g. Fausch and White 1981; Schaefer et al. 1999; Leavy and Bonner 2009), and studies have also shown differences in flow selection between different size classes of the same species (e.g. Heggenes et al. 1999), but for now the question of whether intraspecific differences in swimming ability of similar-sized animals contributes to different flow selection behavior remains open.

The two populations selected for this study differed slightly in their maximal sprint performance ($P=0.046$) and there was a slight tendency for fish from the faster reaches to be better sprinters. Population-level differences in sprint performance in blacknose dace have been reported upon before (Nelson et al. 2008) but were not the focus of the present study.

In summary, the flow selection chamber designed by Katzman et al. (2010) produced significantly repeatable flow selection behavior in the laboratory by individual blacknose dace. There was no relationship between an animal's sprinting ability and this type of individual flow selection. Dace from relatively fast

reaches of streams chose significantly slower flow velocities than did fish from relatively slow stream reaches of the same population. Similar flow selection chambers should prove useful for discerning the causal factors for intraspecific variance in flow preference in a multitude of aquatic species, irrespective of confounding factors such as food availability and predator presence.

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