Preliminary Understanding of Complexities in Swimming Performance of Common Minnow (Cyprinidae) Taxa

CRYSTAL NICHOLS, Aquatic Biology and Fisheries Center, Department of Biology, Ball State University, Muncie, IN, USA; AUSTIN SMITH, STEPHEN HUELSMAN, and CARA SCHEMMEL, Wright State University - Lake Campus, Celina, OH, USA; JASON C. DOLL, Quantitative Fisheries Center, Department of Fisheries and Wildlife, Michigan State University, East Lansing, MI, USA; and STEPHEN J. JACQUEMIN[1], Department of Biological Sciences, Wright State University - Lake Campus, Celina, OH, USA.

ABSTRACT. Understanding swimming performance of native freshwater fishes has implications for ecology, conservation, and management. In particular, this type of information has practical importance for improving the understanding of fish dispersal, occurrence, migration, and invasive potential. The objective of this study was to characterize swimming performance of 2 taxa from the comparatively understudied minnow family (Cyprinidae) and test for potential drivers as a function of total length, sex, habitat, morphology, or some combination. The study assessed Spotfin Shiner (*Cyprinella spiloptera;* n = 66) and Bluntnose Minnow (*Pimephales notatus;* n = 24) populations from an ontogenic range of male and female individuals from lentic and lotic habitats in Indiana and Ohio. Akaike information criterion (AIC) model selection identified the most parsimonious linear regression model to predict swimming performance of Spotfin Shiner and Bluntnose Minnow independently. Overall, larger Spotfin Shiners were superior swimmers compared with smaller individuals. In both species, individuals having more streamlined heads and elongated caudal regions were better swimmers. Additionally, Spotfin Shiners that were collected from lotic environments were generally better swimmers than individuals from lentic environments. Models did not recover sex-specific effects in either species—or meaningful total length, or habitat effects, in Bluntnose Minnows. Overall, this study provides evidence of a complex series of swimming performance covariates when assessing or understanding performance. This has implications for aquatic population, assemblage, and community ecology as well as management and conservation efforts.

Publication Date: June 2018 **https://doi.org/10.18061/ojs.v118i2.6117** **OHIO J SCI 118(2):16-24**

INTRODUCTION

Alterations to flow regimes are almost ubiquitous globally (Poff et al. 1997). Dams constitute the most obvious and recognizable form of these alterations; however, while dams do act as barriers at any scale, numbers of dams pale in comparison to often-overlooked flow alterations caused by stream crossings (e.g., culverts; Tchir et al. 2004; Goerig et al. 2016). Estimates place the number of dams in the United States at 90,580 with the number of culverts at over 1.4 million (National Inventory of Dams database 2016; Infrastructure Report Card: Dams 2017; Pess et al. 2005). This alteration of habitat has been linked to changing assemblages, environmental shifts, and species extirpation (Foster and Keller 2011).

Swimming performance may provide additional information for understanding how flow regime alterations affect fish distribution and abundance. Swimming performance is particularly informative when connections between habitats exist but limited movement is documented (Warren and Pardew 1998; Sofia et al. 2006). Swimming performance has been classically described using several terms that categorize the amount of time an individual is able to swim at a given velocity, including sustained (>200 minutes), prolonged (>20 seconds), and burst (<20 seconds) swimming performance (Brett 1964; Beamish 1978). However, the most commonly used metric or protocol is critical swimming speed (U_{crit}), which estimates prolonged swimming performance using an incremental step-wise increase in water velocity until subject exhaustion (Brett 1964). These different ways of assessing swimming performance are specific to life history, and may provide different interpretations of swimming performance depending on the study objective or taxa. For example, Farrell (2008) identified

---

[1] Address correspondence to Dr. Stephen Jacquemin, Department of Biological Sciences, Wright State University – Lake Campus, 7600 Lake Campus Drive, Celina, OH 45822. Email: stephen.jacquemin@wright.edu

higher swimming performance values in taxa when assessing short-term constant acceleration compared with prolonged U_{crit} tests, indicating that U_{crit} is likely conservative to assess maximum speed.

Regardless of whether a study assesses sustained, prolonged, or burst performance, the information gleaned from studies can provide a better understanding of ecology, inform management, and facilitate conservation. However, until recently, the majority of freshwater swimming performance studies have focused on game fish (e.g., salmonids, centrarchids, etc.) compared with non-game fishes as reviewed in Wolter and Arlinghaus (2003). A focus on non-game fishes is necessary as these fishes—most notably small-bodied Cypriniformes and Perciformes—represent the majority of diversity in North American waterways, and occupy essential roles within ecosystems (Page and Burr 2011).

Recent studies have attributed swimming performance variation to family, species, population, total length, body morphology, macro habitat (e.g., lotic, lentic), within-stream habitat (e.g., riffles, pools, substrate), water quality (e.g., temperature, pH, pollutants, turbidity), schooling behaviors, sex, and a multitude of interactions therein (Adams and Parsons 1998; Boyd and Parsons 1998; Adams et al. 2000; Nelson et al. 2003; Scott and Magoulick 2008; Leavy and Bonner 2009; Goertzen et al. 2011; Williamson et al. 2012; Yan et al. 2012; Hildebrandt and Parsons 2016). Despite a recent increase in non-game fish studies, the extensive variability and biodiversity of these small-bodied taxa (greater than 450 species of minnows and darters in North America; Page and Burr 2011) indicates that more research on swimming performance is needed.

The objective of this study was to describe swimming performance of 2 common species of minnow (Cyprinidae): Spotfin Shiner (*Cyprinella spiloptera)* and Bluntnose Minnow (*Pimephales notatus*). This study describes and tests for swimming performance variation to evaluate predictors, including total length, body shape (morphology), habitat type, and sex. The hypothesis was that all of these factors would relate to individual swimming performance—specifically that larger, male, streamlined specimens from lotic habitats would exhibit comparatively higher swimming performance than smaller, female, robust specimens from lentic habitats.

METHODS AND MATERIALS

Fish Collection

Individuals were collected using beach seines from 4 sites (2 river and 2 reservoir localities) during summer 2016 (Indiana DNR Scientific Purposes License No. 16-175, Ohio DNR Scientific Collection Permit No. 18-78). Bluntnose Minnow were collected from reaches along the West Fork White River (n = 20) as well as Prairie Creek Reservoir (n = 11) in Delaware County, Indiana. Spotfin Shiners were collected from reaches along the St. Marys River (n = 26) as well as Grand Lake St. Marys (n = 40) located in Mercer County, Ohio. River sites were similar third-order streams that exhibited good habitat variability in substrate, structure, and flow. Both reservoir sites were similar in relatively shallow lake habitat (sand/silt bottom) with recreational use designations. Both sets of river and reservoir sites exhibit connections between them, but whether gene flow between sites can or does occur has not been tested.

Swimming Performance Assessment

Upon collection, fish were transported in aerated coolers to the laboratory. They were stocked into filtered and aerated aquaria at maximum densities of 1 fish per 2 gallons at a constant room temperature (20 °C). During housing, all approved institutional animal care and use protocols (Ball State University IACUC – AUP No. 935360-2, Wright State University IACUC – AUP No. 1063) were followed. These protocols involved a 12:12-hour light cycle, daily feeding (brine shrimp and commercial flake food), as well as frequent (multiple times per week) water quality testing and partial water changes to ensure appropriate conditions were maintained. No examples of death or stress were witnessed at any point during housing. Fish were held in acclimation tanks for a period of 2 weeks, after which swimming performance trials were undertaken midday during weeks 3 and 4.

Swimming performance testing utilized Blazka (Spotfin Shiners) and Brett (Bluntnose Minnows) style swimming performance chambers, as these were available in close proximity to collection and study locales (species were not run in both types). Chambers employed in this study ensured similar flow using flow straighteners, which produced laminar conditions, and were calibrated using an electromagnetic Marsh-McBirney Flo-Mate™ flowmeter. Flow speeds between 0 cm/s to 150 cm/s were plotted in 5 cm/s increments against DC motor voltage to allow reproducible flows during trials. The testing protocol followed a $^{5/5}U_{crit}$ protocol as outlined in Nelson et al. (2003) and was chosen due to its biological relevance for smaller-bodied fishes and published use. This protocol began with an initial 1-hour acclimation period (which included 30 minutes of flow at 0 cm/s followed by 15-minute periods of 5 cm/s and 10 cm/s flow) followed by an increase of 5 cm/s every 5 minutes until fatigue. Fatigue was defined as the point in time when the fish became impinged on the chamber's back screen for longer than 3 seconds. U_{crit} was calculated by adding the penultimate speed prior to fatigue to the final velocity multiplied by the fraction of time completed successfully in the last velocity step. Fish that did not swim when placed in the chamber were excluded from analyses (this included 7 Bluntnose Minnows). Post trial, fish were euthanized with MS-222 for photography (lateral view with scale, using a Canon® Rebel T3i camera and macro zoom lens), measurement (total length), and determination of sex (dissection to determine gonad type; 30F and 36M Spotfin Shiners, 14F and 10M Bluntnose Minnows). Fish shape was described using 14 landmarks along the margin of the fish (lateral perspective) using geometric morphometric methodologies (Zelditch et al. 2004) implemented in the freely available tps suite of software from SUNY Stony Brook, including tpsUtil (Rohlf 2010), tpsDig (Rohlf 2001), and tpsRelw (Rohlf 2015). Fourteen landmarks were placed along the lateral margin of each individual following Jacquemin and Pyron (2016), including 4 that were used to digitally unbend specimens prior to further analysis (see unbend function in tpsUtil; Rohlf 2010). General Procrustes analysis was used to superimpose and scale digitized individuals to a common reference shape prior to any analyses. Relative warp analysis by species was performed on the aligned landmark points to describe individual morphologies. Resulting axes were interpreted based on percent variation explained and axes which explained the majority of variation were retained for inclusion into swimming performance models (see below). Given the configuration of the model, it was not possible to include all shape axes in the analysis (as is often seen in MANOVA type approaches common in the morphometric literature). Upon completion of the data collection all fish were preserved and archived in the biological museums of Ball State University (Bluntnose Minnows) and Wright State University – Lake Campus (Spotfin Shiners).

Statistical Analysis

The Akaike information criterion (AIC) model selection identified the most parsimonious linear regression model to predict swimming performance of Spotfin Shiner and Bluntnose Minnow independently. Candidate predictors of the model included total length, sex (male or female), habitat (lentic or lotic), significant relative warp axes, and interaction terms of each relative warp axis with sex and habitat. Thus, the full model for each species included 3 predictors plus significant relative warp axes and interactions. Total length was included in all models. The best subset of models were identified as those having a change of less than 2.0 in AIC (adjusted for small sample size; AICc). Model averaging was used to draw conclusions when more than one model was included in the subset. All analyses were performed in the *R Statistical Environment* (R Core Team 2016). Model selection was conducted using the dredge function in the MuMIn package version 1.15.6 (Barton 2016) and model averaging was conducted using the AICcmodavg package version 2.1-0 (Mazerolle 2016).

RESULTS

Spotfin Shiner

A total of 66 Spotfin Shiners, ranging from 27 to 95 mm in total length, were used in swimming performance trials and analysis (Table 1). Morphology was described along 12 axes which explained 98% of the total variation among individuals. This was primarily driven by the first 2 axes which explained a total of 53% of the variation. Relative warp axis 1 described 33% of the variation, separating positively loading individuals (those with comparatively distended abdomens and more robust caudal peduncles) from more negatively loading individuals (exhibiting opposite trends; Fig. 1). Relative warp axis 2 described 20% of the variation, separating positively loading individuals (those with comparatively streamlined heads and reduced caudal peduncle areas) from more negatively loading individuals (exhibiting opposite trends; Fig. 1). Mean swimming performance (U_{crit}; Table 1) across all individuals was 60.8 cm/s (SD = 11.3) and coefficient of variation (CV) was 18.6%. Swimming performance was found to be positively associated with total length (Fig. 2A), relative warp axis 1, and relative warp axis 2 (Fig. 3A and B). There was also a trend towards higher swimming performance for Spotfin Shiners from the lotic environment and males compared to the lentic environment and females (Fig. 3C and D).

Table 1
Spotfin Shiner (*Cyprinella spiloptera)* and Bluntnose Minnow (*Pimephales notatus)* swimming performance U_{crit} summary statistics

Habitat	Sex	N	Swimming performance (cm/s)				Total length range (mm)
			Mean	SD	Minimum	Maximum	
Spotfin Shiner							
Lentic	Female	21	56.8	11.6	36.3	76.1	34-70
Lentic	Male	19	57.1	9.4	36.7	68.3	27-85
Lotic	Female	9	64.1	10.8	44.5	75.4	35-90
Lotic	Male	17	68.3	9.7	52.6	92.2	41-95
Combined		66[a]	60.8[b]	11.3[c]	36.3[d]	92.2[e]	27-95[f]
Bluntnose Minnow							
Lentic	Female	3	58.5	18.9	41.8	79.0	55-60
Lentic	Male	4	73.6	21.5	52.9	101.3	49-65
Lotic	Female	11	62.1	26.1	14.8	92.8	49-83
Lotic	Male	6	59.8	22.1	26.7	91.7	58-80
Combined		24[a]	63.0[b]	22.7[c]	14.8[d]	101.3[e]	49-83[f]

[a] Column total.
[b] Mean across all individuals.
[c] Mean across all SDs in column.
[d] Minimum value in column.
[e] Maximum value in column.
[f] Total range in column.

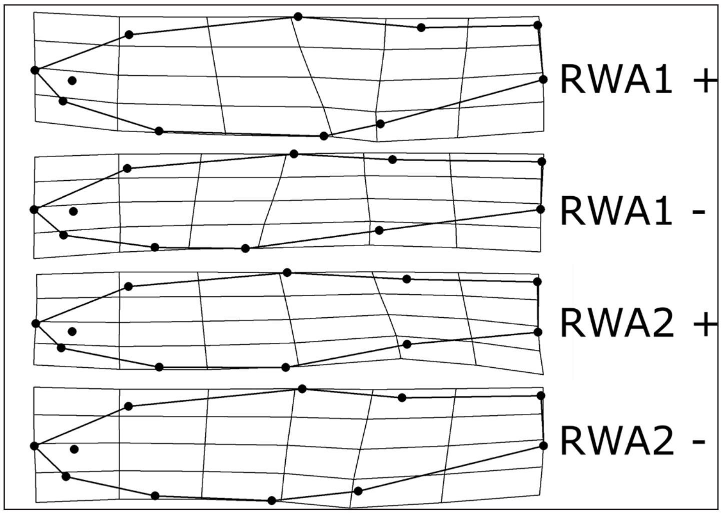

FIGURE 1. Spotfin Shiner (*Cyprinella spiloptera)* deformation grids displaying a gradient of maximum and minimum relative warp axis 1 (RWA1) and relative warp axis 2 (RWA2)

Three models were identified as being supported by the data (Table 2). The best model included only total length and had an Akaike's weight of 0.51, which is interpreted as having a 51% probability of being the best model out of the top models. The second-best model included total length and habitat (Akaike's weight = 0.30) and the third-best model included total length and relative warp axis 1 (Akaike's weight = 0.19). No interaction terms were included in the top models. Model-averaged coefficients indicated that there was an increase in swimming performance as total length increased and relative warp axis 1 increased (i.e., larger individuals with a more distended abdomen and more robust caudal peduncle exhibited better swimming performance; Table 3). Additionally, fish from the lotic system had a higher swimming performance value compared to lentic fish (Table 3).

Bluntnose Minnow

A total of 24 Bluntnose Minnows, ranging from 49 to 83 mm in total length, were used in swimming performance trials and analysis (Table 1). Morphology was described along 10 axes which explained 98% of the total variation among individuals. This was primarily driven by the first 2 axes which explained a total of 55% of the variation. Relative warp axis 1 described 37% of the variation, separating positively loading individuals (those with comparatively reduced caudal peduncles and slightly distended midsections) from more negatively loading individuals (exhibiting opposite trends; Fig. 4). Relative warp axis 2 described 18% of the variation, separating positively loading individuals (those with comparatively streamlined heads and forward arching dorsal surfaces) from more

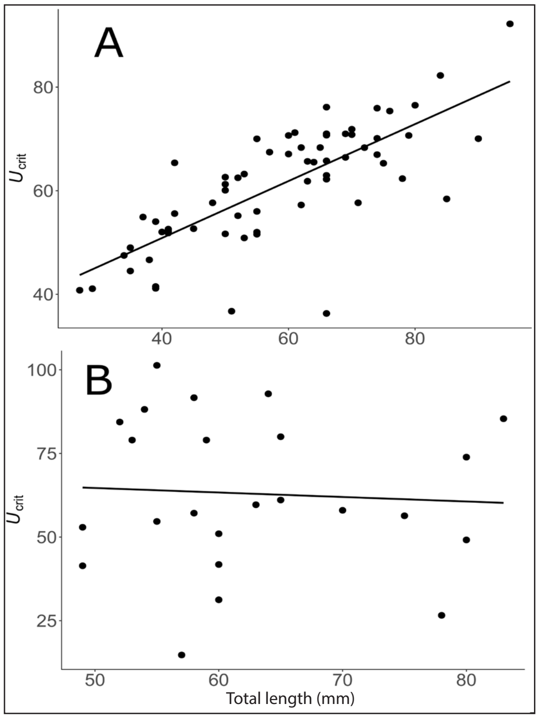

FIGURE 2. Relationship between swimming performance and total length of Spotfin Shiner (*Cyprinella spiloptera;* A) and Bluntnose Minnow (*Pimephales notatus*; B). Solid circles represent individual fish and solid lines represent best fit linear regression.

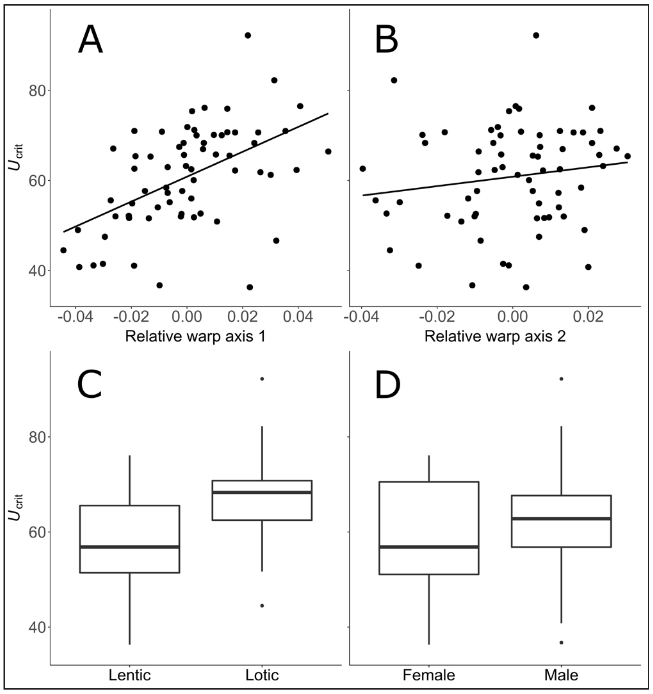

FIGURE 3. Relationship between swimming performance of Spotfin Shiner (*Cyprinella spiloptera)* with morphometric axes (A, B), habitat (C), and sex (D). Solid circles represent individual fish, solid lines represent best fit linear regression line. Modified boxplots include median, 25th and 75th percentiles, whiskers extend to the upper and lower non-outlier, and points are outliers calculated as 1.5 × inter-quartile range.

Table 2

Results of top AICc models (change of <2) for Spotfin Shiner (*Cyprinella spiloptera)* and Bluntnose Minnow (*Pimephales notatus)*

Model	Number of parameters	ΔAICc	AICc weight
Spotfin Shiner			
Total length	3	0.00	0.51
Total length, habitat	4	1.05	0.30
Total length, relative warp axis 1	4	1.97	0.19
Bluntnose Minnow			
Total length	3	0.00	0.53
Total length, relative warp axis 2	4	0.28	0.47

Table 3
Model-averaged coefficients (full average) for the most parsimonious models (see Table 2) predicting swimming performance of Spotfin Shiner (*Cyprinella spiloptera)* and Bluntnose Minnow (*Pimephales notatus)*

Spotfin Shiner			Bluntnose Minnow		
Effect	**Estimate**	**Standard error**	**Effect**	**Estimate**	**Standard error**
Intercept	29.471	3.859	Intercept	72.954	29.978
Total length	0.535	0.067	Total length	-0.159	0.473
Relative warp axis 1	5.850	27.673	Relative warp axis 2	208.804	298.312
Habitat (lotic)	0.688	1.563			

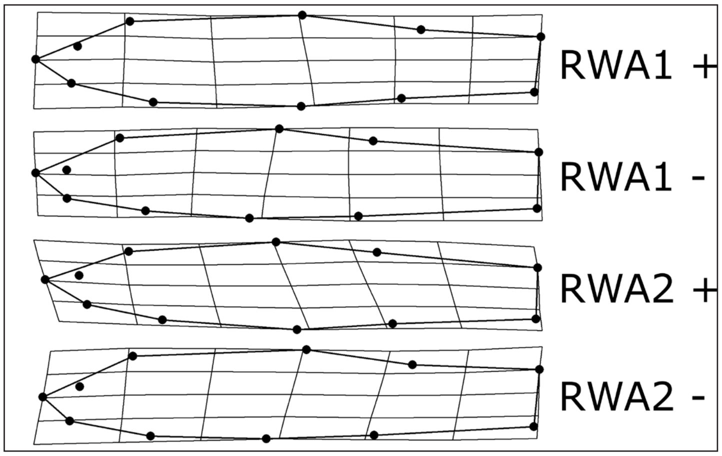

FIGURE 4. Bluntnose Minnow (*Pimephales notatus)* deformation grids displaying a gradient of maximum and minimum relative warp axis 1 (RWA1) and relative warp axis 2 (RWA2)

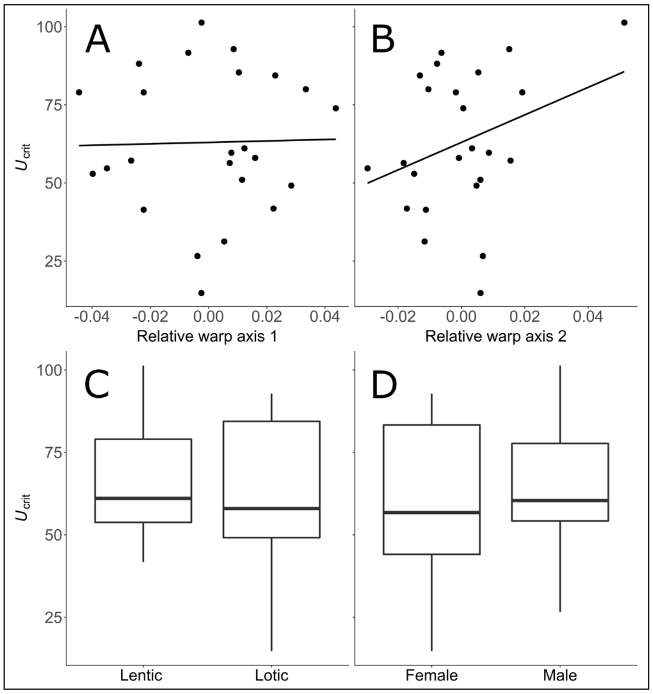

FIGURE 5. Relationship between swimming performance of Bluntnose Minnow (*Pimephales notatus)* with morphometric axes (A, B), habitat (C), and sex (D). Solid circles represent individual fish, solid lines represent best fit linear regression line. Modified boxplots include median, 25th and 75th percentiles, whiskers extend to the upper and lower non-outlier, and points are outliers calculated as 1.5 × inter-quartile range.

negatively loading individuals (exhibiting opposite trends; Fig. 4). Mean swimming performance (U_{crit}; Table 1) across all Bluntnose Minnows was 63.0 cm/s (SD = 22.7) and CV was 36.0%. There was not a strong relationship between swimming performance and total length (Fig. 2B). Swimming performance was found to be positively associated with relative warp axis 2 only (Fig. 5A and B) as no associations were noted with relative warp axis 1 or between lentic and lotic environments or females and males (Fig. 5C and D).

Two models were identified as being equally plausible (Table 2). The best model included only total length and had an Akaike's weight of 0.53. The second best model included total length plus the additional predictor of relative warp axis 2. These models suggest swimming performance increased as total length decreased (although only marginally; Fig. 2B) and relative warp axis 2 increased (Table 3 and Fig 5B). That is, swimming performance was found to be lower among individuals with a more robust head and body and smaller caudal shape. Total length results here are not concordant with exploratory analysis, where a strong relationship was not found. This suggests that the most plausible models to describe observed trends in Bluntnose Minnow swimming performance are not a good description of the observed data and that total length is only marginal in this study.

DISCUSSION

This study provides evidence that (1) swimming performance of Spotfin Shiners could be explained by total length, morphology, and habitat; but (2) the only larger trend observed in Bluntnose Minnows related to morphology. Spotfin Shiners and Bluntnose Minnows both exhibited higher swimming performance when morphologically streamlined in the head region and extended/increased surface area in the caudal region. In addition, Spotfin Shiners from lotic habitats were better swimmers than those from lentic sites; habitat had no effect on Bluntnose Minnows in this study. Larger Spotfin Shiners exhibited higher U_{crit} values; however, no biologically-relevant total length pattern was observed in Bluntnose Minnows. Finally, males of both taxa exhibited slightly higher mean U_{crit} values compared to females, but none of the models included these sex-specific effects. Overall, this indicates variation in swimming performance of cyprinid taxa may be different among species, complicating a single interpretation for smaller-bodied Cyprinidae when managing flow alterations.

Similar results were expected across both taxa. Ultimately, the relationships between swimming performance, morphology, total length, and habitat were consistent with the hypotheses in Spotfin Shiners, but the lack of effects detected in Bluntnose Minnows was surprising. The comparative lack of effects in Bluntnose Minnows could be due to greater variability in swimming performance. The team found the coefficient of variation in swimming performance of Bluntnose Minnow to be twice that of Spotfin Shiner. The large variability in Bluntnose Minnow swimming performance suggests a larger sample size would be needed to identify trends. However, other studies have documented lower variability in swimming performance in other species using similar sample sizes. For example, Nelson et al. (2003) conducted 2 swimming performance trials on 14 Blacknose Dace (*Rhinichthys atratulus*) and found a CV of 27.7% and 19.8%. Thus, future work on swimming performance of Bluntnose Minnows and other Cyprinidae should consider the variability observed in this study when designing experiments.

Importantly, these observations provide additional links between morphology and swimming performance among both species, and are consistent with laboratory experiments on other taxa that have shown particular shapes (mainly related to fusiformity) to exhibit increased swimming performance (Qu et al. 2013; Bell and Jacquemin 2017). In the field, morphological differences among individuals of the same or similar cyprinid species have been linked to specific macro and micro habitats (i.e., flow regime) and are often discussed in relation to swimming abilities or selection. For example, Hass et al. (2010) found Blacktail Shiners (*Cyprinella venusta*) to be more compressed and deeper bodied in lentic compared to lotic environments as a result of selective pressures. Similarly, Jacquemin et al. (2013) found that Bluntnose Minnows from high-velocity stream sites were comparatively more fusiform than those from streams with lower velocities.

Linking the field and laboratory, other cyprinid studies have found that species such as Blacknose Dace exhibit swimming performance values that covary with current velocity and basin (Nelson et al. 2003). Thus, abiotic conditions (e.g., flow) are often attributed as the major influence on swimming performance through the morphological connection.

Additional studies should be conducted with these taxa, as the conclusions point to a complex suite of swimming performance covariates. Known limitations of this study are that it only included 2 populations of each species, did not incorporate schooling behavior, did not test for water quality parameter effects, and did not consider assemblage makeup from collection sites (Bergstrom 2002; Gvozdik and Smolinsky 2015). Future work should include analysis of additional parameters, plus sample collection from larger geographic ranges and more diverse biological settings, to provide a more complete depiction of swimming performance in Cyprinidae. Ultimately, understanding whether swimming performance is plastic, and to what degree, would be useful in managing small non-game fish populations. Although it would not necessarily be expected that a single explanation could unilaterally apply to an entire family, it would be reasonable to have some degree of overlap among the variation between taxa and even population levels. Given the general links between total length and swimming performance across North American fishes, the smaller-bodied fishes of Cyprinidae may be among the most susceptible to alterations in flow regimes from the flow obstructions in North America (Poff et al. 1997; Tchir et al. 2004; Goerig et al. 2016). These study conclusions have far-reaching implications for management and conservation of resources, as documenting swimming performance is essential to understanding dispersal, occurrence, and persistence (Peake et al. 1997).

ACKNOWLEDGEMENTS

The authors thank the Ohio Sea Grant College Program, The Ohio State University, that provided partial funding for this project (Grant No. 60055609: R/ER-119-PD). The authors also acknowledge Lauren Fuelling (Wright State University – Lake Campus, science lab technician) and Kaleb Eden (Ball State University, undergraduate lab technician) for assistance in the field and/or laboratory. Thanks to the Ball State University Environmental Sciences Program for providing the Brett style swimming performance chamber and a special thanks to the Wright State University – Lake Campus Engineering Program for designing and building the Blazka style swimming performance chamber used in this project.

LITERATURE CITED

Adams SR, Hoover JJ, Killgore KJ. 2000. Swimming performance of the Topeka Shiner (*Notropis topeka*) an endangered midwestern minnow. Am Midl Nat. 144(1):178-186. https://doi.org/10.1674/0003-0031(2000)144[0178:SPOTTS]2.0.CO;2

Adams SR, Parsons GR. 1998. Laboratory-based measurements of swimming performance and related metabolic rates of field-sampled Smallmouth Buffalo (*Ictiobus bubalus*): a study of seasonal changes. Physiol Zool. 71(4):350-358. https://doi.org/10.1086/515419

Barton K. 2016. MuMIn: Multi-Model Inference. R package version 1.15.6. [accessed 2017 Dec 1]. https://CRAN.R-project.org/package=MuMIn

Beamish FWH. 1978. Swimming capacity. In: Hoar WS, Randall DJ, editors. Fish Physiology. Vol. 7. New York (NY), London (UK): Academic Press. p. 101–187. https://doi.org/10.1016/S1546-5098(08)60164-8

Bell AJ Jr, Jacquemin SJ. 2017. Evidence of morphological and functional variation among Bluegill *Lepomis macrochirus* populations across Grand Lake St. Mary's watershed area. J Freshw Ecol. 32(1):415-432. https://doi.org/10.1080/02705060.2017.1319429

Bergstrom CA. 2002. Fast-start swimming performance and reduction in lateral plate number in Threespine Stickleback. Can J Zool. 80(2):207-213. https://doi.org/10.1139/z01-226

Boyd GL, Parsons GR. 1998. Swimming performance and behavior of Golden Shiner, *Notemigonus crysoleucas*, while schooling. Copeia. 1998(2):467-471. https://doi.org/10.2307/1447443

Brett JR. 1964. The respiratory metabolism and swimming performance of young Sockeye Salmon. J Fish Res Board Can. 21(5):1183–1226. https://doi.org/10.1139/f64-103

Farrell AP. 2008. Comparisons of swimming performance in Rainbow Trout using constant acceleration and critical swimming speed tests. J Fish Biol. 72(3):693-710. https://doi.org/10.1111/j.1095-8649.2007.01759.x

Foster HR, Keller TA. 2011. Flow in culverts as a potential mechanism of stream fragmentation for native and nonindigenous crayfish species. J N Am Benthol Soc. 30(4):1129-1137. https://doi.org/10.1899/10-096.1

Goerig E, Castro-Santos T, Bergeron NE. 2016. Brook Trout passage performance through culverts. Can J Fish Aquat Sci. 73(1):94-104. https://doi.org/10.1139/cjfas-2015-0089

Goertzen MM, Driessnack MK, Janz DM, Weber LP. 2011. Swimming performance and energy homeostasis in juvenile laboratory raised Fathead Minnow (*Pimephales promelas*) exposed to uranium mill effluent. Comp Biochem Physiol C. 154(4):420–426. https://doi.org/10.1016/j.cbpc.2011.07.012

Gvozdik L, Smolinksy R. 2015. Body size, swimming speed, or thermal sensitivity? Predator-imposed selection on amphibian larvae. BMC Evolutionary Biology. 15:238. https://doi.org/10.1186/s12862-015-0522-y

Haas TC, Blum MJ, Heins DC. 2010. Morphological responses of a stream fish to water impoundment. Biol Lett. 6(6):803-806. https://doi.org/10.1098/rsbl.2010.0401

Hildebrandt EK, Parsons GR. 2016. Effect of turbidity on the swimming performance of the Golden Shiner, *Notemigonus crysoleucas*. Copeia. 104(3):752-755. https://doi.org/10.1643/CI-14-149

Infrastructure Report Card: Dams. 2017. Reston (VA): American Society of Civil Engineers. [updated 2017; accessed 2018 June 6]. https://www.infrastructurereportcard.org/cat-item/dams/

Jacquemin SJ, Martin E, Pyron M. 2013. Morphology of Bluntnose Minnow *Pimephales notatus* (Cyprinidae) covaries with habitat in a central Indiana watershed. Am Midl Nat. 169(1):137-146. https://doi.org/10.1674/0003-0031-169.1.137

Jacquemin SJ, Pyron M. 2016. A century of morphological variation in Cyprinidae fishes. BMC Ecology. 16:48. https://doi.org/10.1186/s12898-016-0104-x

Leavy TR, Bonner TH. 2009. Relationships among swimming ability, current velocity association, and morphology for freshwater lotic fishes. North Am J Fish Manage. 29(1):72–83. https://doi.org/10.1577/M07-040.1

Mazerolle MJ. 2016. AICcmodavg: Model selection and multimodel inference based on (Q)AIC(c). R package version 2.1-0. [accessed 2017 Dec 1]. https://cran.r-project.org/package=AICcmodavg

National Inventory of Dams database. 2016. Washington (DC): US Army Corps of Engineers. [updated 2016; accessed 2018 June 6]. http://nid.usace.army.mil/cm_apex/f?p=838:12

Nelson JA, Gotwalt PS, Snodgrass JW. 2003. Swimming performance of Blacknose Dace (*Rhinichthys atratulus*) mirrors home-stream current velocity. Can J Fish Aquat Sci. 60(3):301-308. https://doi.org/10.1139/f03-023

Page LM, Burr BM. 2011. Peterson field guide to freshwater fishes, 2nd ed. Boston (MA): Houghton Mifflin Harcourt. 688 p.

Peake SJ, McKinley RS, Scruton DA. 1997. Swimming performance of various freshwater Newfoundland salmonids relative to habitat selection and fishway design. J Fish Biol. 51(4):710–723. https://doi.org/10.1111/j.1095-8649.1997.tb01993.x

Pess G, Morley S, Roni P. 2005. Evaluating fish response to culvert replacement and other methods for reconnecting isolated aquatic habitats. In: Roni P, editor. Monitoring stream and watershed restoration. Bethesda (MD): American Fisheries Society. p. 267-276.

Poff NL, Allan JD, Bain MB, Karr JR, Prestegaard KL, Richter BD, Sparks RE, Stromberg JC. 1997. The natural flow regime. BioScience. 47(11):769-784. https://doi.org/10.2307/1313099

Qu Y, Duan M, Yan J, Feng G, Liu J, Zhang L, Zhuang P. 2013. Effects of lateral morphology on swimming performance in two sturgeon species. J Appl Ichthyol. 29(2):310–315. https://doi.org/10.1111/jai.12131

R Core Team. 2016. R: A language and environment for statistical computing. Version 3.3.2. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/

Rohlf FJ. 2001. tpsDig–thin plate spline digitizer, version 2.11. New York (NY): Stony Brook University, Stony Brook.

Rohlf FJ. 2010. tpsUtil – thin plate spline utility program, version 1.46. New York (NY): Stony Brook University, Stony Brook.

Rohlf FJ. 2015. tpsRelw–relative warp analysis, version 1.67. New York (NY): Stony Brook University, Stony Brook.

Scott MK, Magoulick DD. 2008. Swimming performance of five warmwater stream fish species. Trans Am Fish Soc. 137(1):209–215. https://doi.org/10.1577/T06-278.1

Sofia SH, Silva CRM, Galindo BA, Almeida FS, Sodre LMK, Martinez CBR. 2006. Population genetic structure of *Astyanax scabripinnis* (Teleostei, Characidae) from an urban stream. Hydrobiologia. 553(1):245-254. https://doi.org/10.1007/s10750-005-1106-4

Tchir JP, Hvenegaard PJ, Scrimgeour GJ. 2004. Stream crossing inventories in the Swan and Notikewin River basins of northwest Alberta: resolution at the watershed scale. In: Scrimgeour GJ, Eisler G, McCulloch B, Silins U, Monita M, editors. Proceedings of the Forest Land-Fish Conference II. Edmonton (Canada): Alberta Conservation Association. p. 53-62.

Warren ML Jr., Pardew MG. 1998. Road crossings as barriers to small-stream fish movement. Trans Am Fish Soc. 127(4):637-644. https://doi.org/10.1577/1548-8659(1998)127<0637:RCABTS>2.0.CO;2

Williamson NE, Cech JJ Jr., Nelson JA. 2012. Flow preferences of individual Blacknose Dace (*Rhinichthys atratulus*); influence of swimming ability and environmental history. Environ Biol Fish. 95(3):407-414. https://doi.org/10.1007/s10641-012-0014-5

Wolter C, Arlinghaus R. 2003. Navigation impacts on freshwater fish assemblages: the ecological relevance of swimming performance. Rev Fish Biol Fisher. 13(1):63–89. https://doi.org/10.1023/A:1026350223459

Yan GJ, He XK, Cao ZD, Fu SJ. 2012. The trade-off between steady and unsteady swimming performance in six cyprinids at two temperatures. J Therm Biol. 37(6):424-431. https://doi.org/10.1016/j.jtherbio.2012.04.006

Zelditch ML, Swiderski DL, Sheets HD, Fink WL. 2004. Geometric morphometrics for biologists: a primer. Cambridge (MA): Elsevier Academic Press. 443 p. https://doi.org/10.1016/B978-0-12-778460-1.X5000-5