

MORPHOLOGY AND ITS EFFECT ON HABITAT SELECTION OF STREAM FISHES

Kevin A. Gaston, Jaclyn A. Eft and Thomas E. Lauer: Department of Biology, Ball State University, Muncie, IN 47306, USA

ABSTRACT. Fishes were sampled in the Mississinewa, Salamonie, Wabash, and White rivers, Indiana to determine whether fish depth ratio (maximum depth/total length) varied between pool and riffle habitats. Fish collections were made using a backpack electrofisher and water velocity measurements were made using a flow meter. Our results indicated median depth ratio differed between fishes located in pool habitats (0.28) compared to fishes in riffle habitats (0.17). These depth ratio findings were consistent among all four rivers, showing fish morphology is related to habitat selection and use. Changes in fish community structure would be expected with habitat changes in flow regimes, either through natural or anthropogenic (e.g., channelization) alterations.

Keywords: Depth ratio, Indiana, riffle, pool

Body morphology for aquatic animals is largely a response to the environmental pressures derived from the medium in which these organisms live (i.e., water; Knouft 2003; Moyle & Cech 2004; Pflieger 2004). The generalized fusiform shape typically found in fishes and other aquatic animals (e.g., mammals, birds) is a convergent evolutionary response to the density of water and the organism's strategies to move through it (Winemiller 1992; Moyle & Cech 2004). Differences in morphology not only influence the organism's ability to maneuver and accelerate, but also the energetics associated with swimming (Webb 1984; Boily & Magnan 2002). For example, sunfish (Centrarchidae) generally have a high depth ratio and truncated form which allows for a smaller turning radius, thereby enhancing maneuverability (Domenici 2003; Blake 2004).

Many fishes have generalist body plans which perform well in the functions of acceleration, cruising, and maneuvering (Webb 1984). However, some fishes may perform better in one of these functions resultant from a unique and distinctive body plan. Northern pike have an elongated and highly muscled body which promotes quick bursts of speed (Webb 1984), an attribute desirable for this ambush predator. However, an enhanced ability in one area typically creates a body plan that restricts the

other two functions, as is the case for northern pike. These types of variations in body morphology promote diversity within communities, as individual species are able to select and use the most appropriate habitats within ecosystems that best suit their morphologies.

Stream fishes exhibit several different morphologies (Winemiller 1992; Matthews 1998; Moyle & Cech 2004; Pflieger 2004), which appear to be directly or indirectly related to changing water velocities (Ross 1986). Deep-bodied or truncated fishes are categorized by a body depth that is approximately one third their standard lengths, usually giving them a laterally flattened shape (e.g., *Lepomis* spp., family Centrarchidae). This flattened body shape allows these fishes to maneuver among the plants and other physical structures that are used for feeding and protection from predators (Werner 1977a; Moyle & Cech 2004; Pflieger 2004). However, this morphology limits quick acceleration and is not energy efficient while cruising or maintaining position in flowing waters (Webb 1984; Moyle & Cech 2004). Alternate fish morphologies have evolved in fishes that occupy other niches, and include bottom clingers (sculpins, *Cottus* spp. and darters, *Etheostoma* spp.), where flattened or sloping heads minimizes energy usage and allows the fish to remain in close proximity to the bottom while moving through the water or remaining stationary in flowing water (Matthews 1985; Webb 1989; Webb et al.

Correspondence: Thomas E. Lauer, e-mail: tlauer@bsu.edu, Fax: 765-285-8804, TX: 765-285-8825.

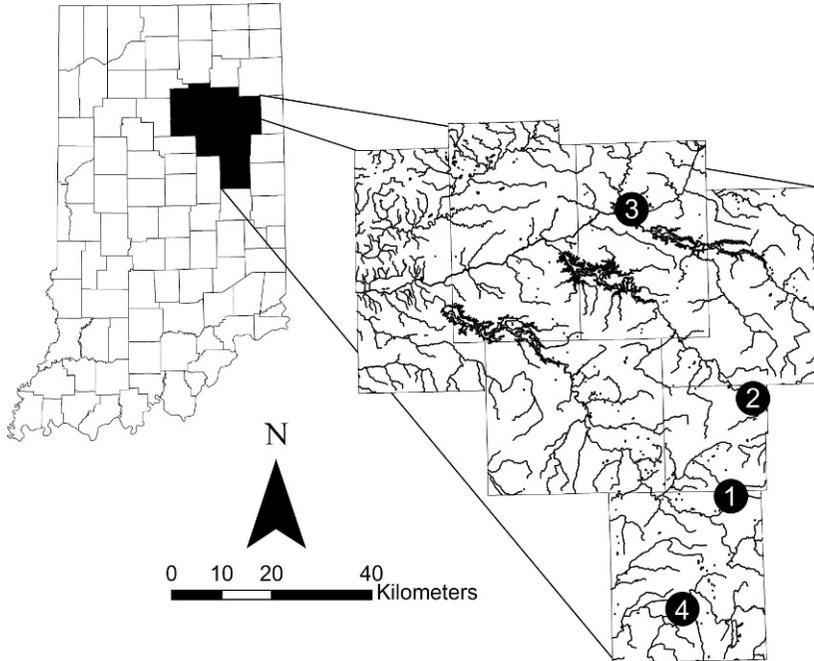


Figure 1.—Location of the study sites sampled for fishes located on the Mississinewa (1), Salamonie (2), Wabash (3), and White (4) rivers, Indiana, during 2009 and 2010.

1996; Moyle & Cech 2004). More streamline fish have elongated caudle peduncles. This design improves the fish's ability to sustain swimming for longer periods of time and minimizes energy lost due to recoiling (McLaughlin & Noakes 1998; Brinsmead & Fox 2002). Further, the streamlined or fusiform body found in black bass species (*Micropterus* spp.) allows for constant movement through water in search of their prey (Webb 1984; Matthews 1998; Moyle & Cech 2004; Pflieger 2004). Collectively, these findings suggest not only that body morphology in fishes relates to the type of habitat where these animals are found, but also provides clues to the theory of niche partitioning in fish communities (Schlosser 1982; Douglas 1987).

The objective of this study was to determine whether fish morphology, specifically depth ratio, is related to habitat selection in Midwestern riverine fishes. We hypothesized fishes located in high water velocity habitats, hereafter referred to as riffles, would have a more streamlined body morphology (high depth ratio) in response to the moving water; whereas, fishes found in low water velocity

habitats, here after referred to as pools, would have a body plan that promotes maneuverability (low depth ratio).

METHODS

Field sampling.—Fish were collected in the Mississinewa, Salamonie, Wabash, and White rivers (Fig. 1) in eastern Indiana between late July to September 2009 and late July 2010 to early October 2010 when river discharges were at or below median values based on U.S. Geological Survey reporting stations (<http://waterdata.usgs.gov/in/nwis/rt>, accessed January 31, 2012). River segments for sampling were selected based on accessibility, but were anecdotally deemed typical of the watercourse. Each segment was required to contain at least one pool and riffle section and was between 100 to 300 m long. Pool and riffle lengths within the sampled segment ranged from 2 to 6 m long and within some segments, multiple pool or riffle areas were sampled.

At each station, we used a Smith-Root Model LR-24 backpack electrofisher to obtain a target sample of 100 fishes taken from both riffles (high velocity) and pools (low velocity). High velocity depths were < 0.25 m, while low

velocity depths were generally > 0.5 m and < 1.5 m. Sampling efficiency (bias) is associated with electrofishing collection gear (Reynolds 1996); but based on our observed catch, we did not feel this materially altered our conclusions, as we were able to sample to the bottom of the stream bed in all habitats. Fish were anesthetized following collection using carbon dioxide, identified to species, measured (total length (mm) using a fish measuring board and maximum depth (mm) using a digital caliper at the maximum depth of the fish) and returned to the water following recuperation. Collection and handling protocol followed Animal Care and Use Committee of Ball State University guidelines.

Water velocity (m/s) was measured using a Global Flow FP101 flow meter in each pool or riffle where fish were collected, with mean (SE) station velocities of pools and riffles for each stream subsequently calculated. Multiple measurements within each station described the variation inherent in velocity and to better define habitat heterogeneity distinguishing pools and riffles.

Data analysis.—Depth ratios were calculated by dividing each fish's maximum depth by its total length. Within each river, we compared depth ratios of fishes found in the pool with those found in the riffle regardless of species distinction. For those species found in both habitats, fish were partitioned proportionally in the analysis. For example, 50 bluegill were collected in the pools at the White River site and included in the pool depth ratio calculations, while two were collected in riffles and included in those respective calculations. Pool and riffle habitat depth ratio comparisons were made (after weighting by abundance) using a non-parametric Mann-Whitney test, as all river data sets did not meet normality assumptions. We adjusted α to 0.0127 using a Bonferroni correction to account for the multiple pairs of data ($N = 4$) in the analysis, effectively using an $\alpha = 0.05$.

RESULTS AND DISCUSSION

A total of 1,461 fishes comprising 46 fish species was collected from the four rivers (Table 1). Twelve species were collected only in pools and included black bullhead, black crappie, blackstripe topminnow, brown bullhead, flathead catfish, gizzard shad, orange-spotted sunfish, pumpkinseed, quillback, red-

ear sunfish, spotted sucker, and white sucker. Eleven species were collected only in riffles and included brook silverside, channel catfish, emerald shiner, mottled sculpin, rainbow darter, redbfin shiner, river carpsucker, shorthead redhorse, smallmouth buffalo, stonecat, and walleye. Twenty-three species were collected in both pools and riffles; however, these species were predominately found in only one habitat. The most common fishes found in pools were bluegill (77%), green sunfish (94%), and rock bass (93%); whereas, in the riffles, central stoneroller (90%), greenside darter (96%), and northern hog sucker (77%) were most common.

Individual species median depth ratios ranged from 0.10 to 0.37, with pools (0.10 to 0.37) and riffles (0.12 to 0.35) showing similar ranges (Table 1). No attempt was made to exclude fishes based on allometric growth changes within a species. The smallest depth ratio of all fish collected came from flathead catfish (0.10), while the largest depth ratio came from redear sunfish (0.37). When combining all fishes in their respective pool or riffle habitats and weighted by abundance, median depth ratios of fishes in pools at individual stations ranged from 0.24 to 0.30, and for riffles 0.13 to 0.18 (Table 2). Depth ratios comparing riffle and pool fishes were significantly different at each of the four river stations, and for all stations and fishes combined (Table 2). Median depth ratios for fishes in pools were approximately 65% greater than those fishes found in riffles.

Mean flow showed water velocities varied between pools and riffles (Table 3). Pools sampled in the four rivers had a mean velocity at or near 0 m/s. Riffle velocities ranged from 0.31 to 1.84 m/s, with three of the river sites > 1.23 m/s.

Our study demonstrated that water flow (velocity) influenced fish habitat selection in the Mississinewa, Salamonie, Wabash, and White rivers in Indiana. Specifically, we demonstrated that pool habitats are characterized by greater numbers of fish with a low depth ratio; whereas, riffle habitats are characterized by greater numbers of fishes with a high depth ratio are more typically found in riffle areas. Presumably, these differences can be attributed at least in part to hydrodynamics as shown by Boily & Magnan (2002). Our findings are not unexpected, as morphological features such as fins and body form, and standard length have

Table 1.—Fish species abundance and their median depth ratios found in pool and riffle fishes located on the Mississinewa, Salamonie, Wabash, and White rivers, Indiana, during 2009 and 2010.

Species	Mississinewa		Salamonie		Wabash		White		Median depth ratio
	Pool	Riffle	Pool	Riffle	Pool	Riffle	Pool	Riffle	
Black bullhead (<i>Ameiurus melas</i>)					1				0.19
Black crappie (<i>Pomoxis nigromaculatus</i>)							2		0.32
Blackside darter (<i>Percina maculata</i>)			1					1	0.15
Blackstripe topminnow (<i>Fundulus notatus</i>)							1		0.13
Bluegill (<i>Lepomis macrochirus</i>)	3	4	4	1	12	14	50	2	0.33
Bluntnose minnow (<i>Pimephales notatus</i>)	12	4	2	20	6	2	46	8	0.17
Brindled madtom (<i>Noturus miurus</i>)	2					2			0.13
Brook silverside (<i>Labidesthes sicculus</i>)								1	0.12
Brown bullhead (<i>Ameiurus nebulosus</i>)			3						0.13
Central stoneroller (<i>Camptostoma anomalum</i>)		9		10		39	11	47	0.17
Channel catfish (<i>Ictalurus punctatus</i>)						1			0.13
Common carp (<i>Cyprinus carpio</i>)	1			1	2	2			0.22
Common shiner (<i>Luxilus cornutus</i>)	3	16	1	9		1		1	0.14
Creek chub (<i>Semotilus atromaculatus</i>)				3	1	1		4	0.17
Emerald shiner (<i>Notropis atherinoides</i>)		1		4		6		2	0.14
Flathead catfish (<i>Pylodictis olivaris</i>)	1								0.10
Freshwater drum (<i>Aplodinotus grunniens</i>)	1				2	5			0.23
Gizzard shad (<i>Dorosoma cepedianum</i>)	1				3				0.28
Golden redhorse (<i>Moxostoma erythrurum</i>)	38			1	1	2	22	3	0.17
Green sunfish (<i>Lepomis cyanellus</i>)	29	1	145		37	17	68		0.29
Greenside darter (<i>Etheostoma blennioides</i>)		4	1	15		9	7	139	0.17
Johnny darter (<i>Etheostoma nigrum</i>)				12		3	4		0.13
Largemouth bass (<i>Micropterus salmoides</i>)					12	6			0.21
Logperch (<i>Percina caprodes</i>)			2			1		4	0.14
Longear sunfish (<i>Lepomis megalotis</i>)	12		2		5	3	18		0.35
Mottled sculpin (<i>Cottus bairdii</i>)								7	0.17
Northern hog sucker (<i>Hypentelium nigricans</i>)	4	7	3	4	2	17	10	37	0.16
Orangespotted sunfish (<i>Lepomis humilis</i>)			6						0.27
Orangethroat darter (<i>Etheostoma spectabile</i>)		1		2		2	4	12	0.20
Pumpkinseed (<i>Lepomis gibbosus</i>)			9				11		0.33
Quilback (<i>Carpionodes cyprinus</i>)							1		0.26
Rainbow darter (<i>Etheostoma caeruleum</i>)		3		5		2		35	0.21
Redear sunfish (<i>Lepomis microlophus</i>)							2		0.37
Redfin shiner (<i>Lythrurus umbratilis</i>)								1	0.18
River carpsucker (<i>Carpionodes carpio</i>)						2			0.25
Rock bass (<i>Ambloplites rupestris</i>)	21	3	1		4	2	75	3	0.32
Sand shiner (<i>Notropis stramineus</i>)							1	2	0.18
Shorthead redhorse (<i>Moxostoma macrolepidotum</i>)						7			0.20
Smallmouth bass (<i>Micropterus dolomieu</i>)	4						49	37	0.23
Smallmouth buffalo (<i>Ictiobus bubalus</i>)						2			0.27
Spotfin shiner (<i>Cyprinella spiloptera</i>)							4	16	0.19
Spotted sucker (<i>Minytrema melanops</i>)	3								0.17
Stonecat (<i>Noturus flavus</i>)								11	0.14
Walleye (<i>Sander vitreus</i>)						1			0.15
White sucker (<i>Catostomus commersonii</i>)							2		0.18
Yellow bullhead (<i>Ameiurus natalis</i>)			2				6	1	0.18

Table 2.—Mann-Whitney test results comparing median depth ratios for fishes taken from pools and riffles located on the Mississinewa, Salamonie, Wabash, and White rivers, Indiana, during 2009 and 2010.

River	<i>N</i>		Median depth ratio		<i>P</i>
	Riffle	Pool	Riffle	Pool	
Mississinewa	53	135	0.13	0.24	< 0.01
Salamonie	88	184	0.14	0.28	< 0.01
Wabash	149	88	0.16	0.29	< 0.01
White	378	419	0.18	0.30	< 0.01
All fish combined	668	826	0.17	0.28	< 0.01

been shown to influence fish location in lakes or rivers (Ehlinger & Wilson 1988; Douglas & Matthews 1992) or habitat selection (Hoagstrom & Berry 2007).

Our sampling indicated that several individual species did not show absolute pool or riffle fidelity. These fishes included some with intermediate depth ratios (e.g., largemouth bass) that might readily move back and forth between habitats, occasionally using one habitat while moving to another showing some degree of niche overlap (Gatz 1979; Ehlinger & Wilson 1988). In addition, some fishes in high abundance may be found in both habitats, as some of the pool-riffle borders were in near proximity. In these latter cases, fish (e.g., green sunfish) were predominately found in one habitat type, expressing a preference.

A deeper bodied fish is comparatively more maneuverable than more streamlined fishes, yet it exerts more energy due to the increased amount of drag while moving in or through fast moving water when compared to slow moving water (Webb 1984; Matthews 1998). For example, bluegill hovered in slow velocity water while foraging for food (Ehlinger & Wilson 1988) moving only its pectoral fins in order to maintain position (Werner 1977a). This feeding strategy alone may suggest why 77% of the bluegill we sampled were found in pool habitats. In contrast, a more streamlined fish, e.g., blackside darters, rainbow darters, and

mottled sculpin in this study, use comparatively little energy while maintaining their position in flowing waters (Webb et al. 1996; Matthews 1998). Collectively, our findings suggest morphology is a driving factor influencing fish habitat selection and use, and agree with Page & Swofford (1984).

Our finding showing fish segregation into pool and riffle habitats is consistent with the theory of niche selection and niche partitioning within a community. Gatz (1979) and Werner (1977b) demonstrated that fishes are not randomly distributed in streams. Rather, fish are often habitat specialists and prefer to live within well-defined niche dimensions (Bain et al. 1998). Although we have only evaluated a single dimension of the stream habitat (i.e., water velocity), other physical habitat characteristics associated with velocity may additionally influence niche selection (Bain et al. 1988). Centrarchids are nest builders and can create spawning areas with fine substrates typically associated with slower moving waters, while darters are lithophilic spawners and need coarse habitat material often found in faster waters to reproduce (Stuber et al. 1982a, 1982b; Aadland 1993). Hence, velocity itself may not be acting on fish selection and use, but rather, velocity may be a determining factor in creating or promoting the habitat features required for individual species. Similarly, greenside darters have been shown to prey on macroinvertebrates

Table 3.—Mean flow (SE) for pools and riffles at each sample site located on the Mississinewa, Salamonie, Wabash, and White rivers, Indiana, during 2009 and 2010. NC = Not calculable.

River	<i>N</i>	Pool (m/s)	<i>N</i>	Riffle (m/s)
Mississinewa	3	0.00 (< 0.01)	2	0.31 (NC)
Salamonie	3	0.00 (< 0.01)	3	1.37 (0.23)
Wabash	3	0.00 (< 0.01)	3	1.84 (0.32)
White	12	0.02 (0.01)	22	1.23 (0.22)

that feed upon aquatic autotrophs (e.g., *Cladophora* and *Fontinalis* spp.; Forbes & Richardson 1920; Fahy 1954; Wehnes 1973; McCormick & Aspinwall 1983; Hlohowskyj & Wissing 1986). These algae are generally confined to larger substrates (Hynes 1970) and may be a contributing reason why darters select riffles for their habitat. It would be naïve to think a single habitat feature is solely responsible for structuring fish communities. Environmental features in sum determine the fish species that are present (Madejczyk 1998) and may include flow regime, channel morphology, pool/glide and riffle/run quality, substrate, in-stream cover, physical and chemical attributes (e.g., oxygen concentration and water temperature) of the river (Schlosser 1990; Raborn & Schramm 2003; Sullivan et al. 2004) along with competitive interactions and predator avoidance (Schoener 1974; Taylor 1996). However, fish species variation also responds to the land type (Jacquemin & Pyron 2011) or land use of the drainage basin (Brown 2000). In our sample locations, a majority of drainage basin use is agriculture (Indiana Agricultural Statistics Service 2000), which typically degrades the fish assemblage (Swales 1988; Shields et al. 1998; Brown 2000; Wang et al. 2003; Yates & Bailey 2010). Although some land types determining fish assemblages may be associated with geological formation and not associated with human activity (Jacquemin & Pyron 2011), anthropogenic influences on land use, such as channelization (Lau et al. 2006), will alter fish community structure. In these cases, fishes such as the blackstripe topminnow, which prefers pool habitats, may not be able to survive the water velocity changes following channelization. (Olden & Poff 2004; Lau et al. 2006). The removal of pools and riffles further creates a homogenous environment with fewer niches and an increasingly unstable environment (Congdon 1971; Gorman & Karr 1978; Carline & Klosiewski 1985; Portt et al. 1986). This instability will alter the community structure in favor of those species whose morphology are adapted for the niches that are present.

Environmental pressures have generally been thought to be a factor in morphological differentiation and speciation among aquatic animals (Brown 2000). Our findings support this hypothesis, demonstrating that fish depth ratios in pools were approximately 65% greater than fishes found in riffle areas. We suggest at

least some of the morphological differences of fishes found in four eastern Indiana rivers are a reflection, directly or indirectly, to variation in water velocity. Identifying the influence of habitat, along with organismal selection and use, is paramount in understanding and managing these natural resources. This understanding may be particularly salient for Indiana and other parts of the Midwest, where land use changes and altered stream habitats in the past 150 years (Carline & Klosiewski 1985) have been common.

ACKNOWLEDGMENTS

We thank the Department of Biology at Ball State University for funding through two undergraduate research grants (KAG and JAE). We also thank C. Carpenter, B. Ciara, A. Dunithan, B. Michaels, C. Miller, S. Raiman, K. Rounds, and J. Walters for assistance in field collections.

LITERATURE CITED

- Aadland, L.P. 1993. Stream habitat types: their fish assemblages and relationship to flow. *North American Journal of Fisheries Management* 13(4):790–806.
- Bain, M.B., J.T. Finn & H.E. Booke. 1988. Stream-flow regulation and fish community structure. *Ecology* 69:382–392.
- Blake, R.W. 2004. Fish functional design and swimming performance. *Journal of Fish Biology* 65:1193–1222.
- Boily, P. & P. Magnan. 2002. Relationship between individual variation in morphological characters and swimming costs in brook charr (*Salvelinus fontinalis*) and yellow perch (*Perca flavescens*). *Journal of Experimental Biology* 205:1031–1036.
- Brinsmead, J. & M.G. Fox. 2002. Morphological variation between lake- and stream-dwelling rock bass and pumpkinseed populations. *Journal of Fish Biology* 61:1619–1638.
- Brown, L.R. 2000. Fish communities and their associations with environmental variables, lower San Joaquin River drainage, California. *Environmental Biology of Fishes* 57:257–269.
- Carline, R.F. & S.P. Klosiewski. 1985. Response of fish populations to mitigation structures in two small channelized streams in Ohio. *North American Journal of Fisheries Management* 5:1–11.
- Congdon, J.C. 1971. Fish populations of channelized and unchannelized sections of the Chariton River, Missouri. *Stream Channelization A Symposium*. Omaha, NE: North Central Division American Fisheries Society Special Publication No. 2.
- Domenici, P. 2003. Habitat, body design, and the swimming performance of fish. Pp. 137–160. *In*

- Vertebrate Biomechanics and Evolution (V.L. Bels, J.P. Gasc & A. Casinos, eds.). BIOS Scientific Publishers, Oxford.
- Douglas, M.E. & W.J. Matthews. 1992. Does morphology predict ecology? Hypothesis testing within a freshwater stream fish assemblage. *Oikos* 65:213–224.
- Douglas, M.E. 1987. An ecomorphological analysis of niche packing and niche dispersion in stream fish clades. Pp. 144–149. *In* Community and Evolutionary Ecology of North American Stream Fishes (W.J. Matthews & D.C. Heins, eds.). University of Oklahoma Press, Norman, OK.
- Ehlinger, T.J. & D.S. Wilson. 1988. Complex foraging polymorphism in bluegill sunfish. *Proceedings of the National Academy of Science* 85:1878–1882.
- Fahy, W.E. 1954. The life history of the northern greenside darter *Etheostoma blennioides* Rafinesque. *Journal of the Elisha Mitchell Scientific Society* 70:139–205.
- Forbes, S.A. & R.E. Richardson. 1920. *The Fishes of Illinois*. 2nd ed. Illinois Natural History Survey.
- Gatz, A.J., Jr. 1979. Community organization in fishes as indicated by morphological features. *Ecology* 60:711–718.
- Gorman, O.T. & J.R. Karr. 1978. Habitat structure and stream fish communities. *Ecology* 59:507–515.
- Hlohowskyj, I. & T.E. Wissing. 1986. Substrate selection by fantail (*Etheostoma flabellare*), greenside (*E. blennioides*), and rainbow (*E. caeruleum*) darters. *Ohio Journal of Science* 86(3):124–129.
- Hoagstrom, C. & C. Berry. 2007. Morphological diversity among fishes in a Great Plains river drainage. *Hydrobiologia* 596:367–386.
- Hynes, H.B.N. 1970. *The Ecology of Running Waters*. University of Toronto Press, Canada.
- Indiana Agricultural Statistics Service. 2000. *Indiana Agricultural Statistics 1999–2000*. Purdue University, West Lafayette, Indiana.
- Jacquemin, S.J. & M. Pyron. 2011. Impacts of past glaciation events on contemporary fish assemblages of the Ohio River Basin. *Journal of Biogeography*.
- Knouft, J.H. 2003. Convergence, divergence, and the effect of congeners on body size ratios in stream fishes. *Evolution* 57:2374–2383.
- Lau, J.K., T.E. Lauer & M.L. Weinman. 2006. Impacts of channelization on stream habitats and associated fish assemblages in East Central Indiana. *American Midland Naturalist* 156:319–330.
- Madejczyk, J.C., N.D. Mundahl & R.M. Lehtinen. 1998. Fish assemblages of natural and artificial habitats within the channel border of the upper Mississippi River. *American Midland Naturalist* 139:296–310.
- Matthews, W.J. 1998. *Patterns in Freshwater Fish Ecology*. New York: Chapman and Hall.
- Matthews, W.J. 1985. Critical current speed and microhabitats of the benthic fishes *Percina roanoka* and *Etheostoma flabellare*. *Environmental Biology of Fishes* 12:303–308.
- McCormick, F.H. & N. Aspinwall. 1983. Habitat selection in three species of darters. *Environmental Biology of Fishes* 8:279–282.
- McLaughlin, R.L. & J.W.A. Grant. 1994. Morphological and behavioural differences among recently-emerged brook charr, *Salvelinus fontinalis*, foraging in slow- vs. fast-running water. *Environmental Biology of Fishes* 39:289–300.
- Moyle, P.B. & J.J. Cech, Jr. 2004. *Fishes: An Introduction to Ichthyology*. New York. Pearson Benjamin Cummings.
- Olden, J.D. & N.L. Poff. 2004. Ecological processes driving biotic homogenization: testing a mechanistic model using fish faunas. *Ecology* 85:1867–1875.
- Page, L.M. & D.L. Swofford. 1984. Morphological correlates of ecological specialization in darters. *Environmental Biology of Fishes* 11:139–159.
- Pflieger, W.L. 2004. *The Fishes of Missouri*. Jefferson City: Missouri Department of Conservation.
- Portt, C.B., E.K. Balon & D.L.G. Noakes. 1986. Biomass and production of fishes in natural and channelized stream. *Canadian Journal of Fisheries and Aquatic Sciences* 43:1926–1934.
- Raborn, S.W. & H.L. Schramm, Jr. 2003. Fish assemblage response to recent mitigation of a channelized warmwater stream. *River Research and Applications* 19:289–301.
- Reynolds, J.B. 1996. Electrofishing. Pp. 221–254. *In* *Fisheries Techniques* (B.R. Murphy & D.W. Willis, eds.). American Fisheries Society, Bethesda.
- Ross, S.T. 1986. Resource partitioning in fish assemblages: a review of field studies. *Copeia* 1986(2):352–388.
- Schlosser, I.J. 1990. Environmental variation, life history attributes, and community structure in stream fishes: implications for environmental management and assessment. *Environmental Management* 14(5):621–628.
- Schlosser, I.J. 1982. Fish community structure and function along two habitat gradients in a headwater stream. *Ecological Monographs* 52:395–414.
- Schoener, T.W. 1974. Resource partitioning in ecological communities. *Science* 185:27–39.
- Shields, F.D. Jr., S.S. Knight & C.M. Cooper. 1998. Rehabilitation of aquatic habitats in warmwater streams damaged by channel incision in Mississippi. *Hydrobiologia* 382:63–86.
- Stuber, R.J., G. Gebhart & O.E. Maughan. 1982a. Habitat suitability index models: bluegill. United States Department of the Interior Fish and Wildlife Service FWS/OBS-82/10.8. 26 pp.
- Stuber, R.J., G. Gebhart & O.E. Maughan. 1982b. Habitat suitability index models: green sunfish.

- United States Department of the Interior Fish and Wildlife Service FWS/OBS-82/10.15. 28 pp.
- Sullivan, B.E., L.S. Rigsby, A. Berndt, M.R. Jones-Wuellner, T.P. Simon, T.E. Lauer & M. Pyron. 2004. Habitat influence on fish community assemblages in an agricultural landscape in four east central Indiana streams. *Journal of Freshwater Ecology* 19:141–148.
- Swales, S. 1988. Fish population of a small lowland channelized river in England subject to long-term river maintenance and management works. *Regulated Rivers Research and Management* 2:493–506.
- Taylor, C. 1996. Abundance and distribution within a guild of benthic stream fishes: local processes and regional patterns. *Freshwater Biology* 36:385–396.
- Wang, L., J. Lyons, P. Rasmussen, P. Seelbach, T. Simon, M. Wiley, P. Kanehl, E. Baker, S. Niemela & P.M. Steward. 2003. Watershed, reach, and riparian influences on stream fish assemblages in the Northern Lakes and Forest Ecoregion, U.S.A. *Canadian Journal of Fisheries and Aquatic Sciences* 60:491–505.
- Webb, P.W., C.L. Gerstner & S.T. Minton. 1996. Station-holding by the mottled sculpin, *Cottus bairdi* (Teleostei: Cottidae), and other fishes. *Copeia* 1996:488–493.
- Webb, P.W. 1989. Station-holding by three species of benthic fishes. *Journal of Experimental Biology* 145:303–320.
- Webb, P.W. 1984. Form and function in fish swimming. *Scientific American* 251:72–82.
- Wehnes, R.E. 1973. The food and feeding relationships of five sympatric darter species (Pisces: Percidae) in Salt Creek, Hocking County, Ohio. M.S. thesis. Ohio State University. Columbus, Ohio.
- Werner, E.E. 1977a. Competition and habitat shift in two sunfishes (Centrarchidae). *Ecology* 58:869–876.
- Werner, E.E. 1977b. Species packing and niche complementarity in three sunfishes. *American Naturalist* 111:553–578.
- Winemiller, K.O. 1992. Ecomorphology of freshwater fishes. *National Geographic Research & Exploration* 8:308–327.
- Yates, A.G. & R.C. Bailey. 2010. Covarying patterns of macroinvertebrate and fish assemblages along natural and human activity gradients: implications for bioassessment. *Hydrobiologia* 637:87–100.

Manuscript received 1 February 2012, revised 11 October 2012.