

## IDENTIFYING LOCAL SCALE FOOD WEB VARIATION USING STABLE $\delta^{13}\text{C}$ AND $\delta^{15}\text{N}$ ISOTOPES IN A CENTRAL INDIANA RESERVOIR AND DOWNSTREAM RIVER

S. J. Jacquemin<sup>1,2</sup>, C. Miller<sup>2</sup> and M. Pyron<sup>2</sup>: <sup>1</sup>Department of Biological Sciences, Wright State University – Lake Campus, Celina, OH 45822, USA; <sup>2</sup>Aquatic Biology and Fisheries Center, Department of Biology, Ball State University, Muncie, IN 47306, USA

**ABSTRACT.** We used stable isotopes of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  were measured from fish and macroinvertebrate consumers, terrestrial and aquatic primary producers, and detritus to describe food webs for a reservoir and downstream riverine habitat. Measurements of  $\delta^{13}\text{C}$  indicated that reservoir energy sources were primarily autochthonous while the riverine habitat was primarily a result of allochthonous carbon sources. Measurements of  $\delta^{15}\text{N}$  indicated that terrestrial primary producers were basal to organic matter, aquatic primary producers, macroinvertebrates, and fishes, respectively. We found significant differences between riverine and reservoir  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  levels among seven fish taxa representing Cyprinidae, Centrarchidae, Percidae, Ictaluridae, and Clupeidae families. Riverine and reservoir overall  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  levels differed by an average of 7.9% and 7.7% by taxa, respectively. Reservoir fish exhibited lower intra specific variation in  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values compared to river fish indicating less variation in diet. Reservoir fish were also found to feed at more extreme trophic positions (high and low) compared to riverine fish. This evidence suggests the presence of habitat-induced variability in local scale food webs and has implications for understanding aquatic ecosystem diversity and organization.

**Keywords:** Food web variation, stable  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  isotopes, reservoir and river habitat, fish ecology

### INTRODUCTION

Variation in food web structure has been linked to a variety of trophic level and productivity patterns associated with freshwater communities (Carpenter et al. 1987; Polis & Strong 1996; Hoinghaus et al. 2008). However, the majority of community food web studies utilize relatively large geographic areas that do not specifically address the potential influence that local habitats may have on food webs (Finlay et al. 2002; Roach et al. 2009). Furthermore, less is understood about the role that habitat may play in driving local variation in food webs among similar or identical taxa within assemblages. Ultimately, describing the role that habitat plays in structuring food webs can serve as a tool for aquatic conservation.

Previous studies have indicated that alterations in habitat (micro- and macro-) can influence food web variation as a result of secondary mechanisms linked with flow, temperature, and nutrient availability (see Boecklen

et al. 2011 for a review). Alteration of flow regime is the primary impetus of aquatic habitat modification globally (Poff et al. 1997; Pringle et al. 2000). Flow regime alteration has been shown to reduce community complexity, homogenize habitats, and shift functional organization (Poff & Ward 1990; Poff & Allan 1995). Impoundment of lotic ecosystems is one of the primary mechanisms of flow regime alteration (Petts 1984). Consequently, two common aquatic ecosystems in North America are reservoirs and subsequent altered downstream riverine segments. Impoundments have been linked with changes in assemblage structure (Taylor et al. 2008) and abiotic attributes of lotic ecosystems (Ward & Stanford 1983) in both the downstream and upstream reach surrounding riverine impoundments (Pringle 1997). However, the study of isotope variation among altered freshwater ecosystems is relatively recent (Diebel & Vander Zanden 2009; Doi 2009). Identification of local scale food web variation in trophic structure and energy sources that occurs due to the presence of impoundments can provide useful information for conservation and restoration by providing additional information to assess the influence

*Correspondence:* Stephen J. Jacquemin, e-mail: stephen.jacquemin@wright.edu.

of habitat alteration on aquatic communities (Hoeinghaus et al. 2008).

Naturally occurring stable isotopes can be used to quantify food web structure (Peterson & Fry 1987; Fry 1988; Doi 2009). Stable isotopes have been used across a wide range of spatial (Fry 1991; Doi 2009) and temporal (Wainwright et al. 1993) aquatic communities (Finlay et al. 2002) and taxa (Genner et al. 2003) to understand trophic and energy dynamics. Compared to classic approaches for understanding trophic relationships (i.e., stomach content analysis, visual observation) isotope analysis allows detailed identification of trophic position ( $\delta^{15}\text{N}$ ), energy origin ( $\delta^{13}\text{C}$ ), and food web complexity (Vander Zanden et al. 1997; Melville & Connolly 2003). Specifically, carbon<sup>13</sup> facilitates detection of autotrophic sources in individuals which may not be readily observable (such as in upper trophic levels) using other diet study approaches (Melville & Connolly 2003). Additionally, nitrogen<sup>15</sup> concentrations increase in organisms with increasing trophic level revealing informative trophic patterns (Cabana and Rasmussen 1996). From a conservation or management perspective, variation in isotopic signatures (Fry 2002) can be used to function as a covariate of habitat heterogeneity or 'quality'. However, application on a local scale to infer effects of habitat differences on trophic dynamics has been limited, particularly in the study of Indiana fishes.

Our study objective was to use stable isotopes to describe local scale variation in trophic position and energy sources and test for variation between riverine and reservoir aquatic communities. We selected taxa that occurred in both habitats to compare food webs by habitat using producers and consumers. Our null hypotheses were that trophic position ( $\delta^{15}\text{N}$ ) and energy origin ( $\delta^{13}\text{C}$ ) would be similar between habitats and among species.

## METHODS

The study area was the West Fork of the White River and Prairie Creek Reservoir in Delaware County, Indiana (Fig. 1). The White River watershed has a drainage area of 712 km<sup>2</sup> in Delaware County (Hoggatt 1975). Prairie Creek Reservoir is a 515 ha impoundment of a headwater tributary of the White River. We collected consumers (fishes and macroinvertebrates), producers (algae, terres-

trial plants, and macrophytes), and detritus (course particulate organic material, CPOM) in September 2009 (fishes) and 2010 (macroinvertebrates, producers, detritus). Samples were collected by seine, hoop net, electrofishing, d-frame kick net, or visual searching.

Three individuals of each fish species (Table 1) were collected from each habitat. River sampling included one wadable site approximately 200 m in length and 15 m in width. Reservoir sampling included approximately 600 m of wadable shoreline within 10 m of shore. All target adult individuals were collected and three individuals from each habitat were randomly selected for tissue samples. To avoid differences in isotope signature due to intraspecific allometric size variation (Genner et al. 2003) only adult individuals of similar body size were used. Sex of individual fish was not determined. A small sample of white muscle tissue was removed from the dorsal / caudal region of each individual fish immediately following collection for isotope analysis. Although our samples did not include the complete assemblage from either the reservoir or riverine habitats, we selected our study taxa based on co-occurrence in both habitats. We collected a minimum of three individuals for each macroinvertebrate taxon from each habitat. Macroinvertebrate individuals were starved for 48 hours prior to processing to reduce confounding effects of retained gut contents (Jardine et al. 2005). Macroinvertebrates were not selected to represent all prey items of the sampled fishes. Rather, the sampled bivalve, gastropod, dragonfly and midge larvae were selected to represent various possible trophic levels within the macroinvertebrate assemblage. The primary producers collected included leaves from overhanging riparian terrestrial trees (*Fagus* sp.), periphytic algae, and the dominant aquatic macrophytes (primarily watermilfoil *Myriophyllum spicatum*) that were present in both habitats. Detritus was collected along shorelines concurrent with consumer sampling and was primarily composed of woody debris and unidentifiable humic material. A minimum of three individual samples for each producer and detritus group were collected from each habitat.

All samples were separated and individually desiccated at 60° C, ground into a homogenous powder using a mortar and pestle, and packed

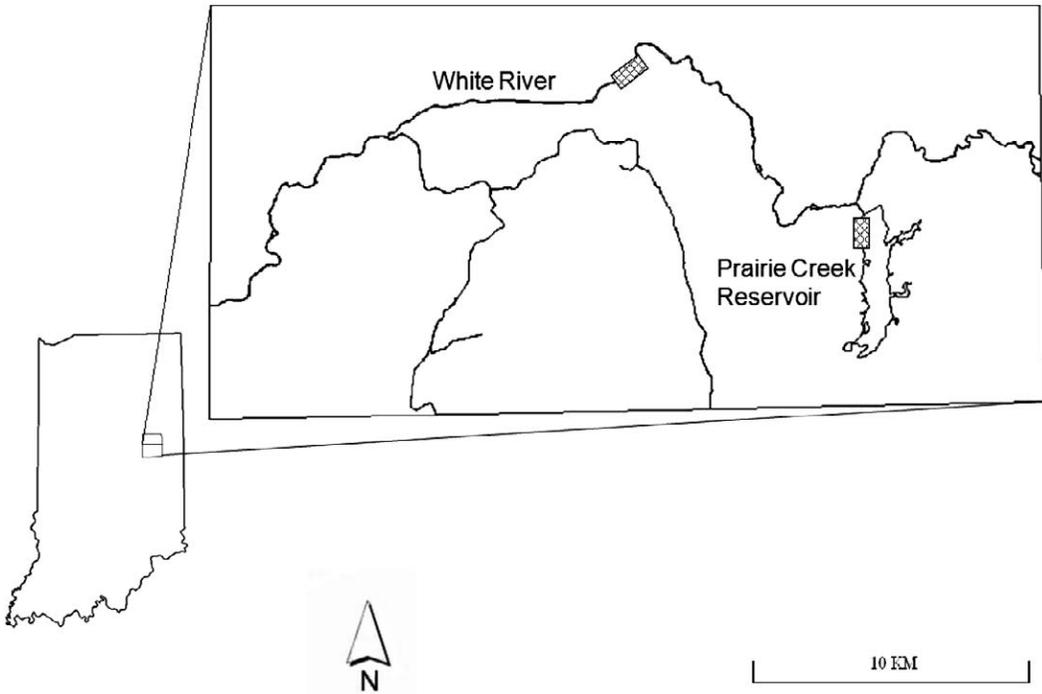


Figure 1.—West Fork of the White River and Prairie Creek Reservoir located in Delaware County, Indiana, USA. Sampling areas are shaded.

into separate tins (Pinnegar & Polunin 1999). Samples were analyzed for  $^{13}\text{C}$  and  $^{15}\text{N}$  enrichment using a continuous flow mass spectrometer (University of Arkansas Stable Isotope Laboratory). Mean  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  levels were compared between reservoir and riverine fish species using two-sample t-tests. In an effort to reduce false discovery rates inherent in multiple pairwise comparisons based on traditional p values we used Q values for tests of significance (Storey 2002). Alpha was set at 0.05 for all tests of significance. To examine variation in  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  for the reservoir and river we calculated and compared coefficient of variation (CV) for all collected fish individuals from each habitat.

Several caveats to this study design are a result of limited resources: multiple collecting years and overall sample size. Fish were collected during summer 2009 and primary producers and macroinvertebrate consumers were collected during summer 2010. Samples were analyzed immediately following processing and were not stored during the interim time period. Variation between 2009 and 2010 may introduce bias when directly comparing fish to primary producers, primary consumers, detri-

tus, etc. However, direct comparisons of taxa within years (e.g. reservoir fish to riverine fish, etc.) are applicable.

## RESULTS

The fish species collected were smallmouth bass (*Micropterus dolomieu*), white crappie (*Pomoxis annularis*), johnny darter (*Etheostoma nigrum*), spotfin shiner (*Cyprinella spiloptera*), yellow bullhead (*Ameiurus natalis*), gizzard shad (*Dorosoma cepedianum*) and common carp (*Cyprinus carpio*) (Table 1). Macroinvertebrate taxa were filter feeding Asian clam (*Corbicula fluminea*), a grazing gastropod (*Physa acuta*), predatory dragonfly larvae (*Odonata*), and omnivorous non-biting fly midge larvae (*Chironomidae*). Only target species of fish and macroinvertebrates were collected and noted. For a full list of fish and macroinvertebrate species richness and assemblages see archived fish and macroinvertebrate annual reports compiled by the City of Muncie, IN, Bureau of Water Quality (<http://www.munciesanitary.org/departments/bureau-of-water-quality/>).

**Trophic position.**—The mean  $\delta^{15}\text{N}$  sample values of all sample groups ranged from 4.4 to

Table 1.—Mean  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values (standard deviation in parentheses) and results of two sample *t* test comparisons by location (Prairie Creek Reservoir - PCR and White River - WR for each fish species. Q values are in parentheses and abbreviations are for Fig. 1 and Fig. 2).

Species	Mean total length (mm)	PCR mean $\delta^{13}\text{C}$	WR mean $\delta^{13}\text{C}$	<i>t</i> -value $\delta^{13}\text{C}$ <sub>dof = 4</sub>	PCR mean $\delta^{15}\text{N}$	WR mean $\delta^{15}\text{N}$	<i>t</i> -value $\delta^{15}\text{N}$ <sub>dof = 4</sub>
Spotfin shiner ( <i>Cyprinella spiloptera</i> ) SFSHR	84.7	-25.0 (0.9)	-28.0 (0.5)	5.1 ( <i>q</i> < 0.01)	13.3 (0.3)	15.4 (0.2)	-9.1 ( <i>q</i> < 0.01)
Gizzard shad ( <i>Dorosoma cepedianum</i> ) SHAD	272.8	-27.0 (0.5)	-31.2 (0.2)	14.0 ( <i>q</i> < 0.001)	14.4 (0.5)	14.1 (0.1)	NS
Carp ( <i>Cyprinus carpio</i> ) CARP	549.8	-27.0 (0.9)	-26.1 (1.2)	NS	14.6 (0.7)	12.0 (0.7)	4.4 ( <i>q</i> < 0.01)
Yellow bullhead ( <i>Ameiurus natalis</i> ) YBLHD	239	-26.3 (0.2)	-25.0 (0.3)	-6.0 ( <i>q</i> < 0.01)	15.1 (0.6)	14.5 (0.1)	NS
Johnny darter ( <i>Etheostoma nigrum</i> ) JDRT	58.5	-23.4 (0.3)	-27.1 (0.6)	9.9 ( <i>q</i> < 0.001)	16.0 (0.0)	15.9 (0.3)	NS
Smallmouth bass ( <i>Micropterus dolomieu</i> ) SMB	347	-24.4 (1.0)	-25.9 (1.0)	NS	16.2 (0.2)	15.4 (0.3)	3.1 ( <i>q</i> < 0.01)
White crappie ( <i>Pomoxis annularis</i> ) WCRP	230.5	-26.7 (0.3)	-26.2 (0.6)	NS	17.1 (0.3)	16.2 (0.2)	4.7 ( <i>q</i> < 0.01)

17.1 in the river and 4.4 to 16.2 in the reservoir habitats (Fig. 2). Terrestrial leaves occupied the lowest trophic position, while white crappie occupied the highest trophic position in both habitats. We did not detect a significant difference in the basal mean levels (CPOM, algae, aquatic macrophytes) of the food webs for the reservoir and river (two sample *t*  $^{15}\text{N}$  [*mean CPOM, algae, aquatic macrophytes*] = -0.95, *q* = 0.36). Given similar basal  $\delta^{15}\text{N}$  values consumer trophic positions were estimated from relative  $\delta^{15}\text{N}$  values (see Vander Zanden et al. 1997 for trophic position formula). Common carp, smallmouth bass, and white crappie occupied a significantly higher trophic position in the reservoir than in the riverine habitat (Table 1). Spotfin shiner in the river had a higher trophic position than in the reservoir. Gizzard shad, johnny darter, and yellow bullhead did not differ significantly in trophic position between habitats. Coefficient of variation for all fish  $\delta^{15}\text{N}$  from the river was 9.4%, comparably higher than the CV for all sampled reservoir fish (8.3%).

**Energy sources.**—The range for  $\delta^{13}\text{C}$  values in the river was -32.0 for Asian clam to -20.1 for aquatic macrophytes (Fig. 2). The ranges for  $\delta^{13}\text{C}$  values in the reservoir were -38.0 for CPOM to -15.2 for aquatic macrophytes (Fig. 2). Mean  $\delta^{13}\text{C}$  values for the fish community (except yellow bullhead) were significantly more positive in the reservoir than the river habitats (Table 1; Fig. 2). The separation of  $\delta^{13}\text{C}$  among fishes corresponded with increasingly negative values of terrestrial primary producers (leaves) and more positive aquatic primary producers (algae). Gizzard shad, johnny darter, and spotfin shiner had higher  $\delta^{13}\text{C}$  levels in the reservoir than in the river habitat. Yellow bullhead had higher  $\delta^{13}\text{C}$  levels in river habitat. Common carp, smallmouth bass, and white crappie  $\delta^{13}\text{C}$  did not differ significantly among habitat types. Coefficient of variation for all fish  $\delta^{13}\text{C}$  from the river was 7.5%, comparably higher than the CV for all sampled reservoir fish (5.7%).

DISCUSSION

**Trophic relationships.**—Fishes are typically the top consumers in aquatic food webs (Pinnegar & Polunin 1999). Our results support this and identified the same top consumer (white crappie) for reservoir and riverine habitats. However, the hierarchical order of mean  $\delta^{15}\text{N}$  values for the other fish taxa

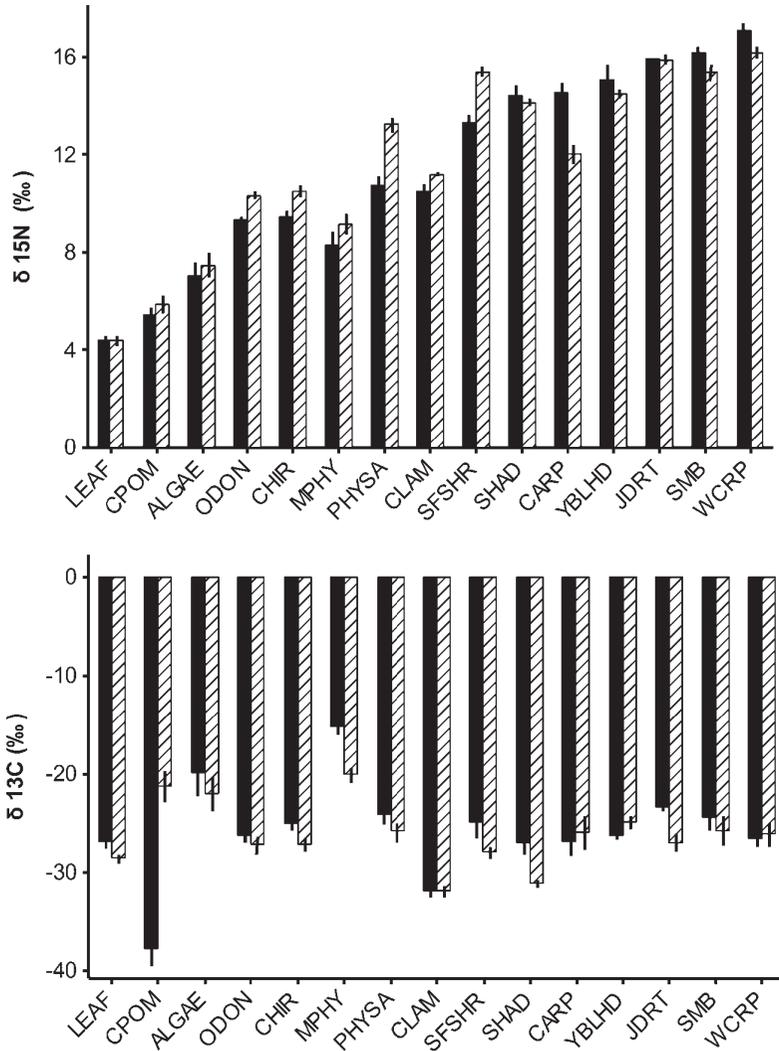


Figure 2.—Mean  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  for White River (striped bars) and Prairie Creek Reservoir (solid bars) taxa (error bars are one standard deviation). Abbreviations are *FISH*: spotfin shiner (SFSHR), gizzard shad (SHAD), common carp (CARP), yellow bullhead (YBLHD), johnny darter (JDRT), smallmouth bass (SMB), and white crappie (WCRP). *PRODUCERS*: algae (ALGAE), submerged macrophytes (MPHY), coarse particulate organic matter (CPOM), and terrestrial leaves (LEAF). *MACROINVERTEBRATE CONSUMERS*: grazing *Physa acuta* snail (PHYSA), non-biting midge larvae (CHIR), dragonfly larvae (ODON), and Asian clam *Corbicula* (CLAM). Note: fish were collected September 2009 and detritus, primary producers, and macroinvertebrates were collected September 2010.

differed between reservoir and riverine food webs. This reorganization is likely a reflection of habitat induced differences in diet and energy assimilation of these taxa. These results may also reflect decreased competition in the reservoir habitat and a more simplified web of interaction. Interestingly, the observed variation in  $\delta^{15}\text{N}$  trophic numbers paralleled habitat associations as inferred by previously

published regional studies such as Trautman (1981). For example, fish taxa that are generally considered more lentic specialists (white crappie and gizzard shad) had greater  $\delta^{15}\text{N}$  variation in reservoir habitats compared with fishes that are generally considered lotic specialists (johnny darter and smallmouth bass) which exhibited greater variation in riverine habitats (Table 1).

**Contribution of energy sources.**—The reservoir and downstream riverine ecosystems contained contributions from both terrestrial and aquatic producers. However, the reservoir food web  $\delta^{13}\text{C}$  values suggested increased importance of autochthonous energy sources compared to the river that used a greater proportion of allochthonous sources as demonstrated through increasingly positive  $\delta^{13}\text{C}$  consumer values (Table 1; Fig. 2). This pattern is expected and has been demonstrated across multiple systems and habitats (Kling et al. 1992). Hoeninghaus et al. (2008) found that trophic web length increased in impounded systems as a function of primary autochthonous productivity. One exception to this pattern is the yellow bullhead individuals from the river habitat resulted in lower  $\delta^{13}\text{C}$  values. In addition, several outliers in the  $\delta^{13}\text{C}$  values of gizzard shad and *Corbicula* clam samples likely indicate the absence of several important biotic components from the riverine foodweb, such as zooplankton and phytoplankton. Overall, we attribute the intra- and interspecific differences in  $\delta^{13}\text{C}$  energy sources to be the result of habitat differences. However, some overlap in energy sources for the ecosystems are expected due to their spatial proximity (Hoeninghaus et al. 2008; Doi 2009).

**Role of habitat degradation on isotope variation.**—Reduced variation in isotope signatures (Fry 2002) and reduced variation in food chain length can indicate that habitats are homogenized and degraded. We suggest that further study of habitat degradation as a source of increased variation in local isotope signatures of aquatic communities is necessary. Further, we suggest that reduced variation in isotope signatures and modified consumer position and variation in food webs in a reservoir is a result of the altered reservoir habitat and is an indicator of loss of ecosystem stability (Hoeninghaus et al. 2008). These results provide additional evidence of negative impacts of altered natural hydrologic regimes. Future studies of food web variation at multiple spatial scales to examine additional impacts including agriculture, urbanization, and channelization are warranted.

#### ACKNOWLEDGEMENTS

This work was funded through an internal Ball State University Department of Biology grant provided by an anonymous donor. The

authors wish to thank L. Etchison, M. Allen, A. Schmelzel and J. Jacquemin for field assistance and M. Bernot for use of laboratory equipment. All fishes were collected under Indiana scientific permit # 09-0233.

#### LITERATURE CITED

- Boecklen, W.J., C.T. Yarnes, B.A. Cook & A.C. James. 2011. On the use of stable isotopes in trophic ecology. *Annual Review of Ecology, Evolution, and Systematics* 42:411–440.
- Cabana, G. & J.B. Rasmussen. 1996. Comparison of aquatic food chains using nitrogen isotopes. *Proceedings of the National Academy of Sciences USA* 93:10844–10847.
- Carpenter, S.R., J.F. Kitchell, J.R. Hodgson, P.A. Cochran, J.J. Elser, M.M. Elser, D.M. Lodge, D. Kretchmer & X. He. 1987. Regulation of lake primary productivity by food web structure. *Ecology* 68:1863–1876.
- Diebel, M.W. & J.M. Vander Zanden. 2009. Nitrogen stable isotopes in streams: effects of agricultural sources and transformations. *Ecological Applications* 19:1127–1134.
- Doi, H. 2009. Spatial patterns of autochthonous and allochthonous resources in aquatic food webs. *Population Ecology* 51:57–64.
- Finlay, J.C., S. Khandwala & M.E. Power. 2002. Spatial scales of carbon flow in a river food web. *Ecology* 83:1845–1859.
- Fry, B. 1988. Food web structure on Georges Bank from stable C, N, and S isotopic compositions. *Limnology and Oceanography* 33:1182–1190.
- Fry, B. 1991. Stable isotope diagrams of freshwater food webs. *Ecology* 72:2293–2297.
- Fry, B. 2002. Stable isotopic indicators of habitat use by Mississippi River fish. *Journal of the North American Benthological Society* 21:676–685.
- Genner, M.J., S.J. Hawkins & G.F. Turner. 2003. Isotopic change throughout the life history of a Lake Malawi cichlid fish. *Journal of Fish Biology* 62:907–917.
- Hoeninghaus, D.J., K.O. Winemiller & A.A. Agostinho. 2008. Hydrogeomorphology and river impoundment affect food-chain length of diverse Neotropical food webs. *Oikos* 117:984–995.
- Hoggatt, R.E. 1975. Drainage area of Indiana streams. Department of the Interior, U.S. Geological Survey, Indianapolis, Indiana.
- Jardine, T.D., R.A. Curry, K.S. Heard & R.A. Cunjak. 2005. High fidelity: isotopic relationship between stream invertebrates and their gut contents. *Journal of the North American Benthological Society* 24:290–299.
- Kling, G.W., B. Fry & W.J. O'Brien. 1992. Stable isotopes and planktonic trophic structure in arctic lakes. *Ecology* 73:561–566.

- Melville, A.J. & R.M. Connolly. 2003. Spatial analysis of stable isotope data to determine primary sources of nutrition for fish. *Oecologia* 136:499–507.
- Peterson, B.J. & B. Fry. 1987. Stable isotopes in ecosystem studies. *Annual Reviews in Ecology and Systematics* 18:293–320.
- Petts, G.E. 1984. *Impounded Rivers: Perspectives for Ecological Management*. John Wiley and Sons, New York, USA.
- Pinnegar, J.K. & N.V.C. Polunin. 1999. Differential fractionation of  $^{13}\text{C}$  and  $^{15}\text{N}$  among fish tissue: implications for the study of trophic interactions. *Functional Ecology* 13:225–231.
- Poff, L.N. & J.V. Ward. 1990. The physical habitat template of lotic systems: recovery in the context of historical pattern of spatio-temporal heterogeneity. *Environmental Management* 14: 629–646.
- Poff, L.N. & J.D. Allan. 1995. Functional organization of stream fish assemblages in relation to hydrological variability. *Ecology* 76:606–627.
- Poff, L.N., J.D. Allan, M.B. Bain, J.R. Karr, K.L. Prestegard, B.D. Richter, R.E. Sparks & J.C. Stromberg. 1997. The natural flow regime: A paradigm for river conservation and restoration. *Bioscience* 47:769–784.
- Poff, L.N., J.D. Olden, D.M. Merritt & D.M. Pepin. 2007. Homogenization of regional river dynamics by dams and global biodiversity implications. *Proceedings of the National Academy of Sciences USA* 104:5732–5737.
- Polis, G.A. & D.R. Strong. 1996. Food web complexity and community dynamics. *American Naturalist* 147:813–846.
- Pringle, C.M. 1997. Exploring how disturbance is transmitted upstream: going against the flow. *Journal of the North American Benthological Society* 16:425–438.
- Pringle, C.M., M.C. Freeman & B.J. Freeman. 2000. Regional effects of hydrologic alterations on riverine macrobiota in the New World: tropical-temperate comparisons. *Bioscience* 50:807–823.
- Roach, K.A., J.H. Thorp & M.D. DeLong. 2009. Influence of lateral gradients of hydrological connectivity on trophic positions of fishes in the Upper Mississippi River. *Freshwater Biology* 54:607–620.
- Storey, J.D. 2002. A direct approach to false discovery rates. *Journal of the Royal Statistics Society Serial B Statistics Methodology* 64:479–498.
- Taylor, C.M., D.S. Millican, M.E. Roberts & W.T. Slack. 2008. Long-term change to fish assemblages and the flow regime in a southeastern U.S. river system after extensive aquatic ecosystem fragmentation. *Ecography* 31:787–797.
- Trautman, M.B. 1981. *The Fishes of Ohio*. Ohio State University Press, Columbus, Ohio.
- Vander Zanden, M.J., G. Cabana & J.B. Rasmussen. 1997. Comparing trophic position of freshwater fish calculated using stable nitrogen isotope ratios ( $\delta^{15}\text{N}$ ) and literature dietary data. *Canadian Journal of Fisheries and Aquatic Science* 54:1142–1158.
- Wainwright, S.C., M.J. Fogarty, R.C. Greenfield & B. Fry. 1993. Long-term changes in the Georges Bank food web: trends in stable isotopic compositions of fish scales. *Marine Biology* 115:481–493.
- Ward, J.V. & J.A. Stanford. 1983. The serial discontinuity concept of lotic ecosystems. Pp. 29–42. *In* *Dynamics of Lotic Ecosystems* (T.D. Fontaine III & S.M. Bartell, eds.). Ann Arbor Science, Ann Arbor, Michigan.

*Manuscript received 17 August 2013, revised 13 February 2014.*