Research Brief

Differences between main-channel and off-channel food webs in the upper Mississippi River revealed by fatty acid profiles of consumers

James H. Larson,[1]* Michelle R. Bartsch,[1] Steve Gutreuter,[2] Brent C. Knights,[1] Lynn A. Bartsch,[1] William B. Richardson,[1] Jonathan M. Vallazza,[1] and Michael T. Arts[3†]

[1] *US Geological Survey, Upper Midwest Environmental Sciences Center, La Crosse, WI, USA*
[2] *Roswell, GA*
[3] *Environment of Canada, National Water Research Institute, Burlington, ON, Canada*
* *Corresponding author: jhlarson@usgs.gov*
† *Current address: Department of Chemistry and Biology, Ryerson University, Toronto, ON, Canada*

Received 11 August 2014; accepted 5 January 2015; published 17 February 2015

Abstract

Large river systems are often thought to contain a mosaic of patches with different habitat characteristics driven by differences in flow and mixing environments. Off-channel habitats (e.g., backwater areas, secondary channels) can become semi-isolated from main-channel water inputs, leading to the development of distinct biogeochemical environments. Observations of adult bluegill (*Lepomis macrochirus*) in the main channel of the Mississippi River led to speculation that the main channel offered superior food resources relative to off-channel areas. One important aspect of food quality is the quantity and composition of polyunsaturated fatty acids (PUFA). We sampled consumers from main-channel and backwater habitats to determine whether they differed in PUFA content. Main-channel individuals for relatively immobile species (young-of-year bluegill, zebra mussels [*Dreissena polymorpha*], and plain pocketbook mussels [*Lampsilis cardium*]) had significantly greater PUFA content than off-channel individuals. No difference in PUFA was observed for the more mobile gizzard shad (*Dorsoma cepedianum*), which may move between main-channel and off-channel habitats even at early life-history stages. As off-channel habitats become isolated from main-channel waters, flow and water column nitrogen decrease, potentially improving conditions for nitrogen-fixing cyanobacteria and vascular plants that, in turn, have low PUFA content. We conclude that main-channel food webs of the upper Mississippi River provide higher quality food resources for some riverine consumers as compared to food webs in off-channel habitats.

Key words: docosahexaenoic acid, DHA, *Dorsoma cepedianum*, *Dreissena polymorpha*, eicosapaentanoic acid, EPA, food webs, gizzard shad, *Lampsilis cardium*, *Lepomis macrochirus*, plain pocketbook mussel, zebra mussel

Introduction

At times, adult bluegill (*Lepomis macrochirus*) are found in relatively high abundance in the main-channel of the Mississippi River (Gutreuter et al. 2010). This observation may be unexpected because bluegill are generally considered a limnophil based on morphology and their common presence in ponds, lakes, and impoundments (e.g., Cross and Collins 1995). Based on observations of channel occupation and other life history information, Gutreuter et al. (2010) proposed that adult bluegill be described as opportunistic feeders that take advantage of more lotic habitats when appropriate food resources are available. This suggests that, at times, main-channel areas of the Mississippi River may offer some food quality advantages for bluegill over nearby off-channel areas.

Do main-channel habitats have higher-quality food resources than off-channel habitats? At the base of the

DOI: 10.5268/IW-5.2.781

food web, off-channel habitats might offer competitive advantages for nitrogen-fixing cyanobacteria (due to low total nitrogen and low total nitrogen to total phosphorus ratio; TN:TP) and vascular macrophytes (which do not establish well in flowing waters; Madsen et al. 2001) compared to main-channel habitats. Cyanobacteria and vascular plants often have poor nutritional quality relative to algae (e.g., diatoms) because they can be low in poly-unsaturated fatty acids (PUFA; fatty acids [FA] with at least 2 double bonds; Ahlgren et al. 1992). Unlike metazoans, algae (and aquatic fungi) are capable of inserting a double bond in the n-3 and n-6 position in 18-carbon FA, and, using these FA as substrates, they can also synthesize long-chain PUFA (LC-PUFA), FA with at least 20 carbons and 3 double bonds, such as eicosapaentanoic acid (EPA; 20:5n-3) and docosahexaenoic acid (DHA; 22:6n-3).

Long-chained PUFA are important for metazoan growth, development, reproduction, and health (Ahlgren et al. 2009, Parrish 2009). Metazoans must either obtain EPA and DHA from the diet or produce them at rates of varying efficiency, from shorter-chained precursors such as α-linolenic (ALA; 18:3n-3) and stearidonic (SDA; 18:4n-3) acids that are synthesized by primary producers. However, LC-PUFA are energetically costly for metazoans to produce from these precursors (Arts and Kohler 2009, Parrish 2009), which leads to the conclusion that the composition and abundance of LC-PUFA in food resources is an important aspect of food quality for many consumers (Ahlgren et al. 2009, Brett et al. 2009b). If off-channel habitats are better suited for cyanobacteria and macrophytes than the main-channel, then the availability of LC-PUFA might be less in off-channel habitats.

To determine if food resources for main-channel consumers are better than those available in off-channel habitats in terms of FA composition, we sampled primary and secondary consumers from main-channel and off-channel habitats in the Mississippi River and determined their FA content. Sampling consumers themselves provides a time-integrated signal of resource availability that would be logistically difficult if food sources themselves were sampled, as in studies using stable isotopes (Peterson and Fry 1987). Adult fish often move among habitats and thus may be accessing a mixture of main-channel and off-channel food resources. To represent main-channel and off-channel food webs, we sampled 2 relatively immobile invertebrate species, zebra mussels (*Dreissena polymorpha*) and plain pocketbook mussels (*Lampsilis cardium*), as well as young-of-year (YOY) bluegill, which have relatively limited home ranges (Ball 1943, Gunnings and Shoop 1963, Gatz and Adams 1994). We also sampled YOY gizzard shad (*Dorosoma cepedianum*) from both habitats, which are a more mobile species, even at small sizes, and therefore are expected to better integrate food resources from both main-channel and off-channel habitats (Schultz et al. 2007).

Methods

Study area

The upper Mississippi River flows ~1400 km from St. Anthony Falls in Minnesota to St. Louis, Missouri. This is a highly regulated system that contains a series of low-head dams and numerous channel-training structures to help support commercial traffic. Our study area encompasses the lower third of Navigation Pool 7 and all of Navigation Pool 8. In 2005, study sites included 3 off-channel locations within Lawrence Lake and 5 main-channel border locations in Navigation Pool 8 and one off-channel location in Lake Onalaska in Navigation Pool 7. In 2006, study sites included 6 main-channel border locations and 4 off-channel locations, including Stoddard Island complex, Lawrence Lake, Target Lake, and Round Lake. In 2007, study sites included 5 main-channel border locations and the same off-channel locations sampled in 2006 (Table 1; Fig. 1).

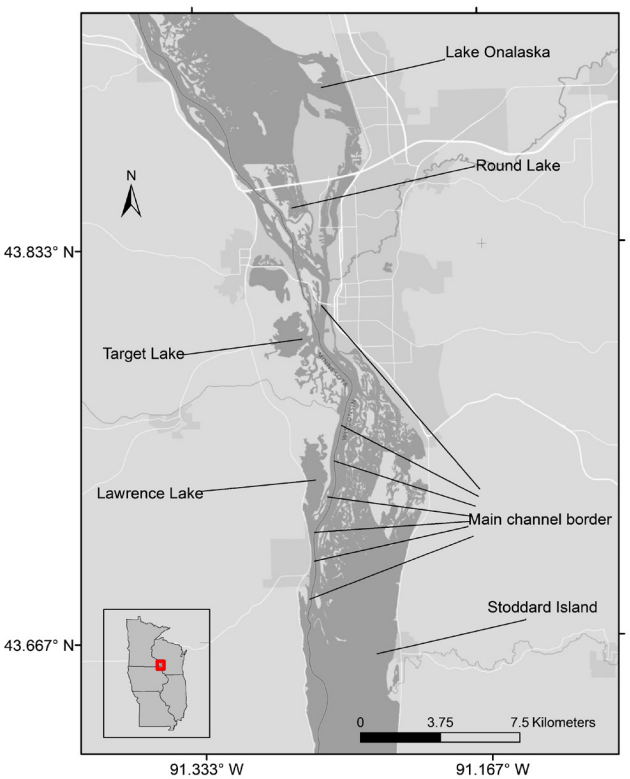

Fig. 1. Main-channel and off-channel sites of the upper Mississippi River sampled for consumers (young-of-year [YOY] bluegill sunfish, YOY gizzard shad, plain pocketbook, and zebra mussel) during 2005–2007.

DOI: 10.5268/IW-5.2.781

Table 1. Number of samples taken from different locations in the upper Mississippi River by species. All sites are off-channel areas except the main-channel border (Fig. 1).

Location	Bluegill[1]	Gizzard shad[2]	Zebra mussel[3]	Plain pocketbook[4]
Lake Onalaska			5	10
Round Lake	5	6		
Target Lake	3	2		
Lawrence Lake	11	1		
Stoddard Island	5	7		
Main-channel border	36	40	4	8

[1] *Lepomis macrochirus*
[2] *Dorosoma cepedianum*
[3] *Dreissena polymorpha*
[4] *Lampsilis cardium*

Field sampling

Consumers at the base of the food web were sampled by electrofishing (fish) or by hand (mussels) from August through October, 2005–2007. YOY bluegill were collected in all years. Due to their small size, whole fish were collected. In 2005 and 2007, each sample (n = 51) consisted of a single individual, but in 2006, composite samples consisting of 5 individuals in a single cryovial (n = 9) were taken at some locations (Table 1). YOY gizzard shad were collected over the same time period, again with analysis of individuals in 2005 and 2007 (42 samples) and composites of 5 individuals in 2006 (14 samples). For gizzard shad, skinless dorsal muscle was removed at the time of sampling. In 2005, plain pocketbook mussels were collected at a main-channel and an off-channel site (18 total; Table 1). Foot tissue from individual mussels was sampled and analyzed. In 2005, zebra mussels were collected in both a main-channel and an off-channel site. All soft tissues were removed from the shell, and several individuals from a single location were grouped together for a single sample (9 samples; Table 1). Samples of each species were placed in cryovials and frozen in liquid nitrogen in the field.

Fatty acids

Prior to FA analysis, samples were freeze-dried at −40 °C with a Labconco freeze dryer and ground to a homogenous powder in liquid nitrogen as described in Hebert et al. (2006). Briefly, fatty acid methyl esters (FAME) were obtained in a 3-step process that included extraction, derivatization, and quantification on a gas chromatograph (GC). An internal standard (5α-cholestane; Sigma-Aldrich; #C8003) was added to the sample tissue before extraction to estimate percent recovery. All of the mussel samples and about half of the fish samples were methylated using fresh boron trifluoride:methanol (10% w/w, Supleco 33021) for 2 h at 70 °C. The remaining fish samples were methylated using sulfuric acid:methanol (1% v/v) overnight at 50 °C (Christie 1989, p. 38). Fish samples were split approximately evenly between habitats among methylation methods (method identified for each sample in the Data Appendix); however, all samples were corrected for differences in methylation efficiency using an internal standard (17:1n-7). FAME was analyzed by GC (Agilent model 6890) using a Supelco 2560 capillary column (100 m, 0.25 mm inner diameter and a 0.2 µm film thickness) and quantified using a flame ionization detector. FAME in samples was identified by comparison of their retention times with a known standard (37-component FAME mix, Supelco 47885-U) and quantified with a 5-point calibration curve using this same standard. An additional single FA standard, docosapentaeonic acid (DPA; 22:5n-3, Supelco 47563-U), was added to the 37-component FAME mix to expand the number of quantifiable FAME. FA contents (i.e., mass fractions; µg FA per unit dry tissue mass) were calculated. Of the 38 FA quantified, 6 LC-PUFA known to be important to metazoans were included in our data analyses (Parrish 2009): linoleic acid (LIN; 18:2n-6), ALA (18:3n-3), arachidonic acid (ARA; 20:4n-6), EPA (20:5n-3), DPA (22:5n-3), and DHA (22:6n-3).

In addition to the individual LC-PUFA mentioned above, we used several FA metrics that are thought to be indicative of FA sources. We calculated the omega-3 to omega-6 (n-3:n-6) FA ratio, which has been used as an indicator of the importance of algal FA (rich in n-3 FA) versus terrestrial or vascular plant FAs (richer in n-6 FA) contributions to a food web (Ahlgren et al. 2009). Omega-3 FA included ALA, 20:3n-3, EPA, DPA, and DHA. Omega-6 FA included LIN, 18:3n-6, 20:2n-6, 20:3n-6, ARA, and 22:2n-6. We calculated total PUFA and also the unsaturation index (UI; by taking the mass

fraction of each FA and multiplying by the number of double bonds and then summing across all FA; similar to Novo and Fonseca 1989). Palmitoleic acid (16:1n-7) was included as a marker for diatoms (Léveillé et al. 1997). Total FAs (the sum of all measured FAs) were also calculated for each sample.

Data analysis

Statistical analyses were conducted using R v3.1.0 (R Development Core Team 2014). Because sample sizes were generally too low to adequately assess among-year differences, we ignored year in our analyses. The average and 95% credible intervals for FA content were sampled using Bayesian Markov Chain Monte Carlo methods (Carlin and Louis 2008) implemented using BRugs (Best and Lunn 2007), which interfaces R to OPENBugs (Thomas et al. 2006). Prior distributions were noninformative and vague (see Statistical Appendix); as a result, posterior distributions are dominated by the data (McCarthy 2007). Statistical differences in the average consumer FA among main-channel and off-channel areas were evaluated by estimating the difference between the mean FA content in each habitat. If the difference had a 95% credible interval that did not include zero, then the main-channel and off-channel sites were considered to be different (raw data to reproduce these results are provided in the Data Appendix).

Results and discussion

The least mobile consumers sampled here were 2 mussel species (zebra and plain pocketbook mussels). For both species, main-channel individuals had higher contents of LIN, EPA, DPA, and DHA than conspecifics in off-channel areas (Fig. 2). Plain pocketbook also had higher ALA content in the main-channel (Fig. 2). Main-channel individuals also had higher n-3:n-6 ratios, UI, PUFA, and 16:1n-7, all of which suggest the main-channel has more algal-derived FA relative to the off-channel areas (Fig. 3). Alternatively, ARA, which plays a role in response to stress in some biota (Koven et al. 2001), was similar between habitats in plain pocketbook and higher in the off-channel habitats for zebra mussels. ARA content is particularly high in freshwater bivalves, suggesting that this FA is of special importance in mussels, although the specific reasons for such high ARA content is as yet unclear (Newton et al. 2013).

Results from the fish species differed based on presumed mobility. As with the sedentary invertebrates, YOY bluegill had higher EPA and DPA contents in main-channel habitats (Fig. 2). Those main-channel individuals also had higher LIN, ALA, and DHA, although differences in those FA did have credible intervals that overlapped with zero (Fig. 2). Main-channel YOY bluegill had higher n-3:n-6 ratios, UI, PUFA, and 16:1n-7, consistent with the mussels and indicative of more algal-derived FA in the main-channel (Fig. 3). YOY bluegill tend to occupy small home ranges relative to larger bluegill (Gunnings and Shoop 1963) and have a diet restricted mainly to small invertebrates (Bauman and Kitchell 1974). In contrast, YOY gizzard shad are quite mobile (Schultz et al. 2007). Gizzard shad may move among aquatic areas and showed no differences between main-channel and off-channel habitats (Fig. 2 and 3). Gizzard shad are also omnivorous, filter-feeding on phytoplankton (Kutkuhn 1957), preying on zooplankton (Drenner et al. 1982), and at times consuming benthic detritus (Yako et al. 1996). Although the individual YOY gizzard shad used in this study were collected from different habitats, their high mobility may mean that individuals fed across habitat types and their flexible feeding strategies might be obscuring habitat comparisons.

The FA profiles of YOY bluegill, plain pocketbook mussels, and zebra mussels suggest that the autotrophic base of food webs in main-channel and off-channel areas

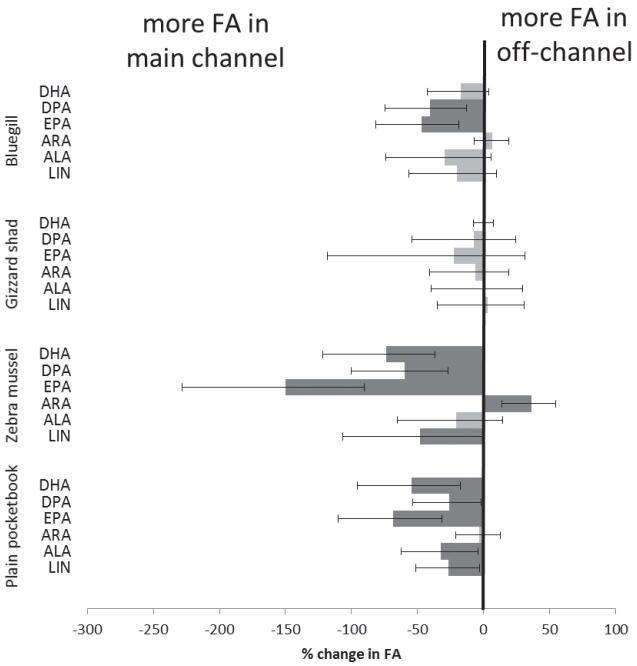

Fig. 2. Percent difference in fatty acid (FA) content between consumers collected in the main-channel and off-channel habitats of the upper Mississippi River (Pools 7 and 8; Fig. 1). Error bars indicate 95% credible intervals. Darkened bars highlight differences that have a 95% credible interval that does not include zero. DHA = docosahexaenoic acid, 22:6n-3; DPA = docosapentaeonic acid, 22:5n-3; EPA = eicosapaentanoic acid, 20:5n-3; ARA = arachidonic acid, 20:4n-6; ALA- α-linolenic, 18:3n-3; LIN = linoleic acid, 18:2n-6.

 DOI: 10.5268/IW-5.2.781

of the Mississippi River is distinct. Long-chain PUFAs such as EPA and DHA were more abundant in tissues from individuals collected in the main channel, and these PUFAs tend to be more prevalent in algal taxa than in cyanobacteria or vascular plants (Ahlgren et al. 1992). Palmitoleic acid (16:1n-7), an FA found in relatively high amounts in diatoms (Napolitano 1999, Reuss and Poulsen 2002), was also more common in the main-channel. Lower n-3:n-6 ratios observed in the less mobile species in off-channel habitats (Fig. 3) may indicate a greater reliance within the off-channel food web on macrophytes (either terrestrial or aquatic) because most vascular plants tend to have lower n-3 FA content (Ahlgren et al. 2009). Terrestrial carbon may be an important food resource for consumers in aquatic systems (Tanentzap et al. 2014), but vascular plants, with the exception of species valued for their seed oils (e.g., canola and camelina), tend to have low PUFA content (Brett et al. 2009a, Taipale et al. 2013). If off-channel food webs rely more on organic material derived from macrophyte production than main-channel food webs, then this could drive the pattern of lower off-channel PUFA in basal consumers observed here. Research on microbial primary producers has not demonstrated consistent differences between main-channel and off-channel habitats (Decker 2012), but off-channel habitats do tend to accumulate macrophytes (Houser et al. 2013).

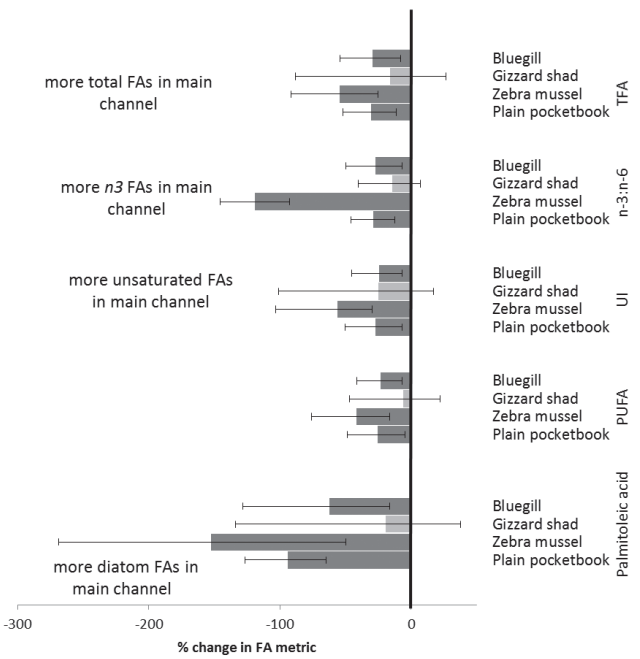

Fig. 3. Percent difference in indices of fatty acid (FA) content and origin between consumers collected in the main-channel and off-channel habitats of the upper Mississippi River (Pools 7 and 8; Fig. 1). Error bars indicate 95% credible intervals. Darkened bars highlight differences that have a 95% credible interval that does not include zero. UI = Unsaturation Index, calculated by taking the mass fraction of each FA and multiply it by the number of double bonds and then summing across all FA; n-3:n-6 = the omega-3 to omega-6 FA ratio (∑[18:3n-3, 20:3n-3, 20:5n-3, 22:5n-3, 22:6n-3]/∑[18:2n-6, 18:3n-6, 20:2n-6, 20:3n-6, 20:4n-6, 22:2n-6]); Palmitoleic acid = 16:1n-7.

Do main-channel habitats have higher-quality food resources than off-channel habitats? These results suggest that, at least in the upper Mississippi River, the main-channel food webs have higher-quality FA than off-channel areas. Whether the increase in food quality is sufficient to increase secondary production or overcome other drawbacks to inhabiting the main-channel (e.g., increased swimming cost for fish) remains unclear. Certainly, opportunistic, mobile consumers such as adult bluegill might find higher-quality food resources in the main channel, potentially explaining their previously unexpected appearance in main-channel habitats (Gutreuter et al. 2010). At a minimum, upper Mississippi River predators of YOY bluegill and the mussel species sampled here would have access to higher-quality food resources in the main-channel than the off-channel areas. The extent to which these results can be extrapolated to other large river systems is unknown.

Acknowledgements

The use of trade names does not constitute endorsement by the US Geological Survey. We are grateful to Robert Kennedy, Jennifer Cavanaugh, Reid Northwick, Alex Schroeder, Dane Cordes, Samantha Olsen, Tammy Yeldon, and Beau Webber for assistance in the field and laboratory. Comments from Jeff Houser and 2 anonymous reviewers greatly improved this manuscript.

References

Ahlgren G, Gustafsson I-B, Boberg M. 1992. Fatty acid content and chemical composition of freshwater microalgae. J Phycol. 28:37–50.

Ahlgren G, Vrede T, Goedkoop W. 2009. Fatty acid ratios in freshwater fish, zooplankton and zoobenthos - Are there specific optima? In Arts MT, Brett MT, Kainz MJ, editors. Lipids in aquatic ecosystems. New York (NY): Springer-Verlag. p. 147–178.

Arts MT, Kohler CC. 2009. Health and condition in fish: the influence of lipids on membrane competency and immune response. In Arts MT, Brett MT, Kainz MJ, editors. Lipids in aquatic ecosystems. New York (NY): Springer-Verlag. p. 237–256.

Ball RC. 1943. A tagging experiment on the fish population of Third Sister Lake, Michigan. T Am Fish Soc. 74:360–369.

Bauman PC, Kitchell JF. 1974. Diel patterns of distribution and feeding of bluegill (*Lepomis macrochirus*) in Lake Wingra, Wisconsin. T Am Fish Soc. 103:255–260.

Best N, Lunn D. 2007. The BRugs Package.

Brett MT, Kainz MJ, Taipale SJ, Seshan H. 2009a. Phytoplankton, not allochthonous carbon, sustains herbivorous zooplankton production. P Natl Acad Sci USA. 106:21197–21201.

Brett MT, Muller-Navarra DC, Persson J. 2009b. Crustacean zooplankton fatty acid composition. In Arts MT, Brett MT, Kainz MJ, editors. Lipids in aquatic ecosystems. New York (NY): Springer-Verlag. p. 115–146.

Carlin BP, Louis TA. 2008. Bayesian methods for data analysis, 3rd ed. Boca Raton (FL): Chapman & Hall/CRC.

Christie WW. 1989. The analysis of fatty acids. In Gas chromatography and lipids. Bridgewater (UK): PJ Barnes & Associates (The Oily Press).

Cross FB, Collins JT. 1995. Fishes in Kansas, 2nd ed. Lawrence (KS): University Press of Kansas.

Decker J. 2012. Nutrient controls on phytoplankton composition and ecological function among hydrologically distinct habitats in the Upper Mississippi River. New York (NY): Fordham University.

Drenner RW, deNovelles F Jr, Kettle D. 1982. Selective impact of filter-feeding gizzard shad on zooplankton community structure. Limnol Oceanogr. 27:965–968.

Gatz AJ, Adams SM. 1994. Patterns of movement of centrarchids in two warmwater streams in eastern Tennessee. Ecol Freshw Fish. 3:35–48.

Gunnings GE, Shoop CR. 1963. Occupancy of home range by longear sunfish, *Lepomis m. megalotis* (Rafinesque) and bluegill, *Lepomis m. macrochirus* (Rafineaque). Anim Behav. 11:325–330.

Gutreuter S, Vallazza JM, Knights BC. 2010. Lateral distribution of fishes in the main-channel trough of a large floodplain river: implications for restoration. River Res Appl. 26:619–635.

Hebert CE, Arts MT, Weseloh DVC. 2006. Ecological tracers can quantify food web structure and change. Environ Sci Technol. 40:5618–5623.

Houser J, Giblin S, James W, Langrehr H, Rogala J, Sullivan J, Gray B. 2013. Nutrient cycling, connectivity and free-floating plant abundance in backwater lakes of the Upper Mississippi River. River Syst. 21:71–89.

Koven W, Barr Y, Lutzky S, Ben-Atia I, Weiss R, Harel M, Behrens P, Tandler A. 2001. The effects of dietary arachidonic acid (20:4n-6) on growth, survival, and resistance to handling stress in gilfhead seabream (*Sparus aurata*) larvae. Aquaculture. 193:107–122.

Kutkuhn JH. 1957. Utilization of plankton by juvenile gizzard shad in a shallow prairie lake. T Am Fish Soc. 87:80–103.

Léveillé J, Amblard C, Bourdier G. 1997. Fatty acids as specific algal markers in a natural lacustrian phytoplankton. J Plankton Res. 19:469–490.

Madsen J, Chambers P, James W, Koch E, Westlake D. 2001. The interaction between water movement, sediment dynamics and submersed macrophytes. Hydrobiologia. 444:71–84.

McCarthy M. 2007. Bayesian methods for ecology. New York (NY): Cambridge University Press.

Napolitano GE. 1999. Fatty acids as trophic and chemical markers in freshwater ecosystems. In Arts MT, Wainman BC, editors. Lipids in freshwater ecosystems. New York (NY): Springer-Verlag. p. 21–44.

Newton TJ, Vaughn CC, Spooner DE, Nichols SJ, Arts MT. 2013. Profiles of biochemical tracers in unionid mussels across a broad geographical range. J Shellfish Res. 32:497–507.

Novo C, Fonseca E. 1989. Change of the unsaturation of the lymphocyte plasma membrane by ethanol and fatty acids. Actas Bioquim. 2:63–70.

Parrish CC. 2009. Essential fatty acids in aquatic food webs, In Arts MT, Wainman BC, editors. Lipids in freshwater ecosystems. New York (NY): Springer-Verlag. p. 309–326.

Peterson B, Fry B. 1987. Stable isotopes in ecosystem studies. Ann Rev Ecol Syst. 18:293–320.

R Development Core Team. 2014. R: A language and environment for statistical computing. Vienna (Austria): R Foundation for Statistical Computing. Available from: http://www.R-project.org

Reuss N, Poulsen LK. 2002. Evaluation of fatty acids as biomarkers for a natural plankton community. A field study of a spring bloom and a post-bloom period off West Greenland. Mar Biol. 141:423–434.

Schultz DW, Garvey JE, Brooks RC. 2007. Backwater immigration by fishes through a water control structure: implications for connectivity and restoration. N Am J Fish Manage. 27:172–180.

Taipale S, Brett M, Hahn M, Martin-Creuzburg D, Yeung S, Hiltunen M, Strandberg U, Kankaala P. 2013. Differing Daphnia magna assimilation efficiencies for terrestrial, bacterial and algal carbon and fatty acids. Ecology. 95:563–576.

Tanentzap AJ, Szkokan-Emilson EJ, Kielstra BW, Arts MT, Yan ND, Gunn JM. 2014. Forests fuel fish growth in freshwater deltas. Nature Comm. 5. doi:10.1038/ncomms5077

Thomas A, O'Hara B, Ligges U, Sturtz S. 2006. Making BUGS open. R News. 6:12–16.

Yako LA, Dettmers JM, Stein RA. 1996. Feeding preferences of omnivorous gizzard shad as influenced by fish size and zooplankton density. T Am Fish Soc. 125:753–759.

Supplementary Material

Supplementary Material is available for download via the Inland Waters website, https://www.fba.org.uk/journals/index.php/IW:

Statistical Appendix
Data Appendix

 DOI: 10.5268/IW-5.2.781