The Prairie Naturalist

Great Plains Natural Science Society

12-2012

Walleye Trophic Position Before and After a Gizzard Shad Extirpation

Bethany J. Bethke
Department of Natural Resources, Finland, bethany.bethke@state.mn.us

Justin A. Vandehey
South Dakota State University & Wisconsin Cooperative Fishery Research Unit

Mark J. Fincel
South Dakota Game, Fish and Parks, Fort Pierre Regional Office

Brian D.S. Graeb
South Dakota State University

Mark T. Porath
Nebraska Game and Parks Commission, Fisheries Division

Bethke, Bethany J.; Vandehey, Justin A.; Fincel, Mark J.; Graeb, Brian D.S.; and Porath, Mark T., "Walleye Trophic Position Before and After a Gizzard Shad Extirpation" (2012). *The Prairie Naturalist*. 49.
https://digitalcommons.unl.edu/tpn/49

The Prairie Naturalist 44:72–78; 2012

Walleye Trophic Position Before and After a Gizzard Shad Extirpation

BETHANY J. BETHKE[1], JUSTIN A. VANDEHEY[2], MARK J. FINCEL, BRIAN D. S. GRAEB, AND
MARK T. PORATH

Department of Natural Resources, Finland, MN 55603, USA (BJB)
Department of Natural Resource Management, South Dakota State University, Brookings, SD 57007, USA (JVDH, BDSG)
South Dakota Game, Fish and Parks, Ft. Pierre Regional Office, Ft. Pierre, SD 57532, USA (MJF)
Nebraska Game and Parks Commission, Fisheries Division, Lincoln, NE 68503, USA (MTP)

ABSTRACT Walleye (*Sander vitreus*) are an ecologically and recreationally important sport fish species. Reduced growth and condition in walleye can occur when prey availability is limited. In two Nebraska reservoirs, walleye consumed gizzard shad (*Dorosoma cepedianum*) as their primary prey until a winterkill extirpated the gizzard shad in 2001. Because of the winterkill, walleye in the two reservoirs had to change to alternative prey items. Our objective was to determine if stable isotope analysis on archived walleye scales can be used to detect a known food web shift in two reservoir food webs. We quantified the changes in walleye trophic position following the loss of gizzard shad using stable isotope analysis of carbon (δ^{13}C) and nitrogen (δ^{15}N) from archived scales. Walleye δ^{15}N decreased and δ^{13}C increased in both reservoirs after the extirpation of gizzard shad, indicating walleye likely fed at a lower trophic level on more benthic or littoral prey resources post winterkill. A replacement of gizzard shad by white perch (*Morone americana*) in Pawnee Reservoir may have ameliorated the loss of gizzard shad; in the other system, walleye appeared to feed on a wider variety of prey items as indexed by increased δ^{13}C variability. Our results indicated that walleye were robust to gizzard shad extirpation.

KEY WORDS *Dorosoma cepedianum*, gizzard shad, Nebraska, *Sander vitreus*, walleye

Walleye (*Sander vitreus)* are a common top predator in aquatic ecosystems across the Northern Great Plains (Hoagstrom and Berry 2010). Many recreational fisheries throughout this region are managed for walleye and stocking programs are common (Berry and Young 2004, Lucchesi 2008). Walleye reach piscivory by age-1 or earlier (Hartman and Margraf 1992, Mittelbach and Persson 1998), but walleye also can consume macroinvertebrates and zooplankton even as adults (Slipke and Duffy 1997, Chipps and Graeb 2011, VanDeHey 2011). However, walleye growth and condition is reduced when prey fish densities are low and walleye feed on invertebrates (Hartman and Margraf 1992, Ward et al. 2007, Graeb et al. 2008, Ward et al. 2008, VanDeHey 2011). Therefore, invertebrates may not be the most energetically efficient prey for walleye (Jones et al. 1994).

Gizzard shad (*Dorosoma cepedianum*) often are an important prey species for walleye where the two species are sympatric (Hartman and Margraf 1992, Michaletz 1997, Porath 2006, VanDeValk et al. 2008, Wuellner et al. 2010). Growth and recruitment of age-0 walleye has been closely related to gizzard shad abundance in western Lake Erie (Madenjian et al. 1996), and age-0 walleye have selected shad over other prey species (Forney 1974, Knight et al. 1984, Hartman and Margraf 1992, Einfalt and Wahl 1997). Juvenile walleye growth in ponds and enclosures increased when fed a diet of larval gizzard shad relative to zooplankton (Stahl and Stein 1994, Michaletz 1997). Additionally, gizzard shad comprised most of the adult walleye diets throughout the growing season in multiple South Dakota reservoirs (Davis 2004, Ward et al. 2007, Wuellner et al. 2010, Fincel 2011). Similarly, walleye were found to consume gizzard shad as a major portion of their diets in Harlan County Reservoir, Nebraska (Olson et al. 2007). Walleye populations appear to benefit from having the soft-rayed, calorie-dense gizzard shad available (Ward et al. 2007, Wuellner et al. 2008, VanDeHey 2011).

During winter 2000–2001, eastern Nebraska experienced unusually cold winter conditions resulting in the extirpation of gizzard shad from several small flood-control impoundments including East Twin Reservoir and Pawnee Reservoir (Porath 2006). Gizzard shad were the only species extirpated during this event, for a description of the aquatic systems evaluated and population assessments methods refer to Porath (2006). These two reservoirs provide important urban fisheries and there were concerns regarding the impacts of the loss of gizzard shad for each respective sport fishery. In addition, white perch (*Morone americana*) were discovered in Pawnee Reservoir shortly after the winterkill; the population rapidly expanded and comprised up to 97% of walleye diets (by weight) in 2006 (Gosch 2008). However, gizzard shad were not replaced with an alternative prey fish in East Twin Reservoir, although other small-bodied fishes (such as *Lepomis* and *Pomoxis* species) remained available. These two systems provided an ideal opportunity for identifying trophic changes in walleye populations following the loss of an important prey species in Midwestern reservoirs. However, without historic information on the diets of walleye, comparing walleye trophic interactions could not be completed with traditional methods (e.g., stomach contents analysis).

---

[1] Corresponding author email address: bethany.bethke@state.mn.us

[2] Present address: Wisconsin Cooperative Fishery Research Unit, Stevens Point, WI 54481, USA

Stable isotope analysis (SIA) is a useful tool for quantifying food web linkages in terrestrial and aquatic systems (Peterson and Fry 1987, Dalerum and Angerbjörn 2005), assessing species introduction and extirpations (Vander Zanden and Rasmussen 1999), evaluating temporal changes in aquatic food webs (Satterfield and Finney 2002), and determining trophic level and energy sources (Peterson and Fry 1987, Grey 2006). Stable isotope analysis also provides a temporally integrated indicator of an organism's position in the food web (Vander Zanden and Rasmussen 1999, McIntyre et al. 2006). Carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotopes can be used to estimate energy sources and trophic position of an organism (Peterson and Fry 1987, Grey 2006).

Muscle tissue is most commonly used for SIA in fishes, but fins, otoliths, and scales also have been used (Sanderson et al. 2009, Fincel et al. 2011*a*). Calcified structures, such as scales, are often available for historic food web studies as management agencies often keep archives for aging purposes. Scales are well suited for retrospective studies, and provide a medium for non-lethal study of a fish's trophic level (Satterfield and Finney 2002, Dalerum and Angerbjörn 2005, Kelly et al. 2006). Despite widespread availability, only a few studies (Perga and Gerdeaux 2003, Pruell et al. 2003, Vander Zanden et al. 2003, Gerdeaux and Perga 2006, Grey et al. 2009) have conducted SIA on scales and the use of SIA on archived calcified structures to assess the impacts of historical extirpations and invasions on food web ecology is a novel concept. Therefore, our objective was to examine changes in walleye trophic position after gizzard shad extirpation using stable isotope analysis (SIA) on archived walleye scales.

STUDY AREA

We studied walleye energy sources at two flood control reservoirs in Lancaster County, Nebraska. East Twin Reservoir was an 85 ha reservoir constructed in 1965. Pawnee Reservoir was a 300 ha reservoir constructed in 1964. Both reservoirs were in the Salt Creek watershed (see Porath 2006 for impoundment characteristics), an intensively cultivated region (Tunink 1991, Jackson 1995). East Twin Reservoir was part of a Nebraska Game and Parks Commission (NGPC) Wildlife Management Area and Pawnee Reservoir was part of a NGPC State Recreation Area; both reservoirs were used for recreational angling.

METHODS

Sample collection

We collected walleye from each lake using experimental gillnets during standardized fish surveys conducted by the NGPC between 1997 and 2007 using methods described in Jackson (1995). We collected a minimum of 10 scales from individual walleye for aging purposes. We kept scales that were not processed for aging and stored them in the envelopes in a climate-controlled office building. We collected total length (TL; mm) and weight (g) of each walleye collected and recorded the total number of fish caught per net night. To allow sufficient turnover of stable isotope values between prey conditions (Buchheister and Latour 2010), we used walleye scales from surveys conducted at East Twin Reservoir in 1997 and 2000 (pre-winterkill), and 2006 and 2007 (post-winterkill). Similarly, we used walleye scales from surveys conducted at Pawnee Reservoir in 1997, 1998, and 2000 (pre-winterkill) and 2007 (post-winterkill).

In addition to walleye sampling, we also obtained stable isotope samples for potential prey of walleye following the winterkill. We targeted a minimum of five individuals of each small-bodied or juvenile fish observed in each system. Gosch et al. (2010) documented Pawnee Reservoir walleye consumed white perch following the winterkill. Pawnee Reservoir walleye diets were comprised of >80% white perch (by weight) in spring, summer, and fall of 2006 and 2007. However, there was no previously available walleye diet information post-gizzard shad winterkill from East Twin Reservoir. Therefore, we collected a variety of small-bodied fishes that could potentially serve as walleye prey from East Twin Reservoir in August of 2009 using night near-shore, AC, boat electrofishing. We placed prey samples on ice for transportation and froze them at -20° C until further processing. We were unable to procure baseline samples retrospectively and therefore assumed a constant $\delta^{15}N$ baseline across the study period.

Stable isotope analysis

We rinsed walleye scales with de-ionized water to remove surface debris and dried them for a minimum of three days at 60° C. We sent scales to the Cornell Stable Isotope Laboratory in Ithaca, NY, where they were ground with a SPEX Certiprep 6750 Freezer/Mill (SPEX SamplePrep, LLC, Metuchen, New Jersey, USA), and weighed (0.25 mg) with a Sartorius MC5 Microbalance (Data Weighing Systems, Inc., Elk Grove, Illinois, USA). We determined stable $\delta^{13}C$ and $\delta^{15}N$ using a Delta V isotope ratio mass spectrometer (Thermo Fisher Scientific, Waltham, Massachusetts, USA) interfaced to a Carlo-Erba NC2500 elemental analyzer (CE Elantech, Inc., Lakewood, New Jersey, USA). We analyzed prey fish samples separately. We removed the head and entrails from prey fish (Fincel et al. 2011*b*) and dried remaining tissue for a minimum of three days at 60° C. We ground dried samples with a mortar and pestle and weighed the contents with a Mettler-Toledo XP26 Delta Range balance (Mettler-Toledo GmbH, Greifensee, Switzerland). We analyzed samples for $\delta^{13}C$ and $\delta^{15}N$ using a Europa 20–20 mass spectrometer (Sercon, Ltd., Cheshire, UK) at the Precision Agriculture Laboratory at South Dakota State University in Brookings, SD. Prey fish $\delta^{13}C$ was corrected for lipid content using the equation recommended by Post et al. (2007). We assumed one trophic level to be equal to 3.4‰ δ^{15}N (Vander Zanden and Rassmussen 2001).

Statistical analysis

Due to fluctuations in walleye population size-structure over time, the TL of walleye sampled for SIA before and after the winterkill was unequal. In piscivores, δ^{15}N generally increases with body size as fish prey become more important in the diet (Vander Zanden and Rasmussen 2001). Therefore, we tested for significant differences in mean TL of walleye from pre- and post-winterkill samples using an analysis of variance (ANOVA) and where differences in mean TL existed between pre- and post-winterkill periods, we corrected isotope ratios for length (covariate) differences between years using adjusted least square means (Ott and Longnecker 2001). We used Student's t-test to determine differences in δ^{13}C and δ^{15}N walleye and two-sample F-tests for variances to compare δ^{13}C variance before and after the gizzard shad winterkill. We conducted all statistical analyses using SAS version 9.2 (SAS Institute, Cary, NC, USA) and set alpha at 0.05.

RESULTS

Mean TL of walleye sampled for scale SIA from Pawnee Reservoir did not differ ($F_{1,65} = 0.36$, $P = 0.55$) pre- and post-winterkill, but East Twin Reservoir mean TL of walleye sampled pre-winterkill were longer ($F_{1,35} = 16.03$, $P < 0.001$) than fish sampled post-winterkill, necessitating the use of adjusted mean SIA values in East Twin Reservoir. Pre-winterkill walleye collected from East Twin Reservoir ranged from 390 to 710 mm TL, with a mean of 527 mm (SE = 20, n = 22). Fish collected post-winterkill ranged from 246 to 625 mm TL with a mean of 389 mm (SE = 29, n = 14). In Pawnee Reservoir, pre-winterkill walleye length ranged from 159 to 558 mm TL, with a mean of 440 mm (SE = 37, n = 24), and post-winterkill length ranged from 285 to 668 mm TL with a mean of 419 mm (SE = 12, n = 44).

In both populations, mean walleye d^{13}C and d^{15}N shifted after the gizzard shad winterkill (Fig. 1). In East Twin Reservoir, adjusted mean d^{13}C of walleye scales increased from –23.01‰ to –19.86‰ ($t_{35} = 9.16$, $P < 0.001$) and became more variable ($F_{1,35} = 4.06$, $P < 0.001$) after the gizzard shad winterkill, indicating walleye consumed a wider variety of prey and likely derived their energy from more benthic than pelagic (gizzard shad) prey after the winterkill. Walleye mean d^{15}N decreased from 17.8‰ to 16.0‰ ($t_{35} = –7.91$, $P < 0.001$), approximately half a trophic level. In East Twin Reservoir, isotopic values of post-winterkill scales were variable but were approximately one trophic level above the common prey fish signature. The small-bodied fishes we sampled from East Twin Reservoir as representative potential prey post-winterkill had similar isotopic signatures compared to pre-winterkill walleye. The green sunfish (*Lepomis cyanellus*), bluegill (*L. macrochirus*), white crappie (*Pomoxis annularis*), white bass (*M. chrysops*), juvenile largemouth bass (*Micropterus salmoides*), and juvenile walleye we sampled all measured about one trophic level below the post-winterkill adult walleye and had similar d^{13}C values (Fig. 1).

In Pawnee Reservoir adjusted mean d^{13}C increased from –23.08‰ prior to extirpation of shad to –18.11‰ following winterkill ($t_{65} = 26.40$, $P < 0.001$) but did not increase in variability ($F_{1,65} = 1.02$, $P = 0.47$). This increase in d^{13}C, indicated walleye in Pawnee Reservoir also consumed more benthic than pelagic prey after the gizzard shad extirpation. Mean d^{15}N of walleye scales decreased from 15.5‰ to 13.5‰ in Pawnee Reservoir ($t_{65} = –10.88$, $P < 0.001$) following the gizzard shad winterkill. In Pawnee Reservoir post-winterkill walleye isotopic signatures were close to values measured for white perch (Fig. 1).

DISCUSSION

In Pawnee and East Twin Reservoirs walleye δ^{13}C became less negative, indicating more reliance on benthic or littoral prey resources post gizzard shad extirpation. Additionally, trophic level of walleye decreased in both systems. These results, consistent among the two populations, provide evidence for change in walleye trophic position following gizzard shad extirpation. The diet breadth of walleye, as indicated by the variability in δ^{13}C values, increased in East Twin Reservoir after the extirpation of gizzard shad, suggesting walleye consumed a wider variety of prey items post-gizzard shad extirpation. Furthermore, the stable isotope values of Pawnee Reservoir walleye scales after the winterkill and introduction of white perch were consistent with the findings of Gosch et al. (2010), suggesting white perch were the dominant energy source for walleye.

One limitation common to archived SIA studies is the lack of comparable archived baseline data. In recent years, much attention has been paid to the variability of stable isotope baselines temporally and spatially within systems (Grey 2006, Solomon et al. 2008, Fincel et al. 2011*b*, Guzzo et al. 2011). Without baseline data for Pawnee and East Twin Reservoirs, it is not possible to wholly attribute the shift in walleye scale stable isotope values to a shift in feeding habits. However, documentation of the same trend in both systems coupled with previous diet information (Porath 2006, Gosch et al. 2010) suggested that shifts in isotopic signatures were likely not a result of shifting baselines. Walleye are adaptable predators as evidenced by numerous studies that have documented diet shifts both experimentally (Lyons 1987, Porath and Peters 1997) and *in situ* (Parsons 1971, Forney 1974, Knight et al. 1984, Lyons and Magnuson 1987). Where walleye exist without soft-rayed prey fishes (e.g., gizzard shad or cisco; *Coregonus artedi*) they primarily consume littoral fishes and invertebrates (Lyons and Magnuson 1987, Liao et al. 2002, Chipps and Graeb 2011). Our data support these previous studies; walleye maintained a high trophic level by consuming a pelagic prey resource before the gizzard shad winterkill, then declined in trophic level when they switched to more benthic or littoral prey resources following gizzard shad elimination. Further, the increase in isotopic variability of walleye in East Twin is indicative of fish consuming a wider variety of prey items and is not necessarily impacted by shifting baselines (Vander Zanden et al. 2000, Bearhop et al. 2004, Paterson et al. 2006, Syvaranta and Jones 2008). Walleye diets in our study shifted and became more variable following the extirpation of gizzard shad.

MANAGEMENT IMPLICATIONS

Many agencies are discontinuing the use of scale collection as they switch to using other structures (e.g., otoliths) to age fishes. However, as scales are relatively inexpensive and non-lethal structures to collect from most fish, we recommend agencies continue collecting scales for stable isotope analysis. As many changes in fisheries trophic structure are

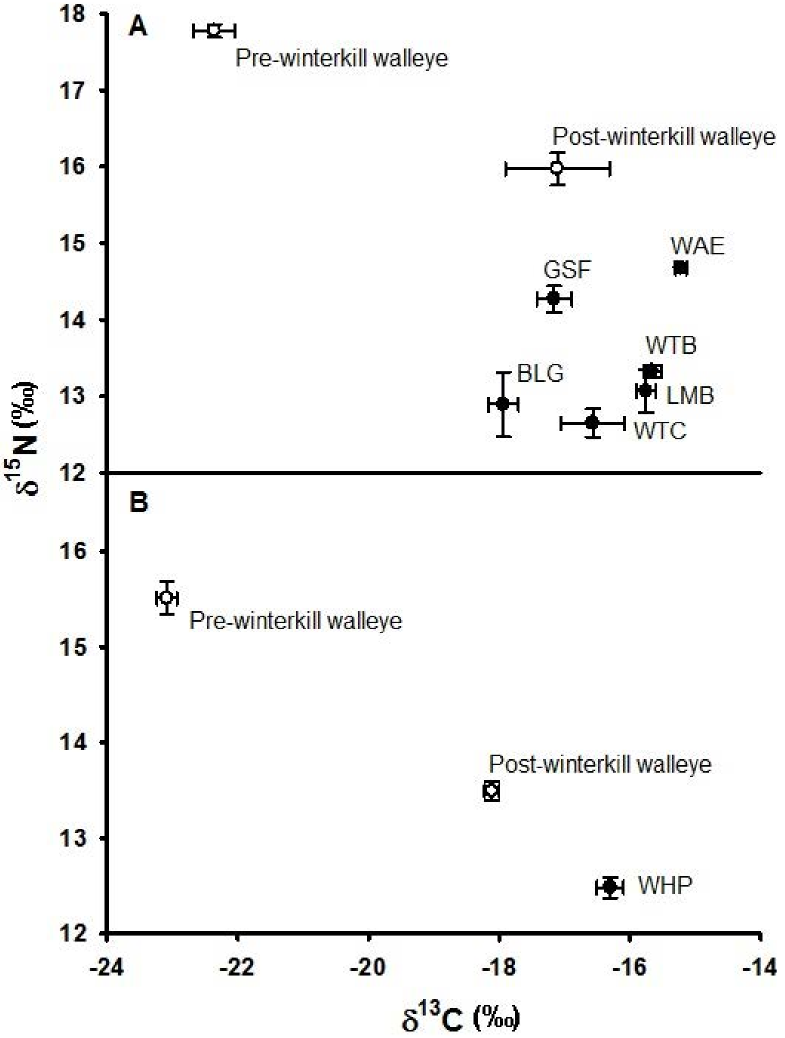

Figure 1. Stable carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotope ratios from adult walleye scales (open circles) collected from East Twin Reservoir (A) and Pawnee Reservoir (B) pre- and post-gizzard shad winterkill that took place in winter 2000–2001. Pre-winterkill walleye were collected in 1997 and 2000 in East Twin Reservoir, in 1997, 1998, and 2000 in Pawnee Reservoir. Post-winterkill walleye were collected in 2006 and 2007 in East Twin Reservoir and in 2007 in Pawnee Reservoir. Potential prey fish (closed circles) stable isotope ratios from East Twin Reservoir are also presented. LMB = juvenile (< 200 mm TL) largemouth bass (*Micropterus salmoides*), WAE = juvenile (< 200 mm TL) walleye, WTC = white crappie (*Pomoxis annularis*), GSF = green sunfish (*Lepomis cyanellus*), BLG = bluegill (*L. macrochirus*), WHP = white perch (*Morone americana*) and WHB = white bass (*M. chrysops*). White perch stable isotope values from Pawnee Reservoir were obtained from Gosch (2008). Error bars represent one standard error.

unforeseeable, having an archived collection of scales may be useful for reconstructing food webs and making comparisons over time. We suggest that while agencies may be without the resources to invest in costly, time-intensive diet studies, the periodic collection of calcified tissue samples and baseline data for SIA may be a viable means for clarifying long-term trends in trophic interactions among fishes. Additionally, we recommend research be conducted comparing isotope signatures from calcified structures temporally to identify if the duration of preservation impacts SIA signatures.

ACKNOWLEDGMENTS

The authors wish to thank N. Gosch and the Nebraska Game and Parks Commission for providing data for this project. Thanks to D. Willis and D. Dembkowski for reviewing a previous draft of this manuscript. Thanks to the Cornell Stable Isotope Laboratory and South Dakota State University Precision Agriculture Laboratory for sample processing. This project was funded by South Dakota State University Research Scholarship Support Fund.

LITERATURE CITED

Bearhop, S., C. E. Adams, S. Waldron, R. A. Fuller, and H. Macleod. 2004. Determining trophic niche width: a novel approach using stable isotope analysis. Journal of Animal Ecology 73:1007–1012.

Berry, C. R., and B. Young. 2004. Fishes of the Missouri National Recreational River, South Dakota and Nebraska. Great Plains Research 14:89–114.

Buchheister, A., and R. J. Latour. 2010. Turnover and fractionation of carbon and nitrogen stable isotope in tissues of a migratory coastal predator, summer flounder (Paralichthys dentatus). Canadian Journal of Fisheries and Aquatic Science 67:445–461.

Chipps, S. R., and B. D. S. Graeb. 2011. Feeding ecology and energetics. Pages 303–320 *in* B. A. Barton, editor. Biology, management and culture of walleye and sauger. American Fisheries Society, Bethesda, Maryland, USA.

Davis, B. A. 2004. Estimating trophic position of Lake Oahe walleye using stable isotope analysis. Thesis, South Dakota State University, Brookings, USA.

Dalerum, F., and A. Angerbjörn. 2005. Resolving temporal variation in vertebrate diets using naturally occurring stable isotopes. Oecologia 144:647–658.

Einfalt, L. M., and D. H. Wahl. 1997. Prey selection by juvenile walleye as influenced by prey morphology and behavior. Canadian Journal of Fisheries and Aquatic Sciences 54:2618–2626.

Fincel, M. J. 2011. Productivity and trophic interactions in the Missouri River impoundments. Dissertation, South Dakota State University, Brookings, USA.

Fincel, M. J., J. A. VanDeHey, and S. R. Chipps. 2011*a*. Nonlethal sampling of walleye for stable isotope analysis: a comparison of three tissues. Fisheries Management and Ecology 19:283–292.

Fincel, M. J., J. A. VanDeHey, A. J. Weustewald, and S. R. Chipps. 2011*b*. Comparing isotope signatures of prey fish: does gut removal affect δ^{13}C or δ^{15}N signatures? Journal of Freshwater Ecology 27:55–62.

Forney, J. L. 1974. Interactions between yellow perch abundance, walleye predation, and survival of alternate prey in Oneida Lake, New York. Transactions of the American Fisheries Society 103:15–24.

Gerdeaux, D., and M. Perga. 2006. Changes in whitefish scales δ^{13}C during eutrophication and reoligotrophication of subalpine lakes. Limnology and Oceanography 51:772–780.

Gosch, N. J. C. 2008. Predation as a mechanism for control of white perch: an investigation of food habits in two Nebraska reservoirs. Thesis, University of Nebraska, Lincoln, USA.

Gosch, N. J. C., L. L. Pierce, and K. L. Pope. 2010. The effect of predation on stunted and nonstunted white perch. Ecology of Freshwater Fish 19:401–407.

Graeb, B. D. S., S. R. Chipps, D. W. Willis, J. P. Lott, R. P. Hanten, W. Nelson-Stastny, and J. W. Erickson. 2008. Walleye response to rainbow smelt population decline and liberalized angling regulations in a Missouri River reservoir. American Fisheries Society Symposium 62:275–292.

Grey, J. 2006. The use of stable isotope analyses in freshwater ecology: current awareness. Polish Journal of Ecology 54:563–584.

Grey, J., C. T. Graham, J. R. Britton, and C. Harrod. 2009. Stable isotope analysis of archived roach (*Rutilis rutilus*) scales for retrospective study of shallow lake responses to nutrient reduction. Freshwater Biology 54:1663–1670.

Guzzo, M. M., D. G. Haffner, S. Sorge, S. A. Rush, and A. T. Fisk. 2011. Spatial and temporal variabilities of delta(13) C and delta(15)N within lower trophic levels of a large lake: implications for estimating trophic relationships of consumers. Hydrobiologia 675:41–53.

Hartman, K. J, and F. J. Margraf. 1992. Effects of prey and predator abundances on prey consumption and growth on walleyes in western Lake Erie. Transactions of the American Fisheries Society 121:245–260.

Hoagstrom, C. W., and C. R. Berry. 2010. The native range of walleyes in the Missouri River drainage. North American Journal of Fisheries Management 30:642–654.

Jackson, J. 1995. A Summary of Pawnee Reservoir fish community changes from 1966 to 1994. Nebraska Game and Parks Commission Report, Lincoln, USA.

Jones, M. S., J. P. Goettl, and S. A. Flickinger. 1994. Changes in walleye food habits and growth following a rainbow smelt introduction. North American Journal of Fisheries Management 14:409–414.

Kelly, M. H., W. G. Hagar, T. D. Jardine, and R. A. Canjak. 2006. Nonlethal sampling of sunfish and slimy sculpin for stable isotope analysis: how scale and fin tissue compare with muscle tissue. North American Journal of Fisheries Management 26:921–925.

Knight, R. L., F. J. Margraf, and R. F. Carline. 1984. Piscivory by walleye and yellow perch in western Lake Erie. Transactions of the American Fisheries Society 113:677–693.

Liao, H., C. L. Pierce, and J. G. Larsheid. 2002. Diet dynamics of the adult piscivorous fish community in Spirit Lake, Iowa, USA 1995-1997. Ecology of Freshwater Fish 11:178–189.

Lucchesi, D. O. 2008. Angler use and harvest surveys on Lake Thompson, Kingsbury County, South Dakota, May 1997-August 2008. South Dakota Department of Game, Fish and Parks Annual Report No. 09–16, Pierre, South Dakota, USA.

Lyons, J. 1987. Prey choice among piscivorous juvenile walleye (*Stizostedion vitreum)*. Canadian Journal of Fisheries and Aquatic Sciences 44: 758–764.

Lyons, J., and J. J. Magnuson. 1987. Effects of walleye predation on the population dynamics of small littoral-zone fishes in a northern Wisconsin Lake. Transactions of the American Fisheries Society 116:29–39.

Madenjian, C. P., J. T. Tyson, R. L. Knight, M. W. Kershner, and M. J. Hansen. 1996. First-year growth, recruitment, and maturity of walleyes in western Lake Erie. Transactions of the American Fisheries Society 125:821–830.

McIntyre, J. K., D. A. Beauchamp, M. M. Mazur, and N. C. Overman. 2006. Ontogenetic trophic interactions and benthopelagic coupling in Lake Washington: evidence from stable isotope and diet analysis. Transactions of the American Fisheries Society 135:1312–1328.

Michaletz, P. H. 1997. Influence of abundance and size of age-0 gizzard shad on predator diets, diet overlap and growth. Transactions of the American Fisheries Society 126:101–111.

Mittelbach, G. G., and L. Persson. 1998. The ontogeny of piscivory and its ecological consequences. Canadian Journal of Fisheries and Aquatic Sciences 55:1454–1465.

Olson, N. W., C. S. Guy, and K. D. Koupal. 2007. Interactions among three top-level predators in a polymictic Great Plains reservoir. North American Journal of Fisheries Management 27:268–278.

Ott, R. L., and M. Longnecker. 2001. An introduction to statistical methods and data analysis. Fifth edition. Wadsworth Group, Pacific Grove, California, USA.

Parsons, J. W. 1971. Selective food preferences of walleye of the 1959 year class in Lake Erie. Transactions of the American Fisheries Society 3:474–485.

Paterson, G., K. G. Drouillard, and G. D. Haffner. 2006. Quantifying resource partitioning in centrarchids with stable isotope analysis. Limnology and Oceanography 51:1038–1044.

Perga, M. E., and D. Gerdeaux. 2003. Using the $\delta^{13}C$ and $\delta^{15}N$ of whitefish scales for retrospective ecological studies: changes in isotope signatures during the restoration of Lake Geneva 1980–2001. Journal of Fish Biology 63:1197–1207.

Peterson, B. J., and B. Fry. 1987. Stable isotopes in ecosystem studies. Annual Review of Ecological Systems 18:293–320.

Porath, M. T. 2006. Climate and habitat factors related to a localized extirpation of gizzard shad (*Dorosoma cepedianum*). Great Plains Research 16:127–135.

Porath, M. T., and E. J. Peters. 1997. Walleye prey selection in Lake McConaughy, Nebraska: a comparison between stomach content analysis and feeding experiments. Journal of Freshwater Ecology 12:511–520.

Post, D. M., C. A. Layman, D. A. Arrington, G. Takimoto, J. Quattrochi, and C. G. Montana. 2007. Getting to the fat of the matter: models, methods, and assumptions for dealing with lipids in stable isotope analysis. Oecologia 152:179–189.

Pruell, R. J., B. K. Taplin, and K. Cicchelli. 2003. Stable isotope ratios in archived striped bass scales suggest changes in trophic structure. Fisheries Management and Ecology 10:329–336.

Sanderson, B. L., C. D. Tran, H. J. Coe, V. Pelekis., E. A. Steel, and W. L. Reichert. 2009. Nonlethal sampling of fish caudal fins yields valuable stable isotope data for threatened and endangered fishes. Transactions of the American Fisheries Society 138:1166–1177.

Satterfield, F. R., and B. P. Finney. 2002. Stable isotope analysis of pacific salmon: insight into the trophic status and oceanographic conditions over the last 30 years. Progress in Oceanography 53:231–246.

Slipke, J. W and W. G Duffy. 1997. Food habits of walleye in Shadehill Reservoir, South Dakota. Journal of Freshwater Ecology 12:11–17.

Solomon, C. T., S. R. Carpenter, J. A. Rusack, and M. J. Vander Zanden. 2008. Long-term variation in isotopic baselines and implications for estimating consumer trophic niches. Canadian Journal of Fisheries and Aquatic Sciences 65:2191–2200.

Stahl, T. P., and R. A. Stein. 1994. Influence of larval gizzard shad (*Dorosoma cepedianum*) density on piscivory and growth of young-of-year saugeye (*Stizostedion vitreum* x *S. canadense*). Canadian Journal of Fisheries and Aquatic Sciences 51:1993–2002.

Syvaranta, J., and R. I. Jones. 2008. Changes in feeding niche widths of perch and roach following biomanipulation, revealed by stable isotope analysis. Freshwater Biology 53:425–434.

Tunink, D. 1991. East Twin Lake rehabilitation projects and long term management plan. Nebraska Game and Parks Commission Report, Lincoln, USA.

VanDeHey, J. A. 2011. Influence of gizzard shad on fish community ecology in northeastern South Dakota glacial lakes. Dissertation, South Dakota State University, Brookings, USA.

Vander Zanden, M. J., S. Chandra, B. C. Allen, J. E. Reuter, and C. R. Goldman. 2003. Historical food web structure and restoration of native aquatic communities in Lake Tahoe (California-Nevada) basin. Ecosystems 6:274–288.

Vander Zanden, M. J., B. J. Shuter, N. P. Lester, and J. B. Rasmussen. 2000. Within- and among-population variation in the trophic position of a pelagic predator, lake trout (*Salvelinus namaycush*). Canadian Journal of Fisheries and Aquatic Sciences 57:725–731.

Vander Zanden, M. J., and J. B. Rasmussen. 1999. Primary consumer δ^{15}N and δ^{13}C and the trophic position of aquatic consumers. Ecology 80:1395–1404.

Vander Zanden, M. J., and J. B. Rasmussen. 2001. Variation in δ^{15}N and δ^{13}C trophic fractionation: implications for aquatic food web studies. Limnology and Oceanography 46:2061–2066.

VanDeValk, A. J., J. L. Forney, and J. R. Jackson. 2008. Relationships between relative weight, prey availability, and growth of walleyes in Oneida Lake, New York. North American Journal of Fisheries Management 28:1868–1875.

Ward, M. C., D. W. Willis, B. R. Herwig, S. R. Chipps, B. G. Parsons, J. R. Reed, and M. A. Hanson. 2008. Consumption estimates of walleye stocked as fry to suppress fathead minnow populations in west-central Minnesota wetlands. Ecology of Freshwater Fish 17:59–70.

Ward, M. J., D. W. Willis, B. H. Miller, and S. R. Chipps. 2007. Walleye consumption and long-term production trends following gizzard shad introductions into a western South Dakota reservoir. Journal of Freshwater Ecology 22:339–345.

Wuellner, M. R., S. R. Chipps, D. W. Willis, and W. E. Adams, Jr. 2010. Interactions between walleyes and smallmouth bass in a Missouri River Reservoir with consideration of the influence of temperature and prey. North American Journal of Fisheries Management 30:445–463.

Wuellner, M. R., B. D. S. Graeb, M. J. Ward, and D. W. Willis. 2008. Review of gizzard shad population dynamics at the northwestern edge of its range. Pages 637–653 *in* M. S. Allen, S. Sammons, and M. J. Maceina, editors. Balancing fisheries management and water uses for impounded river systems. American Fisheries Society, Symposium 62, Bethesda, Maryland, USA.

Submitted 1 February 2012. Accepted 29 September 2012.
Associate Editor was B. Blackwell.