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Effects of gizzard shad introductions on walleye and yellow perch populations in prairie glacial lakes

Justin A. VanDeHey[a,*], David W. Willis[a], Jason M. Harris[a,1], Brian G. Blackwell[b]

[a] Department of Natural Resource Management, South Dakota State University, NPB Lab 138, Box 2140B, Brookings, SD 57007, USA
[b] South Dakota Department of Game, Fish and Parks, 603 E. 8th Avenue, Webster, SD 57274, USA

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ABSTRACT

Fisheries managers often stock prey fish to increase abundance and growth of predatory sport fishes. One species commonly used in the U.S. Midwest is gizzard shad *Dorosoma cepedianum*; gizzard shad have been used to increase growth and condition of walleye *Sander vitreus* in many Midwestern systems. Additionally, with warming climates and stocking, gizzard shad are experiencing a natural range expansion. While this expansion may be beneficial for top predators like walleye, mixed results exist on the effects of gizzard shad on other recreationally important fishes in these systems. Our objectives were to determine if annual growth, relative abundance, and condition of yellow perch, *Perca flavescens* and walleye populations changed following the introduction of gizzard shad. Adult, pre-spawn gizzard shad were introduced in 2008 and 2009 at densities higher than those which resulted in self-sustaining populations in other South Dakota reservoirs. Yellow perch and walleye population dynamics were estimated during 2007 (pre-shad), 2008–2009 (shad present) and 2010 (post-shad) in two glacial lakes stocked with adult gizzard shad and a reference lake (not stocked with shad). Our results suggest that at the densities documented in this study and in the time frame assessed, gizzard shad did not negatively impact yellow perch as total length at age was similar, condition remained high and zooplankton resources were likely not limiting. Walleye did consume gizzard shad when available and shad appeared to have a neutral or positive effect on walleye growth, relative abundance and condition in these systems during this study. The addition of shad may be a viable option to improve walleye populations without negatively impacting sympatric yellow perch populations under the conditions tested in this study. However, the introduction of a non-indigenous species should be done with caution, especially a potential competitor like gizzard shad.

1. Introduction

Stocking of fishes by management agencies to create or enhance recreational fisheries has become a widely accepted and successful practice worldwide (Moffitt et al., 2010). Many of these introductions have occurred to enhance sport fisheries through the direct stocking of desirable sport fishes or through the stocking of prey fishes to enhance the prey base. While these introductions often yield desired outcomes (i.e., species establishment, increased prey abundance) they can also have unforeseen impacts on the fish community as a whole (Vander Zanden et al., 1999; Rahel, 2000, 2002). For example, common carp *Cyprinus carpio* was introduced across North America by the U.S. Fish Commission with the goal of establishing food resources for the growing human population (Nielsen, 1999). However, after stocking common carp, fisheries managers now expend substantial effort and funds in attempt to control the invasive carp, as well as other invasive species (Koehn, 2004; Schrage and Downing, 2004; Weber and Brown, 2009) and reduce its ecological impacts on native fish communities (Lougheed et al., 1998; Parkos et al., 2003; Weber and Brown, 2009).

One species frequently used as an additional prey resource in freshwater lakes and reservoirs is the gizzard shad *Dorosoma cepedianum* (Noble, 1981; Eichner and Ellison, 1983; Porath, 2006). Gizzard shad is a highly fecund, warm water, riverine species prevalent throughout the southern United States (Noble, 1981), although its native range has increased in recent years (White et al., 1987; Fetzer et al., 2011) and now encompasses most of the eastern continental United States and extends from Florida to New Mexico in the south and as far north as North Dakota in the west and New York in the east (Heidinger, 1983; Pflieger, 1997). In fact, it

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* Corresponding author. Present address: College of Natural Resources, University of Wisconsin – Stevens Point, 800 Reserve Street, Stevens Point, WI 54481, USA. Tel.: +1 715 346 2090; fax: +1 715 346 3624.
E-mail address: justin.vandehey@uwsp.edu (J.A. VanDeHey).

[1] Present address: Minnesota Department of Natural Resources, Hutchinson, MN 55350, USA.

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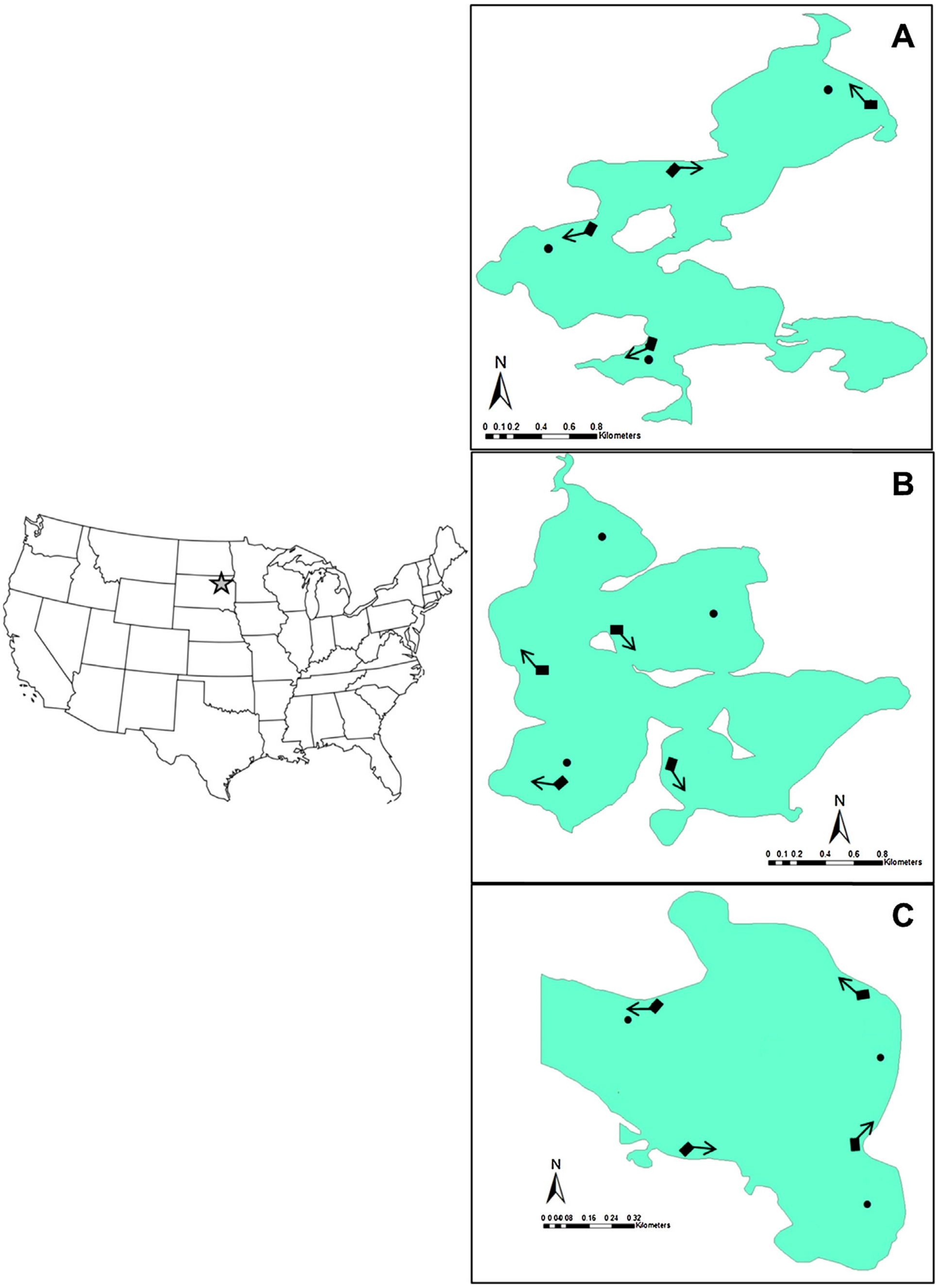

Fig. 1. Left panel: Map of the United States with gray star denoting Day County, South Dakota (study area). Right panel: (A) Lardy (reference), (B) Middle Lynn and (C) East Krause Lakes, Day County, South Dakota. Black circles symbolize locations of standardized gill net sets. Black rectangles indicate starting location for standardized autumn age-0 walleye electrofishing transects; arrows indicate boat direction from starting location.

has become a common practice for fisheries managers of Great Plains states to collect adult gizzard shad brood stock and transfer them to receiving waters in the spring prior to spawning (Eichner and Ellison, 1983; Porath, 2006). For example, gizzard shad introductions in western South Dakota irrigation reservoirs provided additional prey that led to increased growth and size structure for walleye *Sander vitreus* populations (Miller et al., 2007; Ward et al., 2007). Similarly, when young gizzard shad were available in two South Dakota reservoirs, Angostura Reservoir (Ward, 2005) and Lake Sharpe (Elrod et al., 1987; Wuellner et al., 2010), walleye preyed almost exclusively on them.

While gizzard shad is an important prey fish (Michaletz, 1998; Porath, 2006; Wuellner et al., 2010) and an important component in nutrient cycling (Schaus and Vanni, 2000), its impacts on recreational fishes varies greatly depending on the system and the fish community. DeVries and Stein (1992) suggested that recruitment of other fishes was reduced by gizzard shad. The authors indicated that the emergence of larval gizzard shad caused massive declines in zooplankton, forcing other fishes into suboptimal habitats and in turn reducing their growth and survival. Aday et al. (2003) confirmed that bluegill *Lepomis macrochirus* growth rates and adult size structure were reduced in systems containing gizzard shad, although direct competition for food resources may not have been the mechanism. Alternatively, the presence of gizzard shad did not have negative impacts on white crappie *Pomoxis annularis* (Pope and DeVries, 1994) or juvenile yellow perch *Perca flavescens*

(Roseman et al., 1996). At Oneida Lake, New York, gizzard shad provided a predation buffer for age-0 yellow perch from walleye and acted to enhance perch recruitment (Fitzgerald et al., 2006). Based on previous research, it seems that the effects of gizzard shad on fish communities are highly variable and often specific to a body of water.

Recently, natural range expansion and overwinter survival of gizzard shad at the northern edge of its native range, specifically in South Dakota, has been documented (Hanten, 2006; Miller et al., 2007; South Dakota Department of Game, Fish and Parks, 2009; VanDeHey et al., 2012a). Given the variable impacts of gizzard shad on fish communities and that most of the research assessing interactions between shad and native species has occurred in reservoirs or large natural lakes with little if any research on eutrophic glacial lakes, a knowledge gap currently exists on the potential impacts of this range expansion. Therefore, to assess the potential for interactions between gizzard shad and percids (walleye and yellow perch) we performed whole-lake manipulations on two northeastern South Dakota glacial lakes by introducing adult pre-spawn shad and then measuring a suite of biotic and abiotic factors within these systems. We hypothesized that gizzard shad would positively influence walleye by providing an additional prey resource and that shad would have little to no impact on yellow perch due to differences in life history (i.e., spawn timing, ontogenetic diet shifts in perch and diet plasticity of shad). If walleye population dynamics did indeed improve without negatively impacting yellow perch, then natural range expansion may represent a positive interaction enhancing predator populations to reach desired management objectives. The specific objective of this research was to determine if annual growth, relative abundance and condition of adult and juvenile yellow perch (potential competitor) and walleye (predator) populations changed following the introduction of gizzard shad. By assessing the impacts of gizzard shad introductions on yellow perch and walleye population dynamic rates, data could be used to elucidate potential interactions from the shad range expansion.

2. Materials and methods

2.1. Study area

Research was conducted on three natural lakes of glacial origin located in Day County, northeastern South Dakota, USA: Lardy, Middle Lynn, and East Krause lakes (Fig. 1; left panel). All three lakes were eutrophic with mean July Trophic State Index (TSI; Carlson, 1977) values ranging from 57 to 58 (TSI_{SECCHI}; East Krause = 58, Middle Lynn = 57, Lardy = 57), and the predominant land-use in their watersheds was agricultural (≈80%). Middle Lynn Lake and East Krause served as the treatment lakes for this study and received annual stockings of adult, pre-spawn gizzard shad. Both treatment lakes were within the Big Sioux and James River drainages and gizzard shad are native to both of these basins. Middle Lynn Lake has a surface area of approximately 280 ha, and East Krause Lake has the smallest surface area of the three lakes at approximately 70 ha (Fig. 1; panels B and C respectively). Lardy Lake (reference: no gizzard shad stocked) has a surface area of approximately 253 ha (Fig. 1A). The fish assemblage of all three lakes predominantly consisted of walleye and yellow perch with low densities of black crappie *Pomoxis nigromaculatus* present in East Krause Lake and northern pike *Esox lucius* in Lardy Lake. Additionally, all three lakes contained fathead minnows *Pimephales promelas* and low densities of bluegill *L. macrochirus*, black bullhead *Ameiurus melas*, brook stickleback *Culaea inconstans* and johnny darters *Etheostoma nigrum*. Air and water temperature data for these lakes can be found in VanDeHey et al. (2012a,b).

2.2. Gizzard shad stockings

During early May of 2008 and 2009 adult, pre-spawn gizzard shad were collected from Lake Sharpe, South Dakota, a mainstem Missouri River reservoir, using daytime electrofishing. After collection, they were placed in a fish hauling truck and transported to the study lakes. Water in the hauling truck tanks was treated with a 1% salt solution and aerated with pure oxygen to reduce stress. During 2008, a total of 50 (0.71/ha) and 117 (0.44/ha) gizzard shad were stocked into East Krause and Middle Lynn, respectively. During 2009, East Krause was again stocked with 50 (0.71/ha) and Middle Lynn was stocked with 125 (0.47/ha) gizzard shad. These stocking rates were selected to be higher than initial stocking densities in western South Dakota reservoirs which resulted in naturally recruiting shad populations (Ward, 2005). In 2009, all adult gizzard shad received a pelvic fin clip to differentiate them from adults stocked in 2008 (un-clipped). Additionally, due to limited natural recruitment of walleye in these lakes, each lake was stocked with walleye fry (2500/ha) during 2008 through 2010.

2.3. Fish collection

Walleye and adult (>130 mm) and juvenile (<130 mm) yellow perch were collected during May and September of 2007 through 2010. The spring (May) fish collection consisted of a standardized gill net survey (3 total net nights/per lake) and included three 38.1 m long, 1.83 m high experimental gill nets with five 7.62 m sections (bar mesh = 1.9, 2.5, 3.2, 5.1, and 6.4 cm) set in the same location at approximately the same time of year each year. Nets were set in early afternoon, allowed to fish overnight and were pulled the next morning. The autumn sample (September) was collected using short-term gill net sets (2–4 h) and supplemented using 1 h (on-time) of nighttime, pulsed-DC electrofishing, with a Smith-Root boat and control unit (7.5 GPP unit; Smith-Root Inc., Vancouver, WA 98686). Additionally, to determine an index of abundance (number/h) of autumn age-0 walleye, pulsed-DC electrofishing was conducted at four standardized sites (10 min transect at each site) per lake. All pulsed DC electrofishing was conducted using approximately 500 V, 8–10 A and 60 pulses/s.

2.4. Laboratory analysis

At South Dakota State University (SDSU), weights (g), total length (TL; mm) and sex of all yellow perch and walleye were recorded, and sagittal otoliths were removed from fish for age analysis. Otoliths were placed in individually labeled plastic vials and left to dry for a minimum of 14 d. Otoliths were either aged whole (fish estimated at ≤3 years) or cracked through the nucleus (fish estimated at >3 years) and viewed using a fiber optic light and dissecting microscope. All fish were aged double-blind by experienced readers and ages were entered into in a database. In the event of non-agreement a third reader was used.

2.5. Data analysis

To estimate growth of yellow perch, mean TL at age (±SE) was estimated and plotted for perch captured during the September sampling period. Because yellow perch often exhibit sexually dimorphic growth (Purchase et al., 2005; Rennie et al., 2008), mean TL at age was also estimated and compared for both males and females within a lake among years using an analysis of covariance [ANCOVA (Proc GLM; SAS Institute, Cary, NC)]. If no significant differences were found, males and females were pooled, and if differences existed, each sex was compared separately. To determine if growth changed following the introduction of gizzard shad, mean total length at age (male, female, or pooled) was compared among years with and without gizzard shad using an ANCOVA (Proc GLM; SAS Institute, Cary, NC). A sex-specific, age-length key was developed for each lake during each individual year and applied to all un-aged fish in our sample (one age-length key per year, per lake; DeVries and Frie, 1996).

Because of lower sample sizes for several ages of walleye, we estimated annual growth increments rather than mean total length at age. To estimate annual growth increments of individual walleye, we first determined the relationship between walleye TL and length from the center of the otolith nucleus to the edge of the otolith (otolith radius; OR). We combined data from all three lakes during 2007 through 2009 (development data) to model this relationship. Using this model we then predicted OR and compared these values with observed OR values from the 2010 data (validation data). These data were then plotted to determine the most appropriate growth model for back-calculation of length at the previous annuli (Francis, 1990). We compared the fit of three back-calculation models including (1) simple linear regression, (2) direct proportion method and (3) Fraser–Lee modification to the direct proportion method with an intercept of 6 mm (approximately the length at which walleye hatch [Nelson, 1968; Oseid and Smith, 1971; Hoxmeier et al., 2006]).

After determining the appropriate back-calculation model, incremental growth of walleye sampled in May (prior to growth starting for the year; Quist et al., 2002) and September (after the annual growth period) was estimated by comparing OR with the distance from the nucleus to the last visible annulus. Fish captured in July were not used in this analysis. Incremental growth analysis involves plotting the growth increment for the last full growing season as a function of initial length at the start of that growing season. Samples were split into three time periods, "pre-shad," "shad present," and "post-shad." Samples from May and September of 2007 and May of 2008 were delineated as "pre-shad," while samples from September 2008, May and September 2009, and May of 2010 were considered the "shad present" period and samples from September 2010 were considered "post-shad." Samples from September 2010 were considered "post-shad" based on additional research which found that no gizzard shad survived the over-winter period and no shad, of any life stage, were collected in either treatment lake during 2010 (VanDeHey et al., 2012a). To determine which time periods had the fastest and slowest growth, we estimated the mean annual growth increment using least squares methods (Proc GLM). Additionally, to determine if incremental growth differed among walleye of different initial lengths, among the different time periods (e.g., pre-shad vs. post-shad in East Krause) and if a significant length by time period interaction (TL*Time period) was present within each lake an analysis of covariance (ANCOVA) was used (Proc GLM; SAS Institute, Cary, NC). For all statistical analyses $\alpha = 0.05$, unless otherwise noted. Due to low sample sizes during some sampling periods, all walleye (males and females) were grouped and sex-specific growth differences were not assessed.

An index of relative abundance (catch per unit effort; CPUE) for yellow perch and walleye was calculated based on catch data from the May standardized sample. Catch per unit effort was estimated as the mean number of fish per net night. Walleye and yellow perch CPUE data were tested for normality using a Shapiro–Wilk's test (PopTools; Hood, 2010). If data approximated normality, they were compared across years within a lake using a repeated-measures analysis of variance (ANOVA) using Proc Mixed (SAS Institute, Cary, NC; Maceina et al., 1994), otherwise the non-parametric equivalent (Freidman's test) was used. If significant differences existed among years, we used the least square means for each lake (effect) by year with alpha adjusted for multiple comparisons (e.g., 2007 vs. 2008, 2009 and 2010) using a Tukey–Kramer adjustment. In addition, mean CPUE estimates for autumn age-0 walleye captured during electrofishing surveys were tested for normality (Shapiro–Wilks test; PopTools; Hood, 2010), plotted and compared among years within each lake using either *t*-tests (parametric) or Mann–Whitney *U* tests (non-parametric) with alpha corrected for multiple comparisons using a Bonferroni correction (Proc *t*-test; SAS Institute, Cary, NC).

The condition of all captured fishes from both treatment and reference lakes was assessed among years by calculating relative weight (W_r; Murphy et al., 1990) for individual fish based on standard weight equations (Murphy et al., 1990; Willis et al., 1991). To determine if length related trends existed in condition, W_r values (dependent) were plotted with fish TL (independent) to visually assess length related trends. We then used an ANOVA (Proc GLM; SAS Institute, Cary, NC) to compare the slope of the W_r values across fish lengths for each population among years. If differences in W_r existed across lengths, we estimated mean W_r values among length categories (substock, stock to quality, quality to preferred and preferred to memorable; Gabelhouse, 1984) within a lake during each season and each year. Typically, W_r values $\geq$90 are considered satisfactory and if fish have W_r values between 95 and 100 they are considered to be in excellent condition (Murphy et al., 1990). We considered fish to be in good condition if their W_r values were $\geq$90.

3. Results

3.1. Gizzard shad stockings

During early May of 2008 and 2009, pre-spawn adult gizzard shad were collected from Lake Sharpe, South Dakota, a mainstem Missouri River reservoir, and transported to the study lakes. In 2008, 167 adult gizzard shad ranging from 370 to 475 mm total length (TL) were collected and stocked into East Krause Lake (50 fish, 0.71 fish/ha) and Middle Lynn Lake (117 fish, 0.42 fish/ha). In 2009, a total of 175 fish were collected and stocked into East Krause Lake (50 fish, 0.71 fish/ha) and Middle Lynn Lake (125 fish, 0.45 fish/ha). Stocking densities were selected to be higher than those that resulted in successful establishment of gizzard shad populations in other South Dakota water bodies (see Wuellner et al., 2008 for details). Gizzard shad successfully reproduced (larvae present) in both 2008 and 2009 in both East Krause and Middle Lynn lakes and recruited to autumn age-0 during both years in Middle Lynn Lake and during 2008 in East Krause Lake (VanDeHey et al., 2012a).

3.2. Fish collection

During the 4 year study, 3407 yellow perch (1232 Middle Lynn, 998 East Krause, and 1177 Lardy) were collected and brought to SDSU for biological analysis. Collected yellow perch ranged in total length from 73 to 284 mm in East Krause, from 87 to 355 mm in Middle Lynn and from 64 to 297 mm in Lardy Lake. Yellow perch estimated ages ranged from 0 to 4 years in both East Krause and Lardy lakes, and from 0 to 10 years old in Middle Lynn, although only one fish was older than age 6. A total of 1462 walleye were collected and transported to SDSU for subsequent analyses over the 4-year study. Walleye collected in East Krause ranged from 0 to 13 years old and from 168 to 682 mm. In Middle Lynn Lake, collected walleye ranged in age from 0 to 9 years and in TL from 146 to 661 mm. Walleye collected from Lardy Lake ranged in age from 0 to 6 years and in TL from 102 to 612 mm.

3.3. Yellow perch growth

Mean TL at age of male and female yellow perch from September samples were significantly different in 10 of 12 lake-year comparisons ($P < 0.01$); therefore, each sex was analyzed separately.

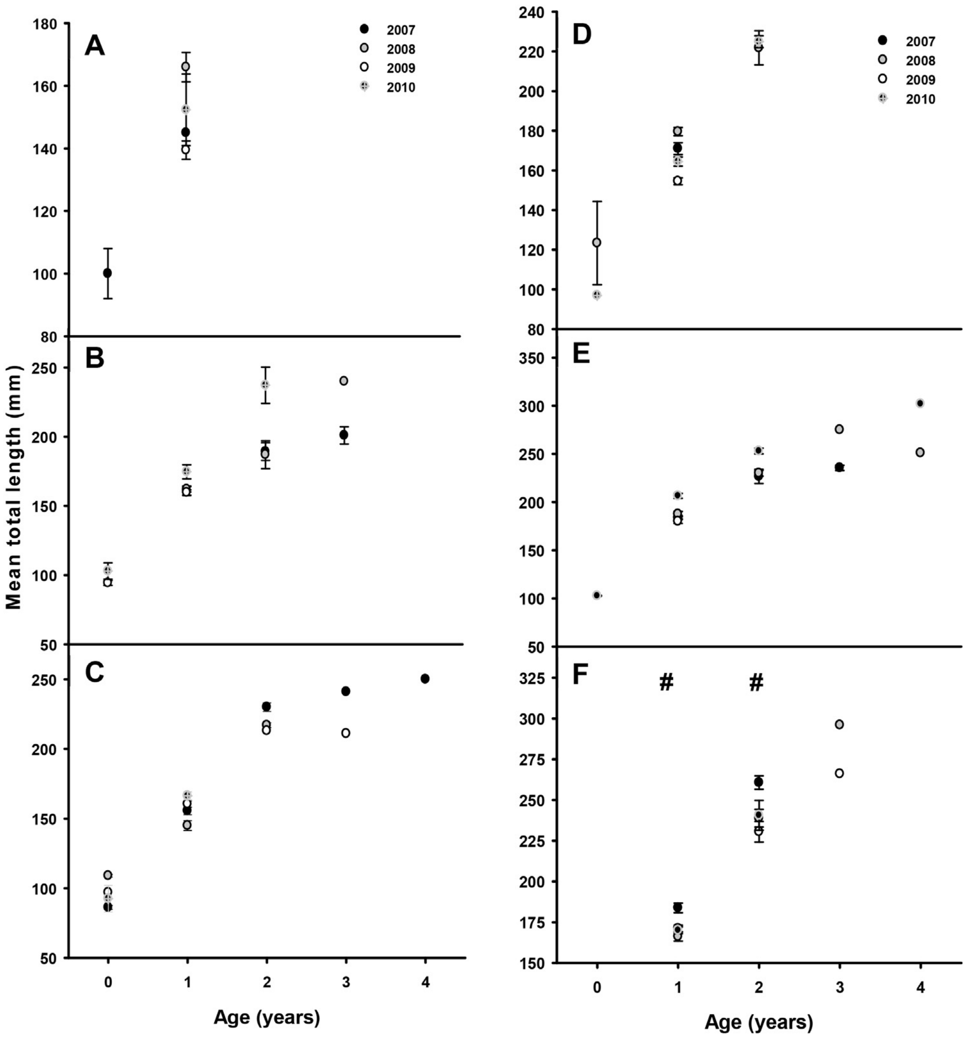

Fig. 2. Mean (±SE) total length at age at capture of male (left) and female (right) yellow perch collected from East Krause (A, D), Middle Lynn (B, E) and Lardy (C, F) lakes in northeastern South Dakota during September of 2007–2010. A "#" above the data denotes significant differences.

Growth of male yellow perch was not statistically different between years with (2008 and 2009) and without (2007 and 2010) gizzard shad present in either of the treatment lakes or the reference lake (Fig. 2A–C). Growth of female yellow perch was not statistically different between years with and without gizzard shad in either treatment lake; female TL at age differed among years in Lardy Lake where mean TL at age-1 was significantly higher in 2007 ($P < 0.028$ for all comparisons; mean TL = 184 mm) than any other year (Fig. 2F). Additionally, in Lardy Lake female yellow perch mean TL at age-2 was the highest in 2007 (mean = 261 mm), and was significantly higher than 2008 ($P = 0.011$) and 2009 ($P = 0.003$; Fig. 2F).

3.4. Walleye growth

The overall models comparing fish OR to TL (2007–2009 data) suggested that nearly 80% of the variation in OR could be explained by fish TL using any of the three competing models. The regression model had the highest r^2 (0.79); however, all three models were nearly identical in model fit. Next, we assessed the fit of all three models again using the validation data (2010 data). The direct proportion model had the best fit for the validation data (lowest residual error) followed by the Fraser–Lee method. Additionally, a significant positive relationship existed when we compared observed OR (2010 validation data) with OR predicted using all three developed models ($P < 0.001$; $r^2 = 0.91$) suggesting that all three models performed similarly. Based on these results and the recommendations from Francis (1990), we chose to use the Fraser–Lee model with the biological intercept as the equation to predict back-calculated lengths at the previous annuli to estimate incremental growth (Table 1). The resulting final equation was as follows:

$$L_i = 1027 \times O_i + 6$$

where L_i is the length of the fish at annulus i, O_i is the otolith radius at annulus i, and 6 is the biological intercept value for walleye (Nelson, 1968; Oseid and Smith, 1971; Hoxmeier et al., 2006).

Mean annual growth of all walleye in East Krause was 64.52 mm, 129.68 mm, and 78.08 mm during the pre-shad, shad present, and post shad periods respectively. Annual growth of walleye in East Krause varied significantly across initial TL ($F = 79.32$; df = 1; $P < 0.001$), time periods ($F = 14.59$; df = 2; $P < 0.001$) and a significant time period by initial TL interaction was present ($F = 9.44$; df = 2; $P < 0.001$; Fig. 3A). In Middle Lynn, mean annual growth increment for walleye was 67.23 mm, 65.05 mm, and 88.96 mm during the pre-shad, shad present and post-shad periods respectively. In Middle Lynn, walleye annual growth also varied significantly with initial TL ($F = 204.59$; df = 1; $P < 0.001$), time period ($F = 18.90$; df = 2; $P < 0.001$), and a significant interaction between initial TL and time

Table 1
Comparison of models for predicting walleye total length from otolith radius. Model evaluation r^2 values were derived from comparing observed total length with predicted total length estimated from the otolith radius using each model. Sum of squares error (SSE) was derived from the residuals of observed total length at time of capture to predicted total length from each model based on otolith radius.

Model development					Model evaluation			
Model	r^2	Slope	Intercept	SSE	Rank	SSE	r^2	Rank
Regression	0.792	986.6	25.5	977,964	1	509,964	0.907	3
Direct proportion	0.789	1045.5	0.0	991,856	3	431,678	0.907	1
Fraser–Lee	0.790	1027.0	6.0	987,990	2	433,642	0.907	2

period was present ($F = 13.07$; df = 2; $P < 0.001$; Fig. 3B). In the reference lake, Lardy, annual growth was 126.75 mm, 76.12 mm, and 64.46 mm during the pre-shad, shad present and post-shad periods respectively. Walleye annual growth in Lardy Lake varied significantly with TL ($F = 33.08$; df = 1; $P < 0.001$), time period ($F = 17.50$; df = 2; $P < 0.001$) and a significant time period by TL interaction was present ($F = 13.96$; df = 2; $P < 0.001$; Fig. 3C).

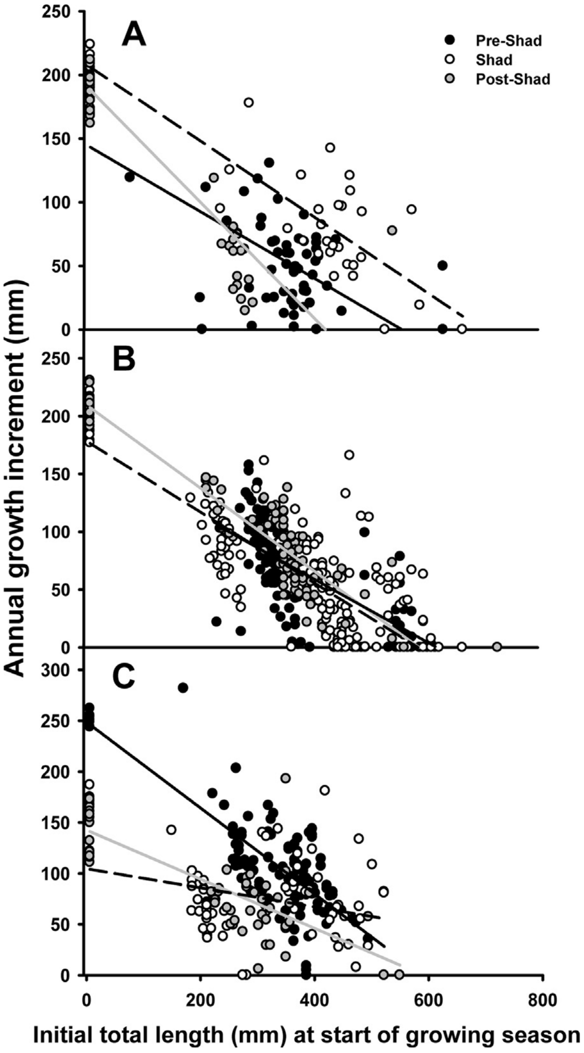

Fig. 3. (A) Annual growth increment of walleye from East Krause Lake (treatment), northeastern South Dakota before (pre-shad period; $r^2 = 0.47$; $P < 0.01$), during (shad period; $r^2 = 0.73$; $P < 0.01$) and after (post-shad period; $r^2 = 0.84$; $P < 0.01$) annual introductions of adult gizzard shad. (B) Annual growth increment of walleye from Middle Lynn Lake (treatment), northeastern South Dakota before (pre-shad period; $r^2 = 0.46$; $P < 0.01$), during (shad period; $r^2 = 0.68$; $P < 0.01$) and after (post-shad period; $r^2 = 0.89$; $P < 0.01$) annual introductions of adult gizzard shad. (C) Annual growth increment of walleye from Lardy Lake (reference), northeastern South Dakota before (pre-shad period; $r^2 = 0.65$; $P < 0.01$), during (shad period; $r^2 = 0.08$; $P = 0.02$) and after (post-shad period; $r^2 = 0.63$; $P < 0.01$) annual introductions of adult gizzard shad. Lines are the linear regressions for the pre-shad period (black), shad (black dashed) and post-shad (gray) periods.

3.5. *Relative abundance estimates*

Mean CPUE of yellow perch from spring gill netting was variable and significant differences were present among years within each lake ($F = 34.67$, df = 3, $P < 0.001$); however, no significant differences existed between lakes ($F = 1.74$, df = 2, $P = 0.197$) and there was not a significant lake-year interaction ($F = 1.35$, df = 3, $P = 0.275$). In East Krause, mean CPUE ranged from 3 to 25 among years, in Middle Lynn it ranged from 2 to 76 among years and in Lardy mean CPUE ranged from 5 to 21 among years (Fig. 4A). Mean CPUE was similar in 2007 and 2010 ($t = -2.85$, df = 8, $P = 0.082$), but was significantly lower in both 2008 ($t = -5.43$, df = 8, $P = 0.003$) and 2009 ($t = -5.35$, df = 8, $P = 0.003$) than in 2010 in East Krause. In Lardy Lake, mean CPUE of yellow perch was significantly higher in 2010 than in 2007 ($t = -5.70$, df = 8, $P = 0.002$), 2008 ($t = -7.23$, df = 8, $P < 0.001$) and 2009 ($t = -7.17$, df = 8, $P < 0.001$), but mean CPUE was not significantly different among any other years ($P > 0.05$). A similar pattern was found in Middle Lynn where mean CPUE was significantly higher in 2010 than in 2008 ($t = -4.71$, df = 8, $P = 0.007$) and 2009 ($t = -4.95$, df = 8, $P = 0.005$), but did not differ among any other years ($P > 0.05$).

Mean CPUE of walleye among years ranged from 3 to 8 fish/gill net night in East Krause from 2 to 26 fish/gill net night in Middle Lynn and from 5 to 17 fish/gill net night in Lardy (Fig. 4B). Data were normally distributed for 8 of 12 lake-years ($P > 0.05$). The overall model from the repeated measures ANOVA indicated that no significant differences were present among years ($F = 1.44$; df = 3, 24; $P = 0.255$), but significant differences existed between lakes ($F = 6.07$; df = 2, 24; $P = 0.001$) and that a lake-year effect was present and significant ($F = 3.67$; df = 6, 24; $P = 0.010$). Mean (±SE) autumn age-0 walleye CPUE among years ranged from 0 (±0.0) to 10.5 (±8.6) fish/h in East Krause, 0 (±0.0) to 447 (±167.9) fish/h in Middle Lynn and from 0 (±0.0) to 174 (±64.2) fish/h in Lardy (Fig. 4C). Data were normally distributed for 11 of 12 lake-year comparisons ($P > 0.05$) and thus we used a parametric analysis. Following Bonferroni adjustment for multiple comparisons, pairwise comparisons between mean CPUE of age-0 walleye were not significantly different for any comparison within a lake between years or between lakes within a year.

3.6. *Condition*

Yellow perch W_r varied significantly with TL during 7 of 12 sampling periods in East Krause, 7 of 12 sampling periods in Lardy and 3 of 12 sampling periods in Middle Lynn throughout the study (Table 2). Because significant differences existed in condition among lengths of fish, mean W_r was estimated for each length category of yellow perch during each sampling period and these length categories were compared during each season among years (e.g., stock to quality [130–200 mm] length perch from July 2008 vs. July 2009 in Middle Lynn).

Table 2

Results from analysis of variance (ANOVA) comparing relative weight (W_r) across all lengths of yellow perch (YEP) and walleye (WAE) collected from three northeastern South Dakota glacial lakes before (2007), during (2008–2009) and following (2010) annual introductions of pre-spawn adult gizzard shad. ML = Middle Lynn (treatment), EK = East Krause (treatment), LL = Lardy Lake (reference). May = M, July = J, September = S. Cells with a dashed line (–) represent a period where too few fish sampled to accurately estimate *F* and *P* values. All tests have one degree of freedom. All significant *P*-values are listed in bold text.

Lake	Test statistic	M 2007	J 2007	S 2007	M 2008	J 2008	S 2008	M 2009	J 2009	S 2009	M 2010	J 2010	S 2010
ML (YEP)	*F*	1.530	1.780	1.040	7.800	9.810	1.060	0.290	0.870	0.330	7.600	0.010	2.760
	P	0.219	0.185	0.311	**0.010**	**0.003**	0.311	0.625	0.353	0.568	**0.006**	0.923	0.102
EK (YEP)	*F*	10.480	1.530	1.180	6.760	6.310	14.600	0.150	1.580	24.760	0.280	24.900	30.670
	P	**0.002**	0.218	0.293	**0.018**	**0.014**	**<0.001**	0.699	0.211	**<0.001**	0.595	**<0.001**	**<0.001**
LL (YEP)	*F*	92.790	65.900	49.980	6.600	7.720	0.370	1.180	2.000	3.610	14.460	3.290	9.020
	P	**<0.001**	**<0.001**	**<0.001**	**0.015**	**0.007**	0.547	0.284	0.159	0.061	**<0.001**	0.074	**0.004**
ML (WAE)	*F*	4.580	6.340	0.470	0.050	0.510	2.840	6.160	0.000	9.980	7.150	0.500	21.740
	P	0.099	**0.045**	0.500	0.821	0.478	0.094	**0.015**	0.953	**0.003**	**0.012**	0.484	**<0.001**
EK (WAE)	*F*	4.850	2.730	29.190	3.280	–	13.630	3.300	2.370	0.890	0.260	3.660	11.500
	P	**0.038**	0.105	**<0.001**	0.082	–	**<0.001**	0.085	0.145	0.445	0.620	0.080	**0.001**
LL (WAE)	*F*	8.060	1.870	0.080	2.710	4.760	9.270	2.800	0.130	0.000	8.070	1.900	4.100
	P	**0.007**	0.220	0.786	0.105	**0.039**	**0.003**	0.118	0.724	0.993	**0.009**	0.186	**0.047**

Across seasons, yellow perch in Middle Lynn tended to have higher mean W_r during 2007 than any other year, but mean W_r never fell below 97 for any length category during any season and no consistent pattern existed among the other 3 years (Table 3). In East Krause Lake, mean W_r was ≥95 for all length categories in all seasons and years except quality to preferred length fish in May of 2008 (mean W_r = 93; Table 3). In Lardy Lake, yellow perch mean W_r values were variable between years within a season among most length classes (8 of 12 comparisons). Although differences existed among some years, mean W_r only dropped below 94 for one length category during one month of one year (July 2007 substock; mean W_r = 88; Table 3).

Walleye W_r varied significantly across TL during 4 of 12 sampling periods in East Krause, and during 5 of 12 sampling periods in Lardy and in Middle Lynn throughout the study (Table 2). Because condition varied significantly with length, we calculated mean W_r for each length category of walleye during each sampling period and compared mean W_r of each length category during each season among years (e.g., substock walleye [<250 mm] from May 2008 vs. May 2009 in East Krause; Table 4). In East Krause Lake, mean W_r was significantly higher in 2008 and 2009 for most length categories of walleye during most seasons. In Middle Lynn, mean W_r was lower for most length categories of fish during most seasons in years when gizzard shad were present; the exception to this was substock walleye collected in September 2009 had the highest mean W_r. The highest mean W_r values in Middle Lynn occurred in 2010 for most length categories of walleye during the majority of seasons. In Lardy Lake, substock walleye had higher mean W_r values in 2010 than any other year. For all other length categories, in all other seasons, fish collected during 2007 had the highest mean W_r values, except for quality to preferred length walleye collected in May, where the 2008 sample had the highest mean W_r of 103. Mean W_r never fell below 93, 95, and 91 during any season of any year in East Krause, Middle Lynn and Lardy lakes, respectively.

4. Discussion

Adult gizzard shad spawned successfully in both treatment lakes during both years and survived to autumn in both lakes during 2008 and in Middle Lynn during 2009 (VanDeHey et al., 2012a). Although further research into their long-term impacts and more focused research into the early life history aspects of introduced gizzard shad would be beneficial, this study does provide significant insights into the potential effects of shad on eutrophic glacial lakes with percid dominated fish communities.

4.1. Effects on yellow perch

The introduction of gizzard shad into northeastern South Dakota glacial lakes at the densities used in this study appeared to have little impact on the yellow perch populations present in these systems. Both gizzard shad and yellow perch generally consume zooplankton as juveniles (Noble, 1975; Fisher and Willis, 1997; Schaus et al., 2002; Graeb et al., 2004; De Brabandere et al., 2009) potentially creating the opportunity for competition (May and Mac

Table 3

Mean (±SD) relative weight (W_r) of yellow perch collected from three northeastern South Dakota glacial lakes before (2007), during (2008–2009) and following (2010) annual introductions of pre-spawn adult gizzard shad. ML = Middle Lynn (treatment), EK = East Krause (treatment), LL = Lardy Lake (reference) [SS = Substock (<130 mm), ST = Stock length (130 mm), QL = quality length (200 mm), PR = preferred length (250 mm) (Gabelhouse, 1984)]. May = M, July = J, September = S. NC = None collected.

Lake	Length Group	M 2007	J 2007	S 2007	M 2008	J 2008	S 2008	M 2009	J 2009	S 2009	M 2010	J 2010	S 2010
ML	SS	125 (9)	130 (9)	NC	NC	109 (4)	107 (12)	NC	121 (5)	102 (11)	98 (12)	117 (0)	102 (9)
	ST-QL	121 (10)	123 (8)	114 (8)	100 (13)	108 (9)	109 (16)	99 (10)	121 (9)	110 (8)	106 (8)	107 (10)	111 (8)
	QL-PR	125 (7)	128 (8)	114 (7)	112 (7)	113 (7)	112 (8)	112 (0)	127 (10)	99 (8)	109 (8)	108 (8)	111 (8)
	PR-ME	118 (7)	NC	117 (0)	NC	109 (0)	110 (6)	NC	116 (7)	NC	NC	106 (7)	105 (6)
EK	SS	125 (6)	128 (19)	109 (12)	114 (2)	116 (7)	112 (14)	106 (11)	114 (4)	101 (12)	NC	120 (6)	116 (5)
	ST-QL	113 (7)	120 (9)	114 (9)	102 (8)	109 (6)	106 (8)	113 (6)	105 (8)	95 (6)	96 (9)	109 (8)	109 (8)
	QL-PR	111 (10)	123 (12)	NC	93 (13)	103 (5)	100 (7)	105 (6)	106 (1)	NC	97 (6)	104 (6)	100 (7)
	PR-ME	NC	115 (7)	NC	NC	NC	NC	NC	NC	NC	NC	98 (0)	99 (2)
LL	SS	129 (9)	128 (6)	127 (15)	NC	88 (13)	112 (16)	117 (0)	124 (7)	104 (14)	125 (11)	116 (4)	116 (17)
	ST-QL	105 (4)	120 (8)	108 (7)	97 (7)	108 (8)	110 (8)	110 (7)	123 (9)	107 (6)	120 (9)	115 (12)	104 (11)
	QL-PR	104 (6)	109 (6)	112 (9)	106 (14)	108 (10)	110 (6)	110 (11)	127 (9)	112 (9)	117 (9)	117 (11)	103 (2)
	PR-ME	94 (9)	105 (8)	NC	104 (7)	108 (4)	104 (6)	104 (4)	119 (0)	108 (5)	113 (7)	NC	120 (0)

Table 4
Mean (±SD) W_r of walleye collected from three northeastern South Dakota glacial lakes before (2007), during (2008–2009) and following (2010) annual introductions of pre-spawn adult gizzard shad. ML = Middle Lynn, EK = East Krause, LL = Lardy Lake [SS = Substock, ST = Stock length, QL = quality length, PR = preferred length, ME = memorable length, TR = Trophy length (Gabelhouse, 1984)]. May = M, July = J, September = S. NC = None collected.

Lake	Length group	M 2007	J 2007	S 2007	M 2008	J 2008	S 2008	M 2009	J 2009	S 2009	M 2010	J 2010	S 2010
ML	SS	109 (0)	NC	110 (13)	NC	NC	105 (8)	108 (12)	102 (5)	117 (8)	NC	NC	116 (6)
	ST-QL	105 (7)	99 (6)	106 (3)	102 (7)	NC	95 (0)	NC	101 (5)	98 (6)	107 (8)	107 (8)	111 (6)
	QL-PR	NC	NC	107 (9)	NC	103 (5)	102 (7)	102 (7)	103 (4)	102 (8)	98 (6)	103 (6)	106 (8)
	PR-ME	94 (11)	NC	104 (8)	103 (10)	104 (6)	103 (13)	103 (9)	97 (0)	105 (5)	103 (2)	NC	111 (13)
	ME-TR	NC	NC	NC	98 (0)	NC	90 (0)	87 (0)	NC	89 (5)	90 (0)	97 (0)	105 (0)
EK	SS	99 (5)	96 (9)	118 (6)	122 (0)	NC	118 (9)	114 (5)	NC	NC	105 (32)	151 (59)	113 (7)
	ST-QL	94 (11)	93 (6)	NC	119 (9)	NC	115 (9)	121 (4)	100 (7)	NC	NC	114 (10)	106 (4)
	QL-PR	89 (5)	90 (7)	109 (6)	110 (9)	101 (6)	106 (7)	106 (11)	104 (6)	94 (0)	90 (0)	98 (15)	NC
	PR-ME	NC	NC	90 (0)	113 (6)	NC	107 (7)	111 (4)	115 (0)	102 (13)	112 (10)	105 (6)	106 (0)
	ME-TR	NC	NC	NC	NC	NC	NC	109 (4)	NC	NC	NC	NC	NC
LL	SS	NC	NC	NC	NC	NC	94 (8)	103 (0)	100 (4)	91 (8)	111 (5)	96 (4)	94 (8)
	ST-QL	110 (7)	110 (12)	108 (5)	106 (4)	NC	NC	NC	NC	92 (6)	103 (6)	98 (10)	97 (12)
	QL-PR	101 (8)	102 (4)	108 (11)	104 (7)	103 (7)	99 (6)	100 (7)	95 (8)	93 (3)	102 (0)	NC	101 (13)
	PR-ME	97 (0)	NC	108 (9)	103 (5)	99 (6)	100 (8)	93 (4)	98 (17)	91 (9)	93 (0)	116 (0)	94 (9)
	ME-TR	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC	NC

Arthur, 1972). While consumption of the same prey resource is a prerequisite for competition, competition between two species likely will only have negative effects if a resource (e.g., food) becomes limiting. While diet samples of larval and small juvenile (<60 mm TL) yellow perch and gizzard shad were not assessed during our study, we did assess TL and condition of autumn-captured age-0 yellow perch. Growth of age-0 yellow perch did not differ statistically within lakes among years and condition of susbstock yellow perch was high during all sample seasons (mean $W_r \geq 100$; Murphy et al., 1990) when gizzard shad were present, suggesting that either perch and gizzard shad occupied different niches or zooplankton resources were not limiting. Zooplankton was collected in these systems approximately every six weeks during the growing season (May–September) and densities never fell below 100/L in any system during all seasons and years (VanDeHey et al., 2012b), suggesting that zooplankton resources were not limiting for yellow perch growth and survival (Werner and Blaxter, 1980; Wu and Culver, 1992; Welker et al., 1994; Dettmers et al., 2003; Graeb et al., 2004). Further, copepod (adult and nauplii) densities, the preferred prey of larval yellow perch (Fisher and Willis, 1997; Graeb et al., 2004), only fell below 100/L during autumn of 2008 in Middle Lynn, spring of 2010 in Lardy Lake and never fell below 100/L in East Krause. Macroinvertebrates dominated autumn-captured yellow perch diets in these systems during the study (VanDeHey et al., 2012b) suggesting that an ontogenetic shift occurred during the first year for perch in these systems (Pycha and Smith, 1955; Whiteside et al., 1985; Graeb et al., 2006). This shift away from zooplankton could have released yellow perch from potential competition with gizzard shad. Alternatively, gizzard shad, if being outcompeted by yellow perch could have switched from zooplanktivory to detritivory if zooplankton resources became depleted (Adams et al., 1983; Schaus et al., 2002). Either way, both species have evolved mechanisms to reduce inter- and intraspecific competition (Mittlebach and Persson, 1998; Schaus et al., 2002).

In addition to assessing the potential for competition between gizzard shad and age-0 yellow perch, we also assessed the potential impacts of shad on larger (≥130 mm TL) yellow perch as little, if any, research had been conducted on this topic. Gizzard shad, at the densities found in this study, apparently had little impact on the population dynamic rates of yellow perch as growth remained similar across years and condition remained high throughout the study. One metric that did change during years with gizzard shad present was the relative abundance of yellow perch. During 2008 and 2009 mean CPUE of yellow perch declined significantly relative to the pre- and post-shad years. However, this pattern was observed in the reference lake as well as both treatment lakes suggesting that environmental factors and variable recruitment (Clady, 1976; Rice et al., 1987; Ward et al., 2007; Isermann et al., 2007; Isermann and Willis, 2008) likely led to the changes in relative abundance rather than gizzard shad causing a reduction in yellow perch abundance.

While it appeared that gizzard shad likely had little impact on yellow perch, there are some precautionary notes regarding this research. First, gizzard shad larval and juvenile abundances in East Krause and Middle Lynn were much lower than those in other South Dakota systems (Ward et al., 2007; Wuellner et al., 2010; VanDeHey et al., 2012a). If gizzard shad adult and juvenile densities had been higher, it is possible that shad may have negatively impacted yellow perch. Three of four adult gizzard shad collected were found to consume zooplankton following stocking into the glacial lakes, and VanDeHey et al. (2012b) found that stable isotope values of age-0 gizzard shad indicated they were feeding in the pelagia, either on zooplankton or phytoplankton. Diet samples of age-0 gizzard shad confirmed the isotope results that shad were indeed consuming zooplankton. If both adult and juvenile gizzard shad were to consume zooplankton and their densities increased, it is possible that they could cause middle-out effects on the food web (DeVries and Stein, 1992; Stein et al., 1995).

Alternatively, if gizzard shad abundances increased, this could potentially have positive effects on yellow perch. When available, age-0 gizzard shad composed a substantial proportion of adult yellow perch diets in Lake Erie (Knight et al., 1984). Gizzard shad are more energetically beneficial than most invertebrates documented in yellow perch diets during this study (Cummins and Wuycheck, 1971; Miranda and Muncy, 1991; Hill, 1997; VanDeHey et al., 2012b) and consumption of juvenile shad would likely increase perch growth. Additionally, Fitzgerald et al. (2006) found that in years when gizzard shad abundance was higher, overwinter survival of yellow perch increased in Oneida Lake, New York. Predation by walleye was suggested to be the mechanism driving overwinter survival of yellow perch and the increased abundance of gizzard shad essentially buffered perch from walleye predation (Fitzgerald et al., 2006).

4.2. Effects on walleye

Overall, it appeared that gizzard shad had a neutral to positive effect on the walleye populations in Middle Lynn and East Krause lakes during this study. When gizzard shad were available (autumn sample), they composed a similar proportion of walleye diets by weight (VanDeHey et al., 2012b) as those found to significantly increase growth and relative abundance of walleye in a western South Dakota reservoir (Ward et al., 2007). Walleye growth

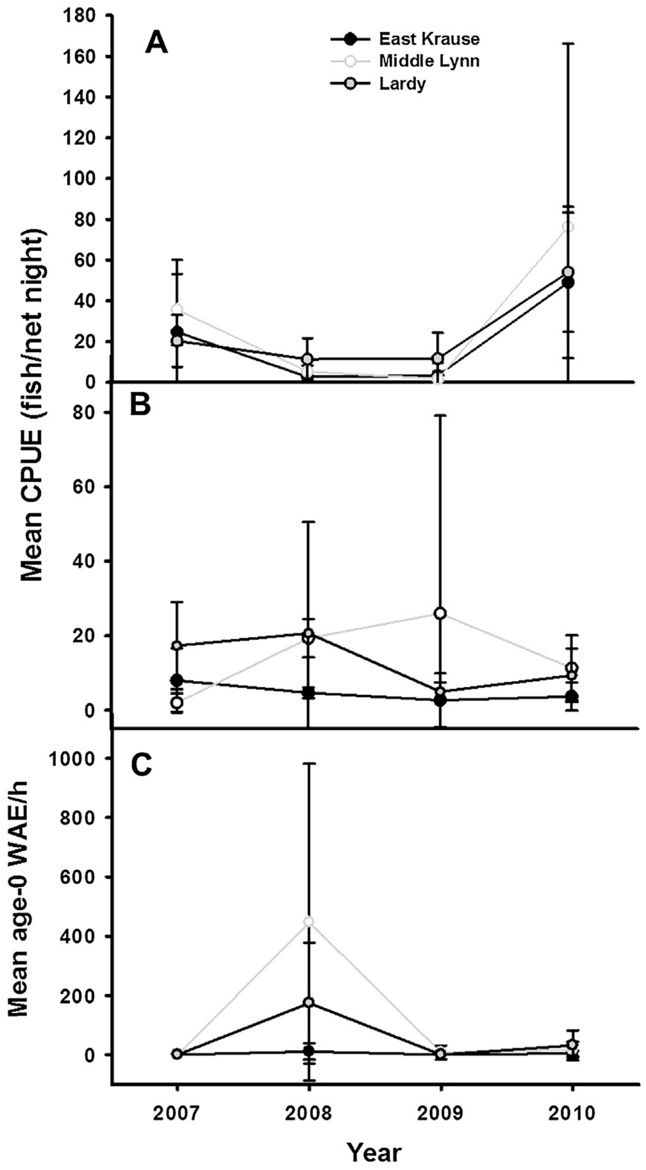

Fig. 4. Mean catch per unit effort (number of fish/net night) for all yellow perch (A) and walleye (B) captured during spring (May) standardized graded mesh gill net surveys during 2007 to 2010 in Middle Lynn, Lardy and East Krause lakes in northeastern South Dakota and mean catch per unit effort of age-0 walleye (C) collected during autumn (September) nighttime electrofishing standardized surveys from 2007 through 2010. Error bars represent 80% confidence intervals.

was highest in East Krause Lake when gizzard shad were present. Additionally, although growth was not faster in Middle Lynn Lake when shad were present, CPUE was the highest during this period and growth was not significantly slower than pre-shad data suggesting that shad may have allowed for increases in walleye density without negative impacts on growth (Wuellner et al., 2010). Walleye growth is often strongly related to the quality and quantity of prey fish available for consumption (Hartman and Margraf, 1992; Michaletz, 1997; Ward et al., 2007; Graeb et al., 2008; Kaufman et al., 2009; Wuellner et al., 2010). Previous research has documented that walleye select for soft-rayed prey species over spinous prey (Forney, 1974; Knight et al., 1984; Hartman and Margraf, 1992) suggesting gizzard shad would likely be preferentially consumed in these systems. Further, gizzard shad have a higher energy density (J/g) than most invertebrates and other fish species commonly found in the diets during this study (see Wuellner et al., 2010 and citations within) suggesting that consumption of shad in place of other fish or invertebrate species should result in increased condition and growth (Ward et al., 2007; Wuellner et al., 2010).

While gizzard shad did not comprise a large portion of the walleye diets throughout the year, they did represent a seasonally important (autumn) prey item (VanDeHey et al., 2012b). This seasonal use of gizzard shad by walleye was similar to that found in Oneida Lake, where shad, despite only seasonal use, are believed to “buffer” yellow perch from walleye predation (Fitzgerald et al., 2006). Our results suggest that during years when yellow perch abundance is low, gizzard shad could potentially help walleye sustain high growth and condition in these systems compared to systems where shad are not present. For example, larval and juvenile yellow perch relative abundance was lowest in 2009 in our reference lake (VanDeHey et al., 2012b; this paper); walleye growth and condition declined during this year in this system.

The addition of an energetically beneficial prey item could also have had positive effects on recruitment. Over 40% of the variability in walleye recruitment in Lake Erie was related to gizzard shad abundance during the previous autumn (Madenjian et al., 1996). In Savanne Lake, Ontario walleye recruitment was both directly and indirectly impacted by bi-annual hatches of the burrowing mayfly *Hexagenia limbata* whereby the adults showed improved condition during years with mayfly hatches and juvenile walleye had an abundant prey source (Richie and Colby, 1988). While natural recruitment of walleye in our study lakes was limited, most likely due to insufficient quality and quantity of spawning habitat, the introduction of a prey species could still have positive impacts on the walleye fry stocked during this research. Growth and survival of larval walleye have been related to prey density (Hoxmeier et al., 2004, 2006) and larval walleye can switch to piscivory as small as 10 mm TL (Schademann, 1987). In both treatment lakes, survival of age-0 walleye to autumn was the highest during 2008. This was also the year with the highest larval gizzard shad abundances (VanDeHey et al., 2012a) suggesting that the presence of shad may have improved survival of age-0 walleye. Autumn age-0 walleye abundance was also the highest in the reference lake during 2008, but larval yellow perch abundances were six times higher in Lardy than in East Krause and 26 times higher in Lardy than Middle Lynn during this year (VanDeHey et al., 2012b). Thus, the addition of gizzard shad to the prey base may have increased walleye survival where larval yellow perch production was low. The availability of an abundant prey fish species for juvenile walleye in these systems may indeed have been a limiting factor, as zooplankton densities were high in all lakes during all years and water temperatures were similar in lakes during all years (VanDeHey et al., 2012b). While it appeared that gizzard shad likely had a positive impact on walleye, abundance of larval and juvenile gizzard in East Krause and Middle Lynn was much lower than in other South Dakota systems (Ward et al., 2007; Wuellner et al., 2010; VanDeHey et al., 2012a). The frequency of occurrence of gizzard shad in walleye diets was relatively low during this study, except during autumn (VanDeHey et al., 2012b), suggesting that if larval and juvenile shad production had been higher it is likely that walleye growth, condition and possibly relative abundance would have increased even more during this study. Had diets been assessed during late July and August, it is likely that gizzard shad would have composed a large portion of walleye diets by weight as this is the time when gizzard shad typically become available (Quist et al., 2002; Ward et al., 2007; Wuellner et al., 2010). A large portion of walleye growth in Great Plains systems is attained during late summer and autumn (Quist et al., 2002) suggesting that a seasonally available prey resource like gizzard shad could have large effects on walleye growth and condition if abundant. Further, walleye in these systems had relatively fast growth and high condition prior to the introduction of gizzard shad. If we had performed this experiment in systems where growth was suppressed and condition was low, it is likely that gizzard shad may have had a larger, positive impact on walleye. For example, in Angostura Reservoir, South Dakota, where walleye growth was slow and abundance was low, growth and abundance of walleye increased significantly following the introduction of gizzard shad (Ward et al., 2007).

4.3. Conclusions

Our results suggest that gizzard shad range expansion, whether natural or human-induced, likely will not have detrimental effects on yellow perch populations and may benefit walleye populations, at least at the abundances documented in this study. Our results also potentially suggest that in highly productive systems with simple fish communities gizzard shad may not have the detrimental impacts they have in more nutrient limited systems. Much research had been conducted on the influence of gizzard shad in more nutrient limited reservoir systems. Gizzard shad can effectively cycle nutrients from the benthos into the pelagia through foraging and excretion and often times they release nutrients not previously available in these systems (Schaus et al., 1997; Vanni, 2002; Vanni et al., 2006). However, given that these systems were eutrophic (VanDeHey et al., 2012b) the release or cycling of nutrients likely did not have a large impact. Regardless, it appears that if sufficient densities of juvenile gizzard shad are achieved, they could improve walleye growth and condition and possibly improve walleye recruitment in eutrophic glacial lakes. Additionally, given the duration and severity of winter, it appears that overwinter mortality will likely limit the ability of gizzard shad to naturally colonize water bodies with thermal regimes similar to these study lakes (Fetzer et al., 2011; VanDeHey et al., 2012a). However, with recent climate warming resulting in decreasing and more variable ice coverage and winter duration (Magnuson, 2002), the natural range expansion of gizzard shad (White et al., 1987; Fetzer et al., 2011) and the associated potential negative impacts of gizzard shad (DeVries and Stein, 1992; Stein et al., 1995), the introduction of any species, especially gizzard shad, should be done with careful consideration (Magnuson, 1976).

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