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Review of Gizzard Shad Population Dynamics at the Northwestern Edge of Its Range

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Abstract.—Gizzard shad *Dorosoma cepedianum* is widely distributed in North America, and South Dakota marks the northwestern edge of its native range. To date, most research regarding population dynamics of gizzard shad has been conducted in more southerly waters. We reviewed the dynamics and biology of gizzard shad populations in South Dakota and compared this information with that reported for southerly populations. Once predicted to become extirpated in some South Dakota systems because of a lack of recruitment, gizzard shad populations today are naturally recruiting and have actually expanded their range, although adult population densities remain low. Recruitment of adult gizzard shad varied depending on the system. One population of gizzard shad introduced into a U.S. Bureau of Reclamation reservoir in western South Dakota exhibited erratic recruitment patterns, with only three age-groups recruited from 1993 to 2004. In contrast, adult gizzard shad samples collected in two Missouri River reservoirs indicated more consistent recruitment over an 8-year period. Peak abundance estimates of larval gizzard shad varied widely by system and by year. From 2004 to 2006, densities of gizzard shad in three western South Dakota reservoirs varied between 3 and 722 fish/100 m^3. Densities of gizzard shad in Missouri River reservoirs in 2004 and 2005 varied between 6 and 24,640 fish/100 m^3. Production of gizzard shad in South Dakota reservoirs may equal or exceed that of southern systems. When available as prey, age-0 gizzard shad are an important component of predator diets (30–100% by weight of all prey consumed by walleyes *Sander vitreus*). Introduction of gizzard shad resulted in increased growth rates for recreational fishes in western South Dakota. Currently, the presence of gizzard shad in South Dakota is considered to be a benefit to recreational fisheries in the state. However, further research should address the relationship between climate and reservoir operation on gizzard shad dynamics and the interactions between age-0 shad and age-0 *Micropterus*, *Perca*, and *Sander* spp.

Introduction

Gizzard shad *Dorosoma cepedianum* have a wide native range, extending as far east as the coast of Virginia and as far west as New Mexico; north–south limits of gizzard shad distribution are the Missouri River basin of the Dakotas and the St. Johns River, Florida (Heidinger 1983). Gizzard shad are often an important component of fish communities throughout their range, providing an important prey resource for several predators such as walleyes *Sander vitreus* (Stroud 1949; Jester and Jensen 1972; Quist et al. 2004;

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Ward et al. 2007), white bass *Morone chrysops* (Jester and Jensen 1972), and white crappie *Pomoxis annularis* (Jahn 1983; Mosher 1983). Because gizzard shad have benefited many recreational fisheries, this fish has been introduced as a prey species both within and outside of its native distribution (Heidinger 1983; Dettmers and Stein 1992, 1996; Moyle and Cech 2003).

Despite the benefits that gizzard shad may provide, management of the species can be problematic. In southern systems, juvenile gizzard shad may experience fast growth and low mortality due to prolonged growing seasons (Swingle 1950; Noble 1981; Michaletz 1997). Resulting intraspecific competition for adult gizzard shad may lead to decreased production of age-0 shad and negative impacts to recreational fishes (Noble 1981). In contrast, gizzard shad on the northern periphery of their range are more susceptible to winterkill (Heidinger 1983; Porath 2006), reducing the probability of intraspecific competition among adults and increasing the likelihood that age-0 shad will be produced on an annual basis (Heidinger 1983; Willis 1987). Evidence suggests that gizzard shad populations in South Dakota are likely limited by winterkill. Walburg (1964) reported no survival of age-0 gizzard shad in years when ice cover lasted more than 103 d in Lewis and Clark Lake (southeastern South Dakota). Furthermore, stocking of juvenile gizzard shad (N = 85,000) into Lake Oahe in April 1982 resulted in no subsequent survival (Hanten 2006). Understanding the environmental factors that affect gizzard shad population dynamics is important to management of predator species (e.g., walleyes) in South Dakota (Ward et al. 2007).

In this paper, we summarized our knowledge of native and introduced populations of gizzard shad in South Dakota and compare this information to southern populations. Because gizzard shad dynamics in South Dakota have changed markedly since the 1970s and 1980s, we examine those changes and hypothesize the future of gizzard shad management in the north-central United States.

Study Sites

Gizzard shad have been extensively studied in six South Dakota reservoirs (Table 1). Gizzard shad have been introduced into three smaller western reservoirs (Angostura, Belle Fourche, and Shadehill). Angostura Reservoir was stocked with prespawn adult gizzard shad in 1990–1992 and 1994, and the population is presently self-sustaining. Belle Fourche and Shadehill reservoirs have been stocked with prespawn adult gizzard shad since 1997 and 1999, respectively (Ward 2005; Ward et al. 2006). All three western reservoirs are operated by the U.S. Bureau of Reclamation (BOR). Angostura and Belle Fourche reservoirs are used for irrigation, and water levels may be reduced during summer to 50% and 15% of full pool, respectively; however, water levels in Shadehill Reservoir are more stable. All three reservoirs are considered eutrophic (Stueven and Stewart 1996).

Gizzard shad are native to three mainstem Missouri River reservoirs: Lewis and Clark Lake, Lake Francis Case, and Lake Sharpe. Construction of these impoundments was authorized by the Pick-Sloan Flood Control Act of 1944 (Public Law 78–534), and all three are managed by the U.S. Army Corps of Engineers for hydropower, recreation, water supply, navigation, flood control, and fish and wildlife. Water-level fluctuations on Lewis and Clark Lake and Lake Sharpe are small (<1.1 m, annually); changes in water levels on Lake Francis Case may vary between 6 and 14 m in a given year. All three Missouri River reser-

Table 1. Managing agency (U.S. Bureau of Reclamations [BOR] or U.S. Army Corps of Engineers [USACOE]), gizzard shad status (native or introduced), physical characteristics, and average annual heating degree days (from nearest National Oceanic and Atmospheric Administration weather station [1971–2000]) for six South Dakota reservoirs.

Water body	Latitude (degrees)	Longitude (degrees)	Managing agency	Native or introduced?	Surface area (ha)	Maximum depth (m)	Mean depth (m)	Annual heating degree-days
Shadehill Reservoir	45.5 N	102.2 W	BOR	Introduced	1,900	18	7	7,995
Angostura Reservoir	43.2 N	103.4 W	BOR	Introduced	1,950	15	8	6,984
Belle Fourche Reservoir	44.4 N	103.7 W	BOR	Introduced	3,250	17	4	6,995
Lewis and Clark Lake	42.9 N	97.5 W	USACOE	Native	10,500	17	5	7,179
Lake Sharpe	44.4 N	99.4 W	USACOE	Native	25,000	24	10	7,282
Lake Francis Case	43.0 N	98.5 W	USACOE	Native	32,000	43	15	7,484

voirs are classified as mesotrophic (Stueven and Stewart 1996).

Methods

Dynamics of Adult Gizzard Shad

Adult gizzard shad were collected in Lakes Sharpe and Francis Case and in Angostura Reservoir using daytime electrofishing during the spring spawning period of 2004. Fish were measured to the nearest millimeter (total length), and sagittal otoliths were removed to determine the age structure of each gizzard shad population (Clayton and Maceina 1999). Annual growth was assessed as the differences in mean length at time of capture by cohort. Total annual mortality was estimated using catch-curve analysis.

Reproduction and Early Life History of Gizzard Shad

Larval gizzard shad were collected in Angostura, Belle Fourche, and Shadehill reservoirs (2004–2006), Lakes Sharpe and Francis Case (2004–2005), and Lewis and Clark Lake (2005) every 10–14 d from early May to mid-August each year. In all reservoirs, larval fish were collected using 1.0-m-diameter ichthyoplankton trawl with 500–1,000-μm mesh (bar measure). A flowmeter was mounted in the mouth of the trawl to estimate the volume of water filtered. Locations were selected using a stratified-random approach. Each reservoir was divided into zones (lower, middle, and two upper zones for BOR reservoirs and upper, middle, and lower zone for the Missouri River reservoirs). In Angostura, Belle Fourche, and Shadehill reservoirs, four 5-min trawls were completed in each zone. Three 10-min trawls were completed in each zone of Lakes Sharpe, Francis Case, and Lewis and Clark. Additionally, Hipple Lake, a 178-ha backwater area of Lake Sharpe, believed to be reproductive and nursery habitat for larval gizzard shad, was sampled separately during each period. Density of larval gizzard shad was calculated as the number of shad per 100 m^3 of water filtered.

Juvenile gizzard shad were collected in all six reservoirs between 2003 and 2006. In the Missouri River reservoirs, fish were collected using a 60-m bag seine with 6.4-mm bar mesh at randomly selected shoreline locations during summer 2003 and 2004. The BOR reservoirs were sampled using a combination of a 30.5-mm bag seining (6.4 mm bar mesh) and daytime electrofishing in summer from 2004 to 2006. Sample sites were selected similarly to those for larval sampling. In all reservoirs, gizzard shad were enumerated and sagittal otoliths were removed from 50 to 100 randomly selected shad. Hatch date for each fish was determined by counting the number of daily growth rings on the otoliths and adding 3 d to account for the first daily ring being formed 3 d posthatch (Davis et al. 1985). Daily growth of juvenile gizzard shad was determined by taking total length at time of capture, subtracting 5 mm for the length at hatching, and dividing by the age of the fish in days (Bremigan and Stein 1999).

Assessing Impacts of Gizzard Shad on Piscivore Dynamics

Walleye diets were assessed monthly in Angostura Reservoir from April through September 2004. In the Belle Fourche and Shadehill reservoirs, walleye diets were assessed seasonally in 2004 (early May, late July, and mid-September). Most walleyes were collected using nighttime electrofishing, but short-term (i.e., <4 h) gill-net and modified fyke-net sets were also used to supplement catches. Diets of walleyes were summarized according to Ward et al. (2007) and compared to diets of walleyes collected pre-gizzard shad introduction. In addition, consumption and growth estimates of walleye cohorts were estimated as described by Ward et al. (2007).

Results and Discussion

Population Dynamics of Adult Gizzard Shad

Recruitment.—Adult gizzard shad were collected in Angostura Reservoir (*N* = 100) and Lakes Francis Case (*N* = 58) and Sharpe (*N* = 118) in spring 2004 (Figure 1). Only Angostura Reservoir exhibited the expected pattern of erratic recruitment. Contrary to a priori hypotheses, Ward et al. (2006) found gizzard shad recruitment in Angostura Reservoir to be regulated by both abiotic (e.g., winter duration) and biotic (e.g., age-0 gizzard shad abundance) factors. Juvenile gizzard shad were most likely to recruit into the adult population in years exhibiting low age-0 shad abundance, warmer summer temperatures, and warmer winters (Ward et al. 2006).

In contrast to Angostura Reservoir, Lakes Francis Case and Sharpe exhibited consistent recruitment of gizzard shad; all year-classes were represented for age-3 and older fish (Figure 1). This result was unexpected given that previous collections of gizzard shad on Lake Sharpe from 1967 to 1974 indicated only one potential year-class recruited during that time period (June 1987). However, stable recruitment of gizzard shad has been documented in other reservoirs and may be linked to productivity

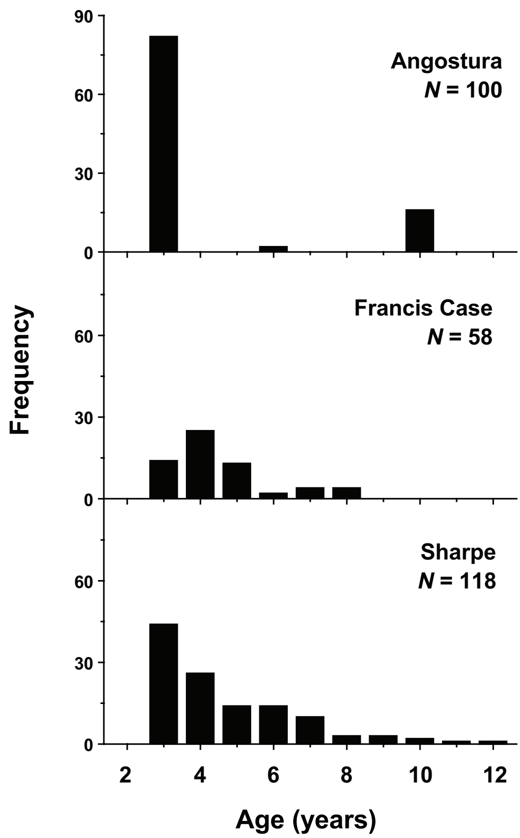

Figure 1. Age structure for adult gizzard shad collected by daytime electrofishing from three South Dakota reservoirs during spring 2004. Ages were determined from sagittal otoliths. Angostura data from Ward et al. (2006).

and availability of thermal refugia. Gizzard shad densities in oligo- or mesotrophic reservoirs are low relative to more productive waters; lower densities may result in consistent recruitment of gizzard shad (DiCenzo et al. 1996; Sammons et al. 1998; Clayton and Maceina 2002). While not quantified, densities of adult gizzard shad in Lakes Sharpe and Francis Case are likely much less than those of southern reservoirs. Further, access to thermal refugia during the winter months could reduce gizzard shad mortality (Heidinger 1983; Porath 2006). Submerged artesian wells are numerous throughout the Missouri River in South Dakota (Davis et al. 1961), and adult gizzard shad have been commonly collected near known artesian wells in both reservoirs (Graeb 2006). Recruitment of adult gizzard shad in the Missouri River may be related to both biotic (adult densities) and abiotic conditions (productivity and water temperature).

Size structure and growth.—Size structure and growth of gizzard shad in South Dakota differed markedly from those reported from other areas. Gizzard shad size structures in Angostura Reservoir and in Lakes Sharpe and Francis Case in 2004 were dominated by large individuals that attained at least 320 mm total length (TL) by age 3 (Table 2). Gizzard shad collected from Angostura Reservoir attained larger lengths at each age on average than those from the Missouri River reservoirs (Table 2), but shad from all three of the above reservoirs were larger than the Texas average reported by Fagan and Fitzpatrick (1978) and the national average reported by Carlander (1969).

Analysis of growth patterns by age in all three reservoirs indicated fast growth at early ages and considerably slower growth after age 3 (Table 2). Rapid growth is likely related to low densities of adult gizzard shad relative to other water bodies (Ward et al. 2006). Clayton and Maceina (2002) reported that gizzard shad mean total length was 250–270 mm at age 2.5 but only 280–300 mm by age 7.5 in two Alabama reservoirs. Growth of gizzard shad in Barataria Estuary, Louisiana, also demonstrated an asymptotic growth pattern at or near age 3 (300–325 mm TL) with a maximum TL of 352 mm for males and 425 mm for females (Fontenot 2006). Thus, gizzard shad in southern

Table 2. Gizzard shad mean total length (mm) by cohort at time of capture in Angostura Reservoir (N = 100) and in Lakes Francis Case (N = 58) and Sharpe (N = 118). All samples were collected by electrofishing during April or May and all fish were aged with sagittal otoliths. Comparison data are mean lengths at age from Carlander (1969; including his nationwide and the highest average lengths from Kansas [KS] to Oklahoma [OK] summaries) and from Fagan and Fitzpatrick (1978; Texas [TX]).

Age	Angostura (SE, N)	Francis Case (SE, N)	Sharpe (SE, N)	Nationwide	KS–OK	TX
3	381 (3, 82)	387 (4, 14)	330 (4, 44)	284	363	249
4		396 (5, 25)	324 (5, 26)	318	411	262
5		454 (15, 13)	358 (14, 14)	345	439	279
6	447 (2, 2)	432 (7, 2)	380 (16, 14)	328	429	303
7		477 (11, 4)	402 (24, 10)	333	401	368
8			388 (42, 3)	373		
9			399 (26, 3)	406		
10	441 (6, 16)		369 (52, 2)	399		

waters appeared to reach asymptotic length at ages similar to South Dakota populations, but at smaller mean lengths.

Adult mortality.—Although adult gizzard shad were collected in Lakes Sharpe and Francis Case and Angostura Reservoir, low sample size and erratic recruitment precluded calculation of total annual mortality in Lake Francis Case and Angostura Reservoir (Figure 2). Total annual mortality in Lake Sharpe was 30% ($r = -0.96$, $P = 0.01$) for ages 3–7. Gizzard shad populations are often characterized as short-lived with high natural mortality (Heidinger 1983). Michaletz (1998) reported average annual mortality rates of 62% for adult (≥age-3) gizzard shad in 15 Missouri reservoirs while mortality rates of 66% were reported for adult shad in Claytor Lake, Virginia (Bonds 2000). No gizzard shad older than age-5 were collected in Barataria estuary, Louisiana (Fontenot 2006). Mortality of gizzard shad in Lake Sharpe appears to be low relative to more southerly waters; survival may be related to low densities of gizzard shad, relatively large sizes of shad prior to winter, and availability of thermal refugia.

Gizzard Shad Reproduction and Early Life History

Larval production.—An important concern for gizzard shad management in South Dakota was the extent of reproduction given the apparent low adult density in our northern populations. Larval densities in the three

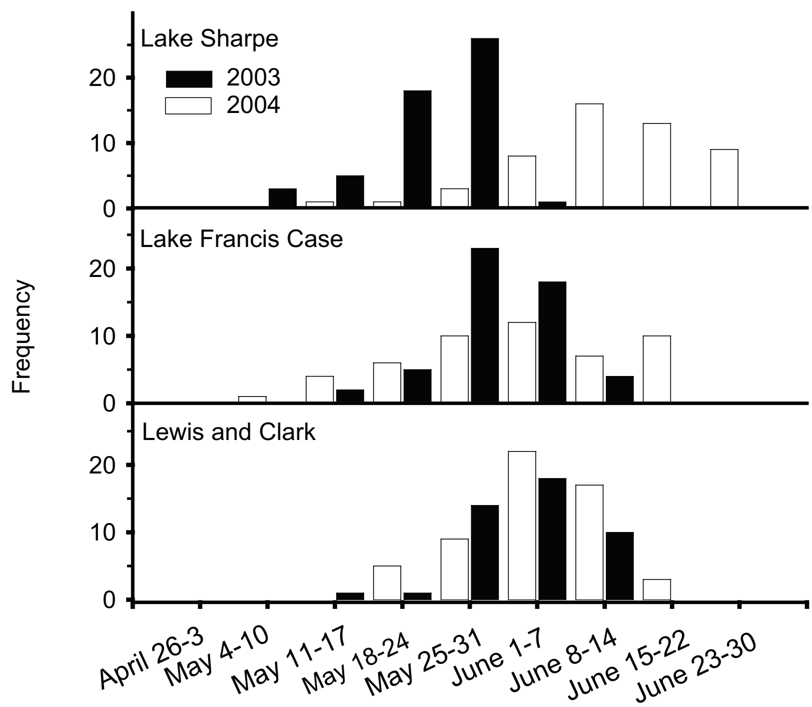

Figure 2. Hatching date distribution (by week) for juvenile gizzard shad collected from three Missouri River reservoirs in late July and early August, 2003 and 2004. Sagittal otoliths were removed for aging and hatching date was determined by counting the number of daily growth rings on the otoliths and then adding 3 d (the first daily ring is formed 3 d posthatch; Davis et al. 1985).

BOR reservoirs ranged from 3 to 722/100 m^3 (Table 3). The one reservoir with an established population of adult gizzard shad (Angostura) had abundance estimates intermediate to the two reservoirs in which prespawn adult shad were stocked annually.

Larval gizzard shad densities in the Missouri River reservoirs equaled or exceeded those of BOR reservoirs and ranged from 6 to 1,374/100 m^3 (Table 3). However, larval densities were 2–25 times greater in Hipple Lake, a shallow backwater area in Lake Sharpe (Table 3). These results suggest that this area may be important for larval rearing

Table 3. Mean abundance estimates for larval gizzard shad indicating peak abundance documented in South Dakota reservoirs. All samples were collected with a 1-m-diameter conical trawl towed for 5–10 min. Number of tows varied by reservoir (see Methods). A flowmeter mounted in the trawl mouth allowed determination of water volume filtered per tow. Comparison data from southern populations are provided.

Water body	State	Year	Peak number/ 100 m^3 (SE)	Source
Angostura	SD	2004	29 (10)	Ward (2005)
		2005	63 (63)	
		2006	152 (152)	
Belle Fourche	SD	2004	558 (192)	Ward (2005)
		2005	722 (351)	
		2006	202 (103)	
Francis Case	SD	2004	32 (24)	Graeb (2006)
		2005	9 (5)	
Lewis and Clark	SD	2005	58 (47)	Graeb (2006)
Shadehill	SD	2004	3 (1)	Ward (2005)
		2005	34 (6)	
		2006	19 (5)	
Sharpe (Hipple Lake)	SD	2004	3,767	Graeb (2006)
		2005	24,630	
Sharpe (reservoir)	SD	2004	6 (3)	Graeb (2006)
		2005	1,374 (1,368)	
Comparisons				
Beaver Reservoir	AK		~180	Netsch et al. (1971)
Clark Lake	OH		8,400	Dettmers and Stein (1992)
Claytor Lake	VA		4–6	Bonds (2000)
Glen Elder Reservoir	KS		4–150	Quist et al. (2004)
Kokosing Lake	OH		8,400	DeVries and Stein (1992)
Lake Carl Blackwell	OK		~4	Downey and Toetz (1983)
Lake Rathbun	IA		1,000	Mayhew (1977)
Lake Texoma	OK/TX		140	Kashuba and Matthews (1984)
Normandy Reservoir	TN		1–118	Sammons et al. (1998)
Smith Mountain Lake	VA		50	Tisa et al. (1985)
Thomas Hill Reservoir	MO		772	Haake (1979)

and production and may supply substantial numbers of gizzard shad to Lake Sharpe.

Assessments of larval gizzard shad densities from South Dakota reservoirs indicated that production in northern latitudes can equal or exceed that in southerly populations (Table 3). Abundance of larval gizzard shad has been linked to biotic (e.g., low adult densities and high adult female condition [Willis 1987; Miranda and Muncy 1988]) and abiotic conditions (e.g., water temperature and rising water levels that trigger spawning activity [Shelton et al. 1982; Willis 1987; Michaletz 1997]).

Dynamics of juvenile gizzard shad.—Juvenile gizzard shad abundance catch per unit effort as indexed by electrofishing in BOR reservoirs varied between 14 and 3,734 fish/h between summer 2004 and 2006 (Table 4). Belle Fourche Reservoir had consistently greater numbers of juveniles, and the least number of juvenile shad were collected in Shadehill Reservoir in 2005. No estimates of relative abundance from were available from seining in the Missouri River or BOR reservoirs, due to lack of effort information. Studies in southern waters have used summer or autumn seining to index juvenile abundance (e.g., Willis 1987; Ploskey et al. 1990) or trawls (Michaletz et al. 1995; Boxrucker et al. 1995); thus, abundance comparisons are difficult. Aday et al. (2003) reported that autumn abundance of age-0 gizzard shad electrofishing (AC) catch per unit effort ranged from 30 to 228 fish/h over 2 years in six smaller central Illinois reservoirs. While electrofishing afforded more precise estimates of abundance compared to seining in BOR reservoirs of South Dakota (Ward 2005), the use of alternative techniques (e.g., hydroacoustics) may provide even higher accuracy (Aday et al. 2003).

Hatch-date distributions from juvenile gizzard shad indicated high variations in reproduction, both among waters and between years. In the three Missouri River reservoirs, gizzard shad spawning appeared to last 5–7 weeks, with peak hatches typically occurring in late May or early June (Figure 2). Gizzard shad appeared to hatch later in 2004 than in 2003 in two reservoirs, likely due to below normal temperatures experienced in 2004, which may have delayed shad spawning (Michaletz 1997). Results from BOR reservoirs indicated a shorter spawning period of 3–6 weeks, with peak activity in mid-June (Ward 2005). However, juvenile estimates of hatch duration in all six reservoirs are likely conservative given that larval gizzard shad (<10 mm TL) were often collected in mid- to late July (Ward 2005; Graeb 2006). Protracted spawning of gizzard shad is not uncommon; spawning periods of 6 weeks were reported for Kansas reservoirs (Willis 1987) and Beaver Reservoir, Arkansas (Netsch et al. 1971). Timing and duration of spawning is often considered important in management of gizzard shad as prey (Willis 1987; Michaletz 1997).

Daily growth rates of juvenile gizzard shad were similar among all six reservoirs. Between 2004 and 2005, growth varied

Table 4. Late summer mean catch per unit effort (number/h) for age-0 gizzard shad collected from three South Dakota reservoirs using daytime electrofishing. Standard errors of the mean are provided in parentheses.

Year	Angostura	Belle Fourche	Shadehill
2004	76 (34)	46 (31)	9 (9)
2005	352 (94)	916 (302)	14 (13)
2006	457 (139)	3,734 (802)	556 (154)

from 0.73 to 1.5 mm/d in the BOR reservoirs (Ward 2005). Growth in the three Missouri River reservoirs ranged from 0.7 to 1.2 mm/d in 2003 and 2004 (Figure 3). Cooler water temperatures in the Missouri River in 2004 may have caused slower growth of age-0 gizzard shad than in 2003. Michaletz (1997) estimated that average growth of juvenile gizzard shad was 0.66 mm/d in reservoirs of southwest Missouri. However, growth may vary within and among cohorts (Michaletz 1997).

Gizzard Shad Community Interactions

Gizzard shad are often the most important prey species for percids in Midwestern U.S. reservoirs (Momot et al. 1977; Stahl and Stein 1994; Carlander 1997; Donovan et al. 1997; Quist et al. 2004; Sieber Denlinger et al. 2006), which also appears to be true for shad in South Dakota. Prior to gizzard shad introductions in Shadehill Reservoir, walleyes primarily consumed invertebrates, suggesting that prey fish abundance was limited (Slipke and Duffy 1997). Gizzard shad were introduced to supplement prey supply in BOR reservoirs beginning in the early 1990s. Recent studies of walleye food habits in these reservoirs have indicated that gizzard shad comprise a substantial proportion of walleye diets (90–100% by weight) from midsummer to September (Ward et al. 2007). Since gizzard shad were introduced into Angostura Reservoir in 1990, both walleye relative abundance (based on catch per effort in annual, standardized gill-net samples) and growth have increased (Ward et al. 2007). Further, walleyes in Angostura Reservoir actually lost weight from April through July but grew rapidly in August and September when gizzard shad became avail-

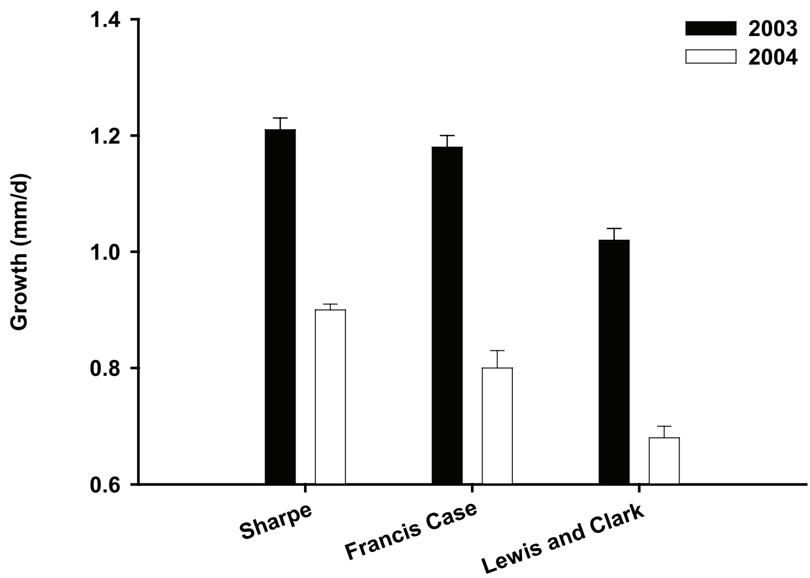

Figure 3. Growth rates (mm/d) of juvenile gizzard shad in three Missouri River reservoirs. Daily growth of juvenile gizzard shad was determined by taking total length at time of capture in late July and early August, subtracting 5 mm for length at hatching, and dividing by the age of the fish in days (Bremigan and Stein 1999). Error bars represent one standard error of the mean.

able (≥25 mm TL; Figure 4). Similar growth patterns have been observed in Pymatuning Sanctuary, Pennsylvania (Kocovsky and Carline 2001), and Glen Elder Reservoir, Kansas (Quist et al. 2002), where gizzard shad were not substantial components of walleye diets until late summer. Further, Santucci and Wahl (1993) noted that walleye growth increments averaged 60 mm/year higher in systems where gizzard shad was the primary prey source versus systems with centrarchid or cyprinid prey bases.

The Missouri River reservoirs contain a more diverse prey fish community than the western irrigation reservoirs (Miller et al. 2006; Sorensen and Knecht 2006; Adams 2007; Lott et al. 2007; Potter and Lott 2007), but gizzard shad have become a primary diet component of piscivorous fish in all of these systems. Gizzard shad were reestablished in Oahe Reservoir in the late 1990s, and shad quickly became a substantial component of walleye diets (often 30–90% by number) during fall and winter months (Hanten 2006; Graeb et al. 2008, this volume). Wickstrom (2006) reported that gizzard shad were an important prey item for walleyes and saugers *Sander canadensis* in Lewis and Clark Reservoir, particularly during autumn. Consumption of gizzard shad rather than other available prey such as yellow perch *Perca flavescens* or emerald shiners *Notropis atherinoides* is probably due to increased predation success on shad relative to other fishes (Wahl and Stein 1988; Einfalt and Wahl 1997).

While gizzard shad do provide benefits to recreational fisheries, they also create many concerns (Dettmers and Stein 1992; DeVries and Stein 1992; Stein et al. 1995; Roseman et al. 1996; Donovan et al. 1997). Larval gizzard shad can influence zooplankton populations through predation or competitive herbivory (i.e., middle-out effects on food webs; DeVries and Stein 1992). However, timing of gizzard shad hatching appears important in interactions with other age-0 species. In southern systems, gizzard shad often spawn during early spring and quick-

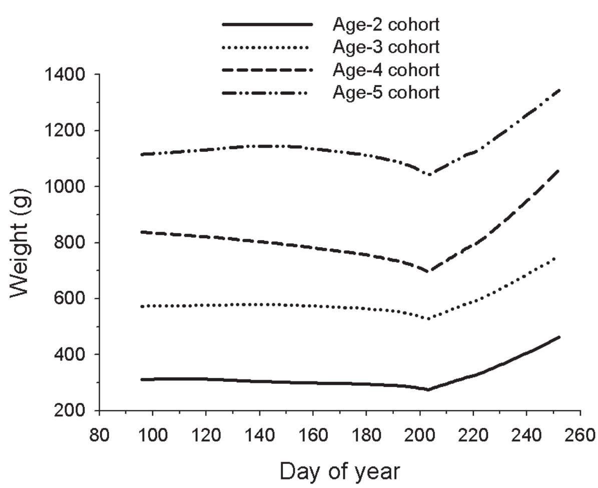

Figure 4. Mean walleye weight (i.e., empirical data) for age-2 through age-5 cohorts from April 5, 2004 until September 8, 2004 in Angostura Reservoir, South Dakota. Commencement of age-0 gizzard shad consumption by walleye corresponds to July 23, 2004. Figure reprinted with permission from Ward et al. (2007).

ly outgrow gape limitations of age-0 centrarchid predators such as largemouth bass *Micropterus salmoides* (Carline et al. 1984; Storck 1986; Garvey and Stein 1998; Allen et al. 1999; Kim and DeVries 2000). However, dynamics between percids and gizzard shad appear to be different. Timing of gizzard shad reproduction appears to be later at the northwestern edge of their range, leaving age-0 shad vulnerable to predation by age-0 walleyes (20–30 mm TL; Momot et al. 1977; Carlander 1997; Quist et al. 2004). Furthermore, timing of diet shifts of gizzard shad may alleviate competition with other percid planktivores. Michaletz et al. (1987) found that larval gizzard shad in Lake Francis Case initially fed mostly on zooplankton but gradually switched to algae and detritus; gizzard shad did not consume zooplankton after July. Age-0 yellow perch in Lake Francis Case did consume zooplankton until July but then switched to insectivory (Michaletz et al. 1987). Thus, competition between the two species may be minimized during the latter half of the growing season. Differences in dynamics of age-0 gizzard shad in South Dakota compared to southerly populations may enhance their benefits to recreational fisheries (DeVries and Stein 1992; Quist et al. 2003).

Management Implications

Managing gizzard shad populations to enhance prey availability is often approached with caution because of the many potential direct and indirect negative effects of shad on aquatic ecosystems. For example, through middle-out food web linkages (Stein et al. 1995), gizzard shad can reduce crustacean zooplankton abundance (DeVries and Stein 1992), decrease growth of planktivores (Aday et al. 2003), and quickly outgrow gape widths of predators in some systems (Garvey and Stein 1998). As such, much research has focused on how to control (i.e., reduce) adult gizzard shad abundance.

Based on our research, we believe that gizzard shad have the potential to greatly enhance the growth rate and size structure of piscivores in South Dakota reservoirs. Currently, multiple systems exist in which adult gizzard shad density is maintained at low levels by high overwinter mortality of juveniles, but at a level sufficient for annual production of larval and juvenile shad as a prey sources for predators. Furthermore, timing of gizzard shad production plays a role in competitive interactions and in their vulnerability to age-0 and older predators. Thus, the potential negative effects of middle-out food web linkages (Stein et al. 1995) are minimized.

Despite the current status of gizzard shad populations in South Dakota, we speculate that climate changes could substantially affect both shad population dynamics and predator–prey interactions in the future. Given the likelihood for increased warming in the northern Great Plains (Poiani et al. 1996) and subsequent effects on fish distributions (Schindler 2001; Stefan et al. 2001), gizzard shad may become more dominant in the fish communities of these reservoirs. Distribution of gizzard shad in the Dakotas has recently expanded. Once believed to be excluded from Lake Oahe (Bailey and Allum 1962; Carufel and Witt 1963), gizzard shad recolonized the reservoir from already established populations upstream beginning in the late 1990s, and a naturally recruiting population has since developed (Hanten 2006; Graeb et al. 2008). Furthermore, gizzard shad have been introduced into several North Dakota reservoirs, and survival of juveniles has been documented in these waters (Gangl 2007).

Increases in temperature would also lead to longer growing seasons and shorter winters, with longer growing seasons potentially allowing age-0 gizzard shad to reach larger sizes prior to winter that, combined with shorter winter duration, could result in increased recruitment and subsequent greater density and biomass of adults. This could benefit gizzard shad management, as biologists may no longer have to stock adult gizzard shad in BOR reservoirs to maintain populations. However, as gizzard shad population abundance becomes less restricted by winter mortality, South Dakota reservoirs may become more prone to the negative middle out effects common in more southerly populations (Stein et al. 1995). High gizzard shad biomass could result in South Dakota biologists suddenly needing to control adult shad abundance through strategies such as predator stocking (Dettmers et al. 1998), use of piscicides (Wydoski and Wiley 1999), and watershed management (Vanni et al. 2005).

Research on native and introduced gizzard shad populations in South Dakota provided insights on shad dynamics that are useful for predator–prey management. However, some key information on adult, juvenile, and larval dynamics is still lacking. Current research is examining the effects of climate and reservoir operation on factors affecting reproductive timing of adult gizzard shad, abundance of age-0 shad, and subsequent overwinter survival in South Dakota reservoirs. Future management and research needs include monitoring reproduction patterns of adult gizzard shad and abundance of age-0 shad, examining potential middle-out food web effects that shad may impose, and determining which abiotic and biotic factors affect adult shad recruitment and mortality.

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References

Adams, G. 2007. Annual fish population surveys of Lewis and Clark Lake, 2006. South Dakota Department of Game, Fish and Parks, Fisheries Division Report 07–25, Pierre.

Aday, D. D., R. J. H. Hoxmeier, and D. W. Wahl. 2003. Direct and indirect effects of gizzard shad on bluegill growth and population size structure. Transactions of the American Fisheries Society 132:47–56.

Allen, M. S., J. C. Greene, F. J. Snow, M. J. Maceina, and D. R. DeVries. 1999. Recruitment of largemouth bass in Alabama reservoirs: relations to trophic state and larval shad occurrence. North American Journal of Fisheries Management 19:67–77.

Bailey, R. M., and M. O. Allum. 1962. Fishes of South Dakota. University of Michigan, Museum of Zoology, Miscellaneous Publication No. 119, Ann Arbor.

Bonds, C. C. 2000. Assessment of the response of piscivorous sportfishes to the establishment of gizzard shad in Claytor Lake, Virginia. Master's thesis. Virginia Polytechnic Institute and State University, Blacksburg.

Boxrucker, J., P. H. Michaletz, M. J. Van Den Avyle, and B. Vondracek. 1995. Sampling shad in reservoirs: overview of gear evaluation study for sampling gizzard shad and threadfin shad populations in reservoirs. North American Journal of Fisheries Management 15:885–890.

Bremigan, M. T., and R. A. Stein. 1999. Larval gizzard shad success, juvenile effects, and reservoir productivity: toward a framework for multi-system management. Transactions of the American Fisheries Society 128:1106–1124.

Carlander, K. D. 1969. Handbook of freshwater fishery biology, volume 1. Iowa State University Press, Ames.

Carlander, K. D. 1997. Handbook of Freshwater Biology, volume 3. Iowa State University Press, Ames.

Carline, R. F., B. L. Johnson, and T. J. Hall. 1984. Estimation and interpretation of proportional stock density for fish populations in Ohio impoundments. North American Journal of Fisheries Management 4:139–154.

Carufel, L. H., and A. Witt, Jr. 1963. Range extension of the gizzard shad (*Dorosoma cepedianum*) into North Dakota. Copeia 1963:178.

Clayton, D. L., and M. J. Maceina. 1999. Validation of annulus formation in gizzard shad otoliths. North American Journal of Fisheries Management 19:1099–1102.

Clayton, D. L., and M. J. Maceina. 2002. Trophic state differences in population characteristics of gizzard shad in two Tennessee River impoundments. Lake and Reservoir Management 8:109–117.

Davis, R. D., T. W. Storck, and S. J. Miller. 1985. Daily growth increments in the otoliths of young-of-the-year gizzard shad. Transactions of the American Fisheries Society 114:304–306.

Davis, R. W., C. F. Dyer, and J. E. Powell. 1961. Progress report on wells penetrating artesian aquifers in South Dakota. U.S. Geological Survey, Water-Supply Paper 1534, Washington, D.C.

Dettmers, J. M., and R. A. Stein. 1992. Food consumption by larval gizzard shad: zooplankton effects and implications for reservoir communities. Transactions of the American Fisheries Society 121:494–507.

Dettmers, J. M., and R. A. Stein. 1996. Quantifying the linkages among gizzard shad, zooplankton, and phytoplankton in reservoirs. Transactions of the American Fisheries Society 125:27–41.

Dettmers, J. M., R. A. Stein, and E. M. Lewis. 1998. Potential regulation of age-0 gizzard shad by hybrid striped bass in Ohio reservoirs. Transactions of the American Fisheries Society 127:84–94.

DeVries, D. R., and R. A. Stein. 1992. Complex interactions between fish and zooplankton: quantifying the role of an open-water planktivores. Canadian Journal of Fisheries and Aquatic Sciences 49:1216–1227.

DiCenzo, V. J., M. J. Maceina, and M. R. Stimpert. 1996. The relation between reservoir trophic state and gizzard shad population characteristics in Alabama reservoirs. North American Journal of Fisheries Management 16:888–895.

Donovan, N. S., R. A. Stein, and M. M. White. 1997. Enhancing percid stocking success through an understanding of age-0 piscivore–prey interactions in reservoirs. Ecological Applications 7:1311–1329.

Downey, P., and D. Toetz. 1983. Distribution of larval gizzard shad (*Dorosoma cepedianum*) in Lake Carl Blackwell, Oklahoma. American Midland Naturalist 109:23–33.

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 54:2616–2626.

Fagan, J. A., and L. C. Fitzpatrick. 1978. Allocation of secondary production to growth and reproduction by gizzard shad *Dorosoma cepedianum* (Clupeidae) in Lewisville, Texas Southwestern Naturalist 23:247–262.

Fontenot, J. F. 2006. Seasonal abundance, GSI, and age structure of gizzard shad (*Dorosoma cepedianum*) in the upper Barataria estuary. Master's thesis. Nicholls State University, Thibodaux, Louisiana.

Gangl, S. 2007. State's newest forage fish. North Dakota Outdoors Magazine 2007:10–12.

Garvey, J. E., and R. A. Stein. 1998. Linking bluegill and gizzard shad prey assemblages to growth of age-0 largemouth bass in reservoirs. Transactions of the American Fisheries Society 127:70–83.

Graeb, B. D. S. 2006. Sauger population ecology in three Missouri River mainstem reservoirs. Doctoral dissertation. South Dakota State University, Brookings.

Graeb, B. D. S. 2008. Walleye response to rainbow smelt popoulation decline and liberalized angling regulations in a Missouri River reservoir. Pages 275–292 *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.

Haake, J. W. 1979. Density and growth of larval gizzard shad, *Dorosoma cepedianum*, in Thomas Hill Reservoir, Randolph County, Missouri. Master's thesis. Northeast Missouri State University, Kirksville.

Hanten, R. 2006. Seasonal food habits, condition, growth and distribution of Lake Oahe, South Dakota walleye during depressed prey fish conditions spring 2001 to spring 2002. South Dakota Department of Game, Fish and Parks, Fisheries Division Report 07–02, Pierre.

Heidinger, R. C. 1983. Life history of gizzard shad and threadfin shad as it relates to the ecology of small lake fisheries. Pages 1–18 *in* Proceedings of the Small Lakes Management Workshop: pros and cons of shad. Iowa Conservation Commission, Des Moines.

Jahn, L. 1983. Effects of gizzard shad and the fishery in a 250-acre Illinois lake. Pages 30–37 *in* Proceedings of the Small Lakes Management Workshop, pros and cons of shad. Iowa Conservation Commission, Des Moines.

Jester, D. B., and B. L. Jensen. 1972. Life history and ecology of the gizzard shad, *Dorosoma cepedianum* (LeSueur) with reference to Elephant Butte Lake. New Mexico Agricultural Experiment Station Research Report 218, Las Cruces.

June, F. C. 1987. Early life history and winter mortality of gizzard shad in Lake Sharpe, South Dakota. Pages 75–83 *in* Limnological and fishery studies on Lake Sharpe, a mainstem Missouri River reservoir, 1964–1975. U.S. Fish and Wildlife Service, Fish and Wildlife Technical Report 8, Washington, D.C.

Kashuba, S. A., and W. J. Matthews. 1984. Physical condition of larval shad during spring-summer in a southwestern Reservoir. Transactions of the American Fisheries Society 113:199–204.

Kim, G. W., and D. R. DeVries. 2000. Effects of a selectively reduced gizzard shad population on trophic interactions and age-0 fishes in Walker County Lake, Alabama. North American Journal of Fisheries Management 20:860–872.

Kocovsky, P. M., and R. F. Carline. 2001. Influence of extreme temperatures on consumption and condition of walleyes in Pymatuning Sanctuary, Pennsylvania. North American Journal of Fisheries Management 21:198–207.

Lott, J., J. Erickson, R. Hanten, and K. Potter. 2007. Annual fish population and angler use, harvest and preference surveys on Lake Oahe, South Dakota, 2006. South Dakota Department of Game, Fish and Parks, Fisheries Division Report 07–26, Pierre.

Mayhew, J. 1977. The effects of flood management regimes on larval fish and fish food organisms at Lake Rathbun. Iowa Fisheries Research Technical Series Number 77–2. Iowa Conservation Commission, Des Moines.

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.

Michaletz, P. H. 1998. Population characteristics of gizzard shad in Missouri reservoirs and their relation to reservoir productivity, mean depth, and sport fish growth. North American Journal of Fisheries Management 18:114–123.

Michaletz, P. H., D. G. Unkenholz, and C. C. Stone. 1987. Prey size selectivity and food partitioning among zooplanktivorous age-0 fishes in Lake Francis Case, South Dakota. American Midland Naturalist 117:126–138.

Michaletz , P. H., J. Boxrucker, S. Hale, and J. R. Jackson. 1995. Comparison of four trawls for sampling juvenile shad. North American Journal of Fisheries Management 15:918–923.

Miller, B., D. James, G. Galinat, and J. Shearer. 2006. Statewide fisheries surveys, 2005: surveys of public waters, part 1, lakes region 1. South Dakota Department of Game, Fish and Parks, Fisheries Division Report 06–10, Pierre.

Miranda, L. E., and R. J. Muncy. 1988. Spawning sequence of largemouth bass, bluegill, and gizzard shad. Proceedings of the Annual Conference Southeastern Association of Fish and Wildlife Agencies 41:197–204.

Momot, W. T., J. Erickson, and F. Stevenson. 1977. Maintenance of a walleye, *Stizostedion vitreum vitreum*, fishery in a eutrophic reservoir. Journal of the Fisheries Research Board of Canada 34:1725–1733.

Mosher, T. D. 1983. A comparison of fish harvested from Kansas lakes with and without gizzard shad with special emphasis on crappie populations. Pages 108–123 *in* Proceedings of small lakes management workshop, pros and cons of shad. Iowa Conservation Commission, Des Moines.

Moyle, P. B., and J. J. Cech, Jr. 2003. Fishes: an introduction to ichthyology, 5th edition. Prentice Hall, Upper Saddle River, New Jersey.

Netsch, N. F., G. M. Kersh, Jr., A. Houser, and R. V. Kilambi. 1971. Distribution of young gizzard shad and threadfin shad in Beaver Reservoir. Pages 95–105 *in* G. E. Hall, editor. Reservoir fisheries and limnology. American Fisheries Society, Special Publication 8, Bethesda, Maryland.

Noble, R. L. 1981. Management of forage fishes in impoundments of the southern United States. Transactions of the American Fisheries Society 110:738–750.

Ploskey, G. R., J. L. Stephen, and D. W. Gabelhouse, Jr. 1990. Evaluation of summer seining in Kansas reservoirs. Proceedings of the Annual Conference Southeastern Association of Fish and Wildlife Agencies 44:76–88.

Poiani, K. A., W. C. Johnson, G. A. Swanson, and T. C. Winter. 1996. Climate change and northern prairie wetlands: simulations of long-term dynamics. Limnology and Oceanography 41:871–881.

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

Potter, K., and J. Lott. 2007. Annual fish population and angler use, harvest, and preference surveys on Lake Sharpe, South Dakota, 2006. South Dakota Department of Game, Fish and Parks, Fisheries Division Report 07–09, Pierre.

Quist, M. C., C. S. Guy, R. J. Bernot, and J. L. Stephen. 2002. Seasonal variation in condition, growth and food habits of walleye in a Great Plains reservoir and simulated effects of an altered thermal regime. Journal of Fish Biology 61:1329–1344.

Quist, M. C., C. S. Guy, R. D. Shultz, and J. L. Stephen. 2003. Latitudinal comparisons of walleye growth in North America and factors influencing growth of walleyes in Kansas reservoirs. North American Journal of Fisheries Management 23:677–692.

Quist, M. C., C. S. Guy, R. J. Bernot, and J. L. Stephen. 2004. Factors related to growth and survival of larval walleyes: implications for recruitment in a southern Great Plains reservoir. Fisheries Research 67:215–225.

Roseman, E. F., E. L. Mills, J. L. Forney, and L. G. Rudstam. 1996. Evaluation of competition between age-0 yellow perch (*Perca flavescens*) and gizzard shad (*Dorosoma cepedianum*) in Oneida Lake, New York Canadian Journal of Fisheries and Aquatic Sciences 53:865–874.

Sammons, S. M., P. W. Bettoli, and F. C. Fiss. 1998. Effect of threadfin shad density on production of threadfin shad and gizzard shad larvae in a Tennessee Reservoir. Environmental Biology of Fishes 53:65–73.

Santucci, V. J., Jr., and D. H. Wahl. 1993. Factors influencing survival and growth of stocked walleye (*Stizostedion vitreum*) in a centrarchid dominated impoundment. Canadian Journal of Fisheries and Aquatic Sciences 50:1548–1558.

Schindler, D. W. 2001. The cumulative effects of climate warming and other human stresses on Canadian freshwaters in the new millennium. Canadian Journal of Fisheries and Aquatic Sciences 58:18–29.

Shelton, W. L., C. D. Riggs, and L. G. Hill. 1982. Comparative reproductive biology of the threadfin and gizzard shad in Lake Texoma, Oklahoma–Texas. Pages 47–51 *in* C. F. Bryan, J. V. Conner, and F. M. Truesdale, editors. Proceedings of the Fifth Annual Larval Fish Conference. Louisiana State University, Louisiana Cooperative Fishery Research Unit, Baton Rouge.

Sieber Denlinger, J. C., R. S. Hale, and R. A. Stein. 2006. Seasonal consumptive demand and prey use by stocked saugeye in Ohio reservoirs. Transactions of the American Fisheries Society 135:12–27.

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

Sorensen, J., and G. Knecht. 2006. Annual fish population and angler use and sport fish harvest surveys on Lake Francis Case, South Dakota, 2004. South Dakota Department of Game, Fish and Parks, Fisheries Division Report 06–20, Pierre.

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 vitreum* × *S. canadense*). Canadian Journal of Fisheries and Aquatic Sciences 51:1993–2002.

Stefan, H. G., Z. Fang, and J. G. Eaton. 2001. Simulated fish habitat changes in North American lakes in response to projected climate warming. Transactions of the American Fisheries Society 130:459–477.

Stein, R. A., D. R. DeVries, and J. M. Dettmers. 1995. Food web regulations by a planktivores: exploring the generalities of the trophic cascade hypothesis. Canadian Journal of Fisheries and Aquatic Sciences 52:2518–2526.

Stueven, E., and W. C. Stewart. 1996. 1995 South Dakota lakes assessment final report. South Dakota Department of Environment and Natural Resources, Pierre.

Storck, T. W. 1986. Importance of gizzard shad in the diet of largemouth bass in Lake Shelbyville, Illinois. Transactions of the American Fisheries Society 115:21–27.

Stroud, R. H. 1949. Growth of Norris Reservoir walleye during the first twelve years of impoundment. Journal of Wildlife Management 13:157–177.

Swingle, H. S. 1950. Relationships and dynamics of balanced and unbalanced fish populations. Alabama Polytechnic Institute, Agricultural Experiment Station Bulletin 274, Auburn.

Tisa, M. S., J. J. Ney, and D. K. Whitehurst. 1985. Spatial and temporal distribution of larval alewives and gizzard shad in a Virginia reservoir. Proceedings of the Annual Conference Southeastern Association of Fish and Wildlife Agencies 39:65–73.

Vanni, J. M., K. K. Arend, M. T. Bremigan, D. B. Bunnel, J. E. Garvey, M. J. González, W. H. Renwick, P. A. Soranno, and R. A. Stein. 2005. Linking landscapes and food webs: effects of omnivorous fish and watersheds on reservoir ecosystems. Bioscience 55:155–167.

Wahl, D. H., and R. A. Stein. 1988. Selective predation by three esocids: the role of prey behavior and morphology. Transactions of the American Fisheries Society 117:142–151.

Walburg, C. H. 1964. Fish population studies, Lewis and Clark Lake, Missouri River, 1956 to 1962. U.S. Fish and Wildlife Service, Special Scientific Report-Fisheries No. 482, Washington, D.C.

Ward, M .J. 2005. Gizzard shad biology and predator-prey relations with walleyes in western South Dakota impoundments. Master's thesis. South Dakota State University, Brookings.

Ward, M. J., D. W. Willis, and G. F. Galinat. 2006. Gizzard shad recruitment patterns in a western South Dakota irrigation reservoir. Journal of Freshwater Ecology 21:201–207.

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

Wickstrom, G. A. 2006. Seasonal distribution, movement, and food habits of walleye and sauger in Lewis and Clark Lake. South Dakota Department of Game, Fish and Parks, Fisheries Division Report No. 06–12, Pierre.

Willis, D. W. 1987. Reproduction and recruitment of gizzard shad in Kansas reservoirs. North American Journal of Fisheries Management 7:71–80.

Wydoski, R. S., and R. W. Wiley. 1999. Management of undesirable fish species. Pages 403–430 in C. C. Kohler and W. A. Hubert, editors. Inland fisheries management in North America, 2nd edition. American Fisheries Society, Bethesda, Maryland.