

Interactions between Walleyes and Smallmouth Bass in a Missouri River Reservoir with Consideration of the Influence of Temperature and Prey

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Abstract.—Walleyes *Sander vitreus* are the most popular fish among South Dakota anglers, but smallmouth bass *Micropterus dolomieu* were introduced to provide new angling opportunities. Some walleye anglers have reported reductions in the quality of walleye fisheries since the introduction of smallmouth bass and attribute this to the consumption of young walleyes by smallmouth bass and competition for shared prey resources. We quantified the diets of walleyes and smallmouth bass in the lower reaches of Lake Sharpe (a Missouri River reservoir), calculated the diet overlap between the two predators, and determined whether they partitioned shared prey based on size. We also quantified walleye diets in the upper reach of the reservoir, which has a different prey base and allowed us to compare the growth rates of walleyes within Lake Sharpe. Age-0 gizzard shad *Dorosoma cepedianum* composed a substantial proportion of the diets of both predators, regardless of location, for most of the growing season; the patterns in shad vulnerability appeared to drive the observed patterns in diet overlap. Smallmouth bass appeared to consume a smaller size range of gizzard shad than did walleyes, which consumed a wide range. Smallmouth bass consumed *Sander* spp. in some months, but in very low quantities. Given that global climate change is expected to alter the population and community dynamics in Great Plains reservoirs, we also used a bioenergetics approach to predict the potential effects of limiting prey availability (specifically, the absence of gizzard shad and rainbow smelt *Osmerus mordax*) and increased water temperatures (as projected from global climate change models) on walleye and smallmouth bass growth. The models indicated that the absence of rainbow smelt from the diets of walleyes in upper Lake Sharpe would reduce growth but that the absence of gizzard shad would have a more marked negative effect on both predators at both locations. The models also indicated that higher water temperatures would have an even greater negative influence on walleye growth; however, smallmouth bass growth was predicted to increase with higher temperatures. Fisheries managers should consider strategies to enhance the prey base or mitigate the effects of increased water temperatures that may occur in the future as a result of global climate change. Such proactive actions may alleviate potential future competition between walleyes and smallmouth bass resulting from changes in the fish community.

Fisheries management relies on an understanding of the dynamics between predators and prey within a given system (Ney 1990; Hayes et al. 1999). Prey fish availability is the primary factor affecting piscivore survival and growth in lakes and reservoirs (Ney and

Orth 1986); thus, a well-functioning and self-sustaining fishery is typically characterized as one in which prey are sufficiently abundant to support top predators (Cyterski and Ney 2005). The introduction of new predators, whether intentional or not, may upset the predator–prey balance through competition for shared prey resources (Kitchell and Crowder 1986), negatively affecting survival, growth, and other fitness-related factors of native predators (Crowder 1990). For

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example, the introduction of lake trout *Salvelinus namaycush* into Bear Lake, Utah, reduced the survival of Bonneville cutthroat trout *Oncorhynchus clarkii utah*, in part because of competition for Bear Lake sculpin *Cottus extensus* (Ruzycki et al. 2001). Similarly, competition for shared prey fish reduced the size structure of Eurasian perch *Perca fluviatilis* after the introduction of zander *Sander lucioperca* into the Grober Vätersee, Germany (Schulze et al. 2006).

Introductions of smallmouth bass *Micropterus dolomieu* throughout North America, Europe, Russia, and Africa could alter existing food webs and negatively affect native predators (Sharma and Jackson 2008). Intentional stockings, angler introductions, and range expansion through drainage networks facilitated by increased water temperatures have extended the range of smallmouth bass northward in North America since the mid-1880s (Jackson 2002; Vander Zanden et al. 2004; Dunlop and Shuter 2006; Sharma and Jackson 2008). Documentation of smallmouth bass in new locations has been associated with reduced abundances of native cyprinids (Jackson 2002). Further, the stocking of smallmouth bass into waters with native lake trout decreased the latter's fecundity, growth, and survival via altered food and feeding habits (Vander Zanden et al. 1999).

In South Dakota, walleyes *Sander vitreus* are native to the Missouri River reservoirs (Hoagstrom et al. 2007) and are the most popular fish among anglers (Gigliotti 2007). Smallmouth bass are native to the northeastern corner of the state (Hoagstrom et al. 2007) but were introduced into the Missouri River reservoirs beginning in the early 1980s to provide new angling opportunities (Milewski and Willis 1990; Berry and Young 2004). Some South Dakota walleye anglers believe that smallmouth bass are consuming young walleyes and reducing the abundance, growth, and condition of walleyes through competition for food (Brian G. Blackwell and John P. Lott, South Dakota Department of Game, Fish and Parks [SDGFP], personal communication).

At present, only one study has attributed walleye year-class failures to predation by smallmouth bass (Johnson and Hale 1977). Several studies have documented the potential for competition between sympatric walleyes and smallmouth bass using food habits information (Fedoruk 1966; Johnson and Hale 1977; Frey et al. 2003; Fayram et al. 2005). These studies have indicated low levels of diet overlap owing to the higher diversity of food items consumed by smallmouth bass (Poe et al. 1991; Lott 1996; Vander Zanden et al. 1997). However, only one study (Lott 1996) has been conducted in an oligotrophic or mesotrophic system such as the Missouri River

reservoirs, where low productivity may contribute to a higher incidence of shared prey resources.

Prey availability may differ by location within a single reservoir (Jackson et al. 1993; Lott 1996). In Lake Sharpe, native gizzard shad *Dorosoma cepedianum* are probably abundant throughout the reservoir and currently recruit on an annual basis (Wuellner et al. 2008). Conversely, rainbow smelt *Osmerus mordax* are more abundant in the upper reaches of Lake Sharpe. Rainbow smelt were not intentionally introduced, and no established population currently persists in the reservoir. However, they compose a large portion of the prey base in Lake Oahe (the reservoir directly upstream of Lake Sharpe) and entrainment of large numbers fish through Oahe Dam has been documented (Unkenholz 1998). In fact, Smith (2000) estimated that 439 million rainbow smelt were entrained through Oahe Dam during the summer of 1997. Rainbow smelt could subsidize the diets of predators in upper Lake Sharpe, particularly during mid to late spring.

Prey availability can also change on an annual basis, and it is possible that both gizzard shad and rainbow smelt are less available to Lake Sharpe predators. Higher water temperatures associated with global climate change could increase the growth rates of age-0 gizzard shad and thereby reduce their window of vulnerability to predation in Lake Sharpe if they quickly outgrow predator gape widths (Stein et al. 1995; Vatland and Budy 2007). Further, increased growth and warmer winter temperatures could increase the overwinter survival of age-0 gizzard shad and their recruitment to the adult stage (Wuellner et al. 2008). High biomass of adults could result in decreased annual reproductive efforts, further reducing the abundance of age-0 gizzard shad in the Lake Sharpe prey base during most years (Wuellner et al. 2008).

In a similar manner, rainbow smelt may cease to be available as a prey resource in Lake Sharpe. The amount of entrainment of rainbow smelt that occurs annually through Oahe Dam is dependent on the timing and depth of the spring thermocline in Lake Oahe (Unkenholz 1998; Smith 2000; Hamel et al. 2008). Recent research has shown that sensory deterrent systems may reduce or prevent rainbow smelt entrainment (Hamel et al. 2008). The absence of gizzard shad or rainbow smelt from the Lake Sharpe prey base could affect predator growth differently, depending on location and species.

In addition to producing changes in fish community structure, global climate change is expected to alter fish population dynamics (Matthews and Zimmerman 1990; Carpenter et al. 1992). Altered thermal regimes have been shown to affect the growth of both walleyes and smallmouth bass; walleye populations at the

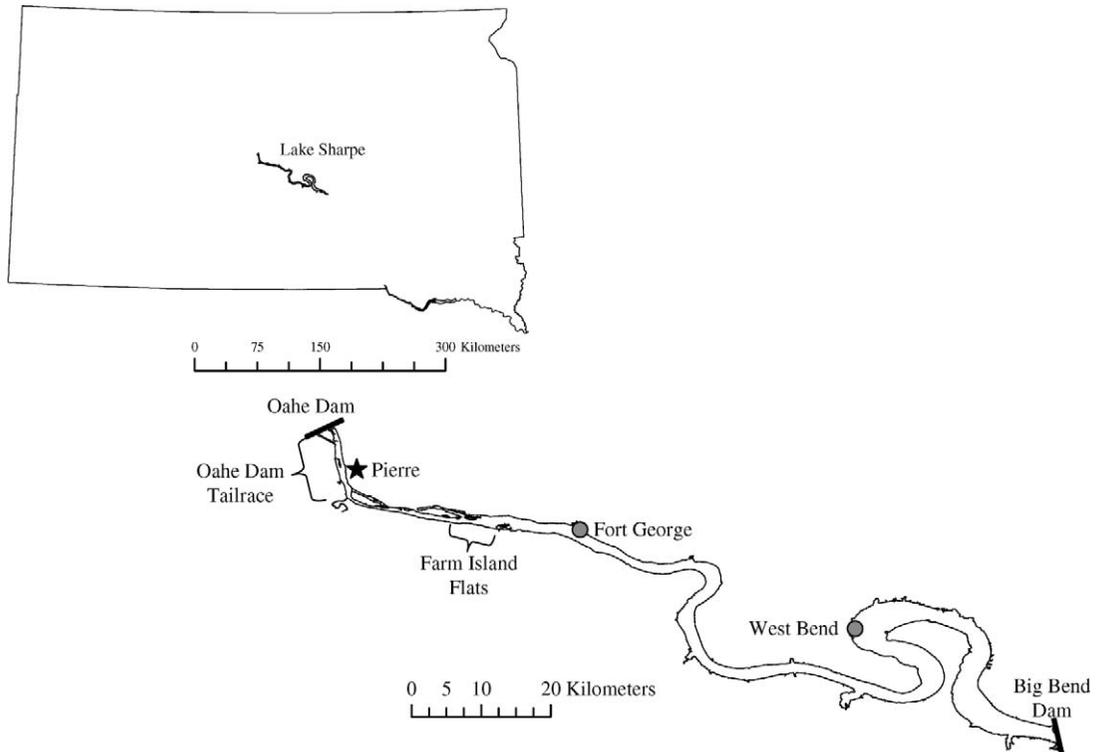


FIGURE 1.—Map of Lake Sharpe showing the upper (Oahe Dam tailrace downstream to Fort George) and lower reaches (West Bend to Big Bend Dam).

central and southern portions of their range may experience lower annual growth rates (Collette et al. 1977; Kocovsky and Carline 2001; Quist et al. 2002), but smallmouth bass in the central and northern portions of their range will probably experience higher annual growth rates (Shuter et al. 1980; Dunlop and Shuter 2006; Sharma and Jackson 2008). Therefore, the objectives of this study were to (1) document the food habits of walleyes and smallmouth bass in Lake Sharpe and determine whether smallmouth bass consume walleyes; (2) quantify the diet overlap and size of prey (specifically, gizzard shad) consumed by walleyes and smallmouth bass; and (3) document the potential impact of changes in prey availability and altered temperature regimes on the growth of both predators using a bioenergetics approach.

Study Site

Lake Sharpe was constructed by the U.S. Army Corps of Engineers (USACOE) and is the fourth-most upstream reservoir on the Missouri River. The impoundment extends from Oahe Dam (completed in 1958) downstream to Big Bend Dam (completed in 1963) and has a surface area of approximately 25,000

ha (Figure 1). The mean and maximum depths of the reservoir are 9.5 and 23.7 m, respectively, and the bottom substrate is classified as sand, gravel, shale, and silt. Lake Sharpe is operated by the USACOE for water control and hydropower, and the annual water fluctuations are less than 1.1 m (Nelson and Walburg 1977). The reservoir does not thermally stratify or does so only weakly owing to high turnover rates (USACOE 2003). In this study, the upper reach of the reservoir was defined as the portion from the Oahe Dam tailrace downstream to Fort George, the lower reach as the portion from West Bend to Big Bend Dam (Figure 1).

The spatial distributions of walleyes and smallmouth bass differ within the reservoir. Walleyes are abundant throughout the upper and lower reaches of the reservoir, while smallmouth bass are found in greater abundance in the lower reach (Figure 1). Other common predators in Lake Sharpe include channel catfish *Ictalurus punctatus*, sauger *Sander canadensis*, and white bass *Morone chrysops*.

Gizzard shad are the primary prey species for Lake Sharpe predators (Johnson et al. 2002). South Dakota marks the northwestern edge of the gizzard shad's native range (Heidinger 1983). Recruitment of gizzard

shad is consistent in Lake Sharpe (Wuellner et al. 2008). Spawning activity may last 5–7 weeks (the timing can depend on water temperatures and flow), but age-0 gizzard shad typically reach lengths at which they are vulnerable to predation beginning in mid-July (Wuellner et al. 2008). Rainbow smelt may be another important prey species in upper Lake Sharpe; they could subsidize the prey base in upper Lake Sharpe before age-0 gizzard shad become vulnerable to predation, thus influencing the growth and body condition of the walleyes inhabiting the upper reach.

Methods

Predators were collected monthly in Lake Sharpe from May to October of 2006 and 2007; these months were considered to be the primary growing season for fish in Lake Sharpe. Walleyes and smallmouth bass were collected from the lower reach of the reservoir for diet comparisons. Walleyes were also collected from the upper reach, where entrained rainbow smelt were available. Although smallmouth bass are present in the upper reach of Lake Sharpe, they are not abundant in this area and were not collected in this region for this study. In both reaches of the reservoir, fish were collected by means of short-term (<4-h) daytime and overnight experimental gill-net sets (bar mesh = 1.3–5.1 cm). The walleye catches from the upper reach were supplemented by nighttime electrofishing. The weights (g), total lengths (TLs; mm), and genders of all collected fish were determined. Sagittal otoliths were removed to determine age. The entire stomach was excised from each fish and preserved in a 90% ethanol solution. The goal of this study was to obtain 20 fish with food in their stomachs each month from each of four length categories for each location and species. For walleyes, the length categories were <300, 300–380, 381–450, and >450 mm TL; for smallmouth bass the length categories were <250, 250–330, 331–410, and >410 mm TL. These length categories were chosen on the basis of length-frequency information from long-term standardized sampling of walleyes and smallmouth bass in Lake Sharpe (Robert P. Hanten and Kyle P. Potter, SDGFP, personal communication).

All diet items were identified to family or order for invertebrates and to species for identifiable fish. The prey items were enumerated and the wet weights (nearest 0.01 g) and lengths (mm) were recorded for each taxonomic group. Counts of prey items were often difficult owing to digestion, so the diets of the walleyes and smallmouth bass were summarized as percent composition by wet weight (Bowen 1996). Food habits data were pooled among all length categories owing to the low numbers of fish sampled within some length categories by month.

The diet overlap between walleyes and smallmouth bass was summarized monthly by means of Pianka's (1973) index of niche overlap. Pianka's index (O_{jk}) is defined as

$$O_{ij} = \frac{\sum_i^n p_{ij}p_{ik}}{\sqrt{\sum_i^n p_{ij}^2 \sum_i^n p_{ik}^2}},$$

where p_{ij} is the proportion of diet item i in the total resources used by species j , p_{ik} is the proportion of diet item i in the total resources used by species k , and n is the total number of diet items. Pianka's index varies between 0 (no diet overlap) and 1.0 (complete diet overlap), with values exceeding 0.75 indicating high diet overlap and values less than 0.40 signifying low overlap (Matthews and Hill 1980; Matthews et al. 1982; Ross 1986). Owing to the low sample sizes among the length categories for walleyes and smallmouth bass, all of the fish from each species were pooled and single diet overlap values were calculated for each month. A bootstrap procedure was used to measure the variability in diet overlap and reduce the effects of outliers on the calculations (Ricklefs and Lau 1980; Smith 1985; Olson et al. 2007; Bellgraph et al. 2008).

Different sizes of predators may consume different sizes of prey, thereby influencing interspecific competition. The size of the gizzard shad consumed by walleyes and smallmouth bass was compared over all months by calculating their mean weighted standard length (SL), where the weights were the numbers of gizzard shad consumed (maximum of 10 shad lengths per individual predator). A one-way t -test was used to determine whether the SLs differed with respect to predator; significance was determined at the 0.05 level.

The relationships between the horizontal gape widths (GWs; mm) of the predators and the SLs of the gizzard shad consumed were also examined. Walleye GWs were determined from predator TLs using the equation of Gosch (2008; $GW = 0.10 \cdot TL - 6.9$). Smallmouth bass GWs were determined using a published equation for butterfly peacock bass *Cichla ocellaris* (Hill et al. 2006; $GW = 0.12 \cdot TL - 2.69$); the genera *Cichla* and *Micropterus* are ecomorphologically similar (Norton and Brainerd 1993). Tests of normality indicated that the gizzard shad SLs were not normally distributed (Kolmogorov–Smirnov test; walleyes: $D = 0.07$, $P < 0.01$; smallmouth bass: $D = 0.08$, $P < 0.01$); thus, predator GW and gizzard shad SL data were \log_e transformed. Linear regression and the 95% prediction interval were used to determine the relationship

TABLE 1.—Energy densities (J/g wet weight) of prey items consumed by walleyes and smallmouth bass in Lake Sharpe during the 2006 and 2007 growing seasons (May–October). The energy densities of unidentified invertebrates or fish were calculated as the average energy densities of known invertebrates or fish; the energy density of unidentified prey was calculated as the average energy density of all known diet items, whether invertebrate or fish.

Group	Taxon	Energy density	Source
Invertebrates	Cambaridae	3,063	Eggleton and Schramm (2002)
	Coleoptera	5,523	Hill (1997)
	Diptera	1,763	Cummins and Wuycheck (1971)
	Ephemeroptera	4,705	Cummins and Wuycheck (1971)
	Hemiptera	5,523	Hill (1997)
	Heteroptera	3,176	Hill (1997)
	Hymenoptera	5,523	Hill (1997)
	Odonata	3,176	Hill (1997)
	Trichoptera	3,176	Hill (1997)
	Unidentified invertebrates	4,349	
Fish	Channel catfish	5,015	Eggleton and Schramm (2002)
	Emerald shiner <i>Notropis atherinoides</i>	5,009	Kelso (1972)
	Fathead minnow <i>Pimephales promelas</i>	4,100	Chipps et al. (2000)
	Gizzard shad	5,108	Miranda and Muncy (1989)
	Rainbow smelt	4,814	Lantry and Stewart (1993)
	<i>Sander</i> spp.	4,606	Kelso (1972)
	Smallmouth bass	4,186	Shuter and Post (1990)
	Unidentified fish	4,640	
	White bass	4,774	Kelso (1972)
	Yellow perch <i>Perca flavescens</i>	4,186	Eggleton and Schramm (2002)
Other	Unidentified prey	4,127	

between the transformed GW and the gizzard shad SL for each predator.

Bioenergetics modeling (Fish Bioenergetics 3.0; Hanson et al. 1997) was used to examine the influences of prey (specifically, rainbow smelt and gizzard shad) and temperature on walleye and smallmouth bass growth. Published caloric values of diet items were obtained from various sources (Table 1) and used along

with the observed diet composition and mean daily temperature to model growth for single individuals in each cohort (Table 2). To estimate growth for the entire growing season, the mean weights of age-3, -4, and -5 walleyes (upper and lower reservoirs separately) and smallmouth bass were calculated in May and October of 2006 and 2007 (Table 2). Two temperature loggers were set near West Bend and one in the Oahe Dam

TABLE 2.—Range of mean daily water temperatures (°C), mean beginning and ending weights (g), and proportion of maximum consumption (p) for age-3, -4, and -5 walleyes and smallmouth bass in Lake Sharpe derived from bioenergetics modeling with actual food habits, growth, and water temperatures during the 2006 and 2007 growing seasons (May–October).

Year	Species	Location	Mean daily temperature range	Age	Mean weight (SD)		p
					May	October	
2006	Walleye	Upper reservoir	4.2–23.9	3	501 (15)	628 (21)	0.29
				4	608 (28)	768 (66)	0.30
				5	752 (23)	775 (46)	0.25
				3	450 (12)	587 (31)	0.32
				4	536 (10)	635 (52)	0.31
	Smallmouth bass	Lower reservoir	3.6–27.9	5	588 (23)	620 (85)	0.33
				3	241 (77)	628 (82)	0.91
				4	455 (40)	850 (34)	0.84
				5	681 (41)	934 (34)	0.72
				3	338 (57)	633 (102)	0.37
2007	Walleye	Upper reservoir	5.2–23.6	4	624 (36)	553 (40)	0.22
				5	615 (36)	758 (92)	0.29
				3	239 (33)	466 (0)	0.41
				4	531 (19)	575 (28)	0.30
				5	673 (51)	953 (152)	0.38
	Smallmouth bass	Lower reservoir	5.3–30.1	3	429 (45)	649 (9)	0.72
				4	555 (39)	885 (32)	0.71
				5	813 (34)	995 (58)	0.57

tailrace area 1–2 m below the water surface; temperatures were recorded hourly and a mean daily temperature was calculated. The proportions of maximum consumption (p) obtained from the observed growth, diet, and temperature data were recorded (Table 2).

Water temperatures in the Great Plains are expected to increase by at least 3°C as a result of global climate change (Eaton and Scheller 1996). This may affect the metabolic rates of fish and their food demand (Biro et al. 2007) while altering prey availability (e.g., Matthews and Zimmerman 1990; Carpenter et al. 1992; Wuellner et al. 2008). To further determine the effects of prey and water temperature on predator growth, walleye and smallmouth bass growth was simulated under several scenarios: (1) the absence of rainbow smelt and gizzard shad from upper Lake Sharpe (walleyes only); (2) the absence of gizzard shad from lower Lake Sharpe (walleyes and smallmouth bass); (3) a 3°C increase in water temperature with no changes in food habits; and (4) the absence of rainbow smelt or gizzard shad (depending on the location and predator) coupled with a 3°C increase in water temperature. Using the values of p obtained from the bioenergetics models with the observed temperatures and food habits, the growth of walleyes and smallmouth bass was simulated over the same growing season under each scenario. The consumption of prey items other than rainbow smelt and gizzard was assumed not to change; instead, the percent composition (by wet weight) of the remaining prey items was recalculated when rainbow smelt or gizzard shad were eliminated.

Results

Food Habits

Upper reservoir walleyes.—Rainbow smelt were found in the diets of walleyes collected from the upper reach of the reservoir almost every month between May and October in both 2006 and 2007 (Figure 2). Invertebrates (primarily dipterans and ephemeropterans) composed a larger proportion of walleye diets from May to July than in other months in both years (see Wuellner 2009). Age-0 gizzard shad were the primary diet item from July to October in 2006 and 2007, representing 47–85% of the total diet.

Lower reservoir walleyes and smallmouth bass.—Invertebrates (mostly ephemeropterans) composed a higher proportion of walleye diets from May to July than from August to October in both years (Figure 2; see also Wuellner 2009). Gizzard shad were the primary prey for walleyes during the latter half of the growing season, representing 25–88% of the total diet

in both years. Walleyes consumed gizzard shad in June of 2006 but not until July in 2007.

The diets of smallmouth bass collected in lower Lake Sharpe varied by month (Figure 2). Smallmouth bass consumed a higher percentage of invertebrates by weight as well as a greater diversity of invertebrates (primarily coleopterans, ephemeropterans, and hemipterans) than did walleyes (see Wuellner 2009). During the early growing season, smallmouth bass also consumed a higher proportion of fish than did lower reservoir walleye in both years. Age-0 gizzard shad represented 2–85% of smallmouth bass diets during the latter part of the growing season in both years, but they did not make a substantial contribution until August in 2007 as opposed to July in 2006.

Distinguishing walleyes from saugers in the stomachs of smallmouth bass was difficult owing to digestion. Even so, the consumption of *Sander* spp. was low in both 2006 and 2007 (Figure 2). Although smallmouth bass consumed *Sander* spp. in May, August, September, and October of 2006, the quantity never exceeded 5% by weight. In 2007, consumption of *Sander* spp. by smallmouth bass was only documented in June and July, and these species constituted 3% or less of the overall diet in both months.

Diet Overlap and Partitioning of Gizzard Shad by Size

Diet overlap between lower Lake Sharpe walleyes and smallmouth bass was low in May and June of 2006 and May and July of 2007 (Table 3). However, overlap was complete or nearly so for each month between August and October in both years and in July 2006 and June 2007. High diet overlap values coincide with patterns of age-0 gizzard shad consumption by both predators (Figure 2).

The weighted SL of gizzard shad consumed was 42 ± 5 mm (95% confidence interval about the mean) and 33 ± 3 mm for walleyes and smallmouth bass, respectively. The size of the shad consumed differed between the two predators ($t = 1.18$; $P = 0.04$); walleyes consumed a wide size range of gizzard shad (8.6–102.0 mm), whereas smallmouth bass consumed a narrower range (12.0–68.2 mm) (Figure 3).

Bioenergetics Modeling and Simulations

Bioenergetics modeling of growth indicated that of the three ages of walleyes collected in upper Lake Sharpe in 2006, fish of ages 3 and 4 grew steadily throughout the growing season while those of age 5 mostly either maintained their weight or grew only a small amount (Figure 4). In 2007, age-4 walleyes lost weight, in contrast to the constant growth displayed by age-3 and age-5 fish (Figure 4). However, this pattern

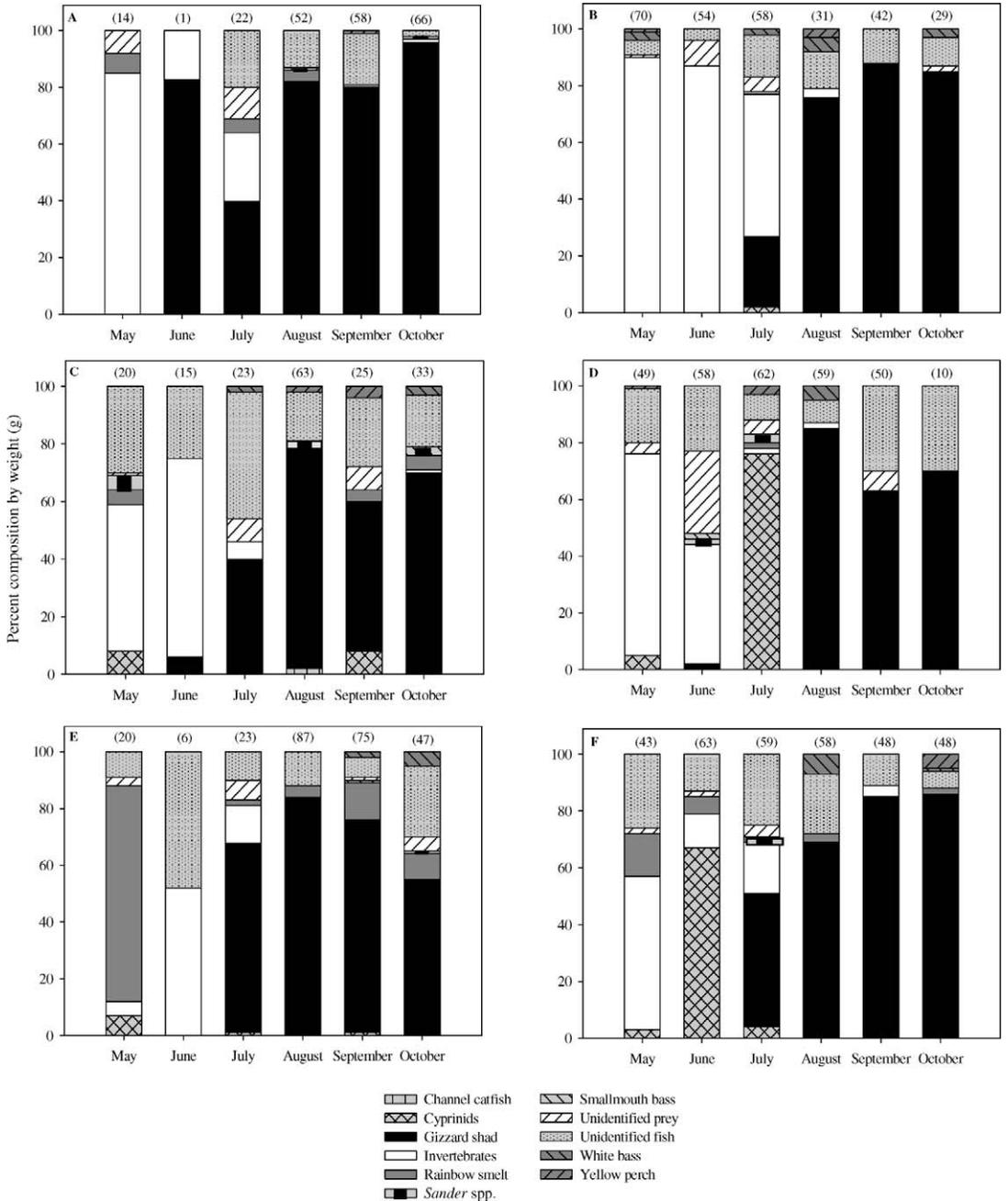


FIGURE 2.—Percent composition of the diets of (A)–(B) walleyes and (C)–(D) smallmouth bass collected from lower Lake Sharpe and (E)–(F) walleyes collected from upper Lake Sharpe in 2006 and 2007, respectively (left and right columns). The numbers in parentheses are the numbers of fish with food in their stomachs in given months.

may have been influenced by the small sample sizes of age-4 fish in May and October. The overall growth rates of age-3 and age-5 fish were higher in 2007 than in 2006.

The growth patterns of the walleyes collected in the lower reservoir differed from those of the fish collected in the upper reservoir. In 2006, the growth of all three ages of walleyes increased steadily from May through

TABLE 3.—Mean Pianka's (1973) niche overlap values based on the diets of lower Lake Sharpe walleyes and smallmouth bass sampled during May–October 2006 and 2007.

Month	Mean overlap index (SE)	
	2006	2007
May	0.06 (0.01)	0.43 (0.01)
Jun	0.30 (0.01)	0.81 (0.10)
Jul	0.94 (0.09)	0.00 (0.02)
Aug	1.00 (0.01)	1.00 (0.01)
Sep	0.98 (0.01)	1.00 (0.01)
Oct	1.00 (0.01)	1.00 (0.01)

October (Figure 4). In 2007, age-3 and age-5 fish grew for most of the growing season but age-4 fish lost weight in the middle of the growing season, possibly owing to the later consumption of gizzard shad (Figure 2).

The growth rates of smallmouth bass differed by month throughout the growing season in both 2006 and 2007 and for all three ages of fish. Growth initially increased after gizzard shad were observed in smallmouth bass diets but reached an asymptote about mid-September (day 258). All three ages of smallmouth bass gained weight at faster rates during the growing season overall than did the walleyes in either part of the reservoir (Figure 4).

Simulations assuming the absence of rainbow smelt and/or gizzard shad resulted in lower growth for all three ages of walleyes in the upper reservoir, but the absence of smelt had less effect than that of shad (Figure 5). Simulations assuming higher temperatures alone resulted in even less growth than the absence of either or both prey items; the absence of both prey types coupled with higher temperatures led to the greatest reduction in growth in both years (Figure 5).

Simulations assuming the absence of gizzard shad resulted in lower growth among all three ages of walleyes in the lower reservoir, but the effect was more pronounced in 2006 than in 2007 (Figure 6). When temperatures were assumed to increase by 3°C, the simulations ceased to provide output after day 193 (July 15) in both years; however, they showed that the walleyes had lost a substantial amount of weight before mid-July, which probably affected their survival.

The results of the growth simulations for smallmouth bass were markedly different from those for walleyes (Figure 7). The absence of gizzard shad resulted in lower growth for all three ages, but growth was still more rapid than that of walleyes under actual conditions. In addition, growth was positively affected by higher temperatures, even when gizzard shad were absent.

Discussion

This study provides useful information about the sharing of prey resources between walleyes and smallmouth bass and how potential changes in prey availability and ambient water temperature could alter the growth rates of these recreationally important predators. The diets of walleyes and smallmouth bass in Lake Sharpe were similar during the latter part of the growing season but differed by species and location in the months before age-0 gizzard shad became vulnerable. Upper reservoir walleyes consumed a higher percentage of fish (especially rainbow smelt and cyprinids) than lower reservoir walleyes, which were more invertivorous in May and June. The importance of invertebrates to walleye diets has been documented for natural lakes (Johnson and Hale 1977; Isaak et al. 1993) and reservoirs (Slipke and Duffy 1997; Quist et al. 2002; Ward et al. 2007), but rainbow smelt and cyprinids are often of greater importance in large systems such as Lake Oahe (Jackson et al. 1993; Bryan 1995; Lott 1996; Graeb et al. 2008) and the Great Lakes (Knight et al. 1984). Higher consumption of fish in the early months may contribute to the observed higher weights of walleyes in upper Lake Sharpe at the beginning and end of the growing season as well as their more rapid growth rates.

Gizzard shad were substantial components of walleye diets in both reaches of Lake Sharpe, but the timing of gizzard shad consumption varied depending on location and year. In 2006, a single walleye collected in the lower reservoir was observed to have consumed 23 gizzard shad in June. The SL of those shad varied from 17 to 22 mm, indicating that they were age-0 fish. The water temperature in upper Lake Sharpe is usually lower than that in the lower reservoir as a result of hypolimnetic discharges from Oahe Dam. Given that the timing of gizzard shad reproduction is at least partially related to water temperature in reservoirs (Shelton et al. 1982; Willis 1987; Michaletz 1997), it is possible that the walleyes in the lower reach of Lake Sharpe have an earlier opportunity to consume shad than do those in the upper reservoir. However, the 2 years of diet data described here suggest some synchronicity between upper and lower reach walleye in terms of gizzard shad consumption.

The food habit patterns of smallmouth bass were similar to those of lower reservoir walleyes. Gizzard shad composed a substantial portion of smallmouth bass diets in the mid to late growing season during both years, and invertebrates were an important diet item prior to shad vulnerability. However, smallmouth bass consumed a wider diversity of invertebrates (eight versus four groups) than did walleyes. Further, small-

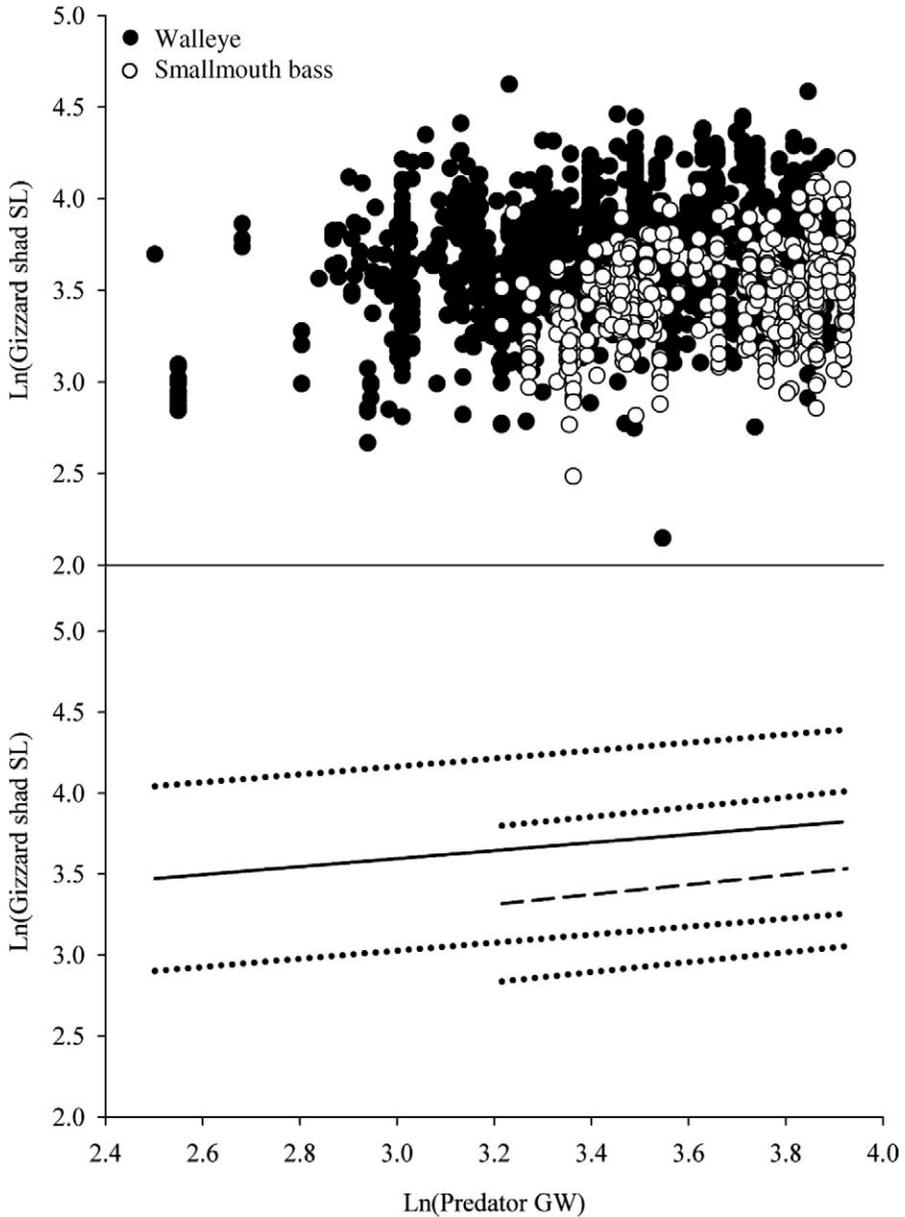


FIGURE 3.—Relationships between the standard lengths (SLs [mm]) of the gizzard shad consumed by walleyes and smallmouth bass in lower Lake Sharpe in 2006 and 2007 and the gape widths (GWs [mm]) of the walleyes and smallmouth bass. The upper panel shows the raw data, the lower panel the estimated regression equations (walleyes: $\log_e(\text{SL}) = 0.24 \cdot \log_e(\text{GW}) + 2.86$ [solid line]; smallmouth bass: $\log_e(\text{SL}) = 0.30 \cdot \log_e(\text{GW}) + 2.34$ [dashed line]). The dotted lines indicate the 95% prediction intervals for the two equations.

mouth bass were more piscivorous than walleyes during the early part of the growing season. The piscivory among Lake Sharpe smallmouth bass is higher than that reported in other studies (Fedoruk 1966; Gangl et al. 1997; Johnson and Hale 1977; Frey et al. 2003), possibly owing to habitat characteristics

and prey availability. Danehy and Ringler (1991) and Lott (1996) compared the diets of smallmouth bass collected from sandy versus rocky habitats within the same water body in Mexico Bay (Lake Ontario) and Lake Oahe, respectively; both studies documented higher rates of piscivory among smallmouth bass

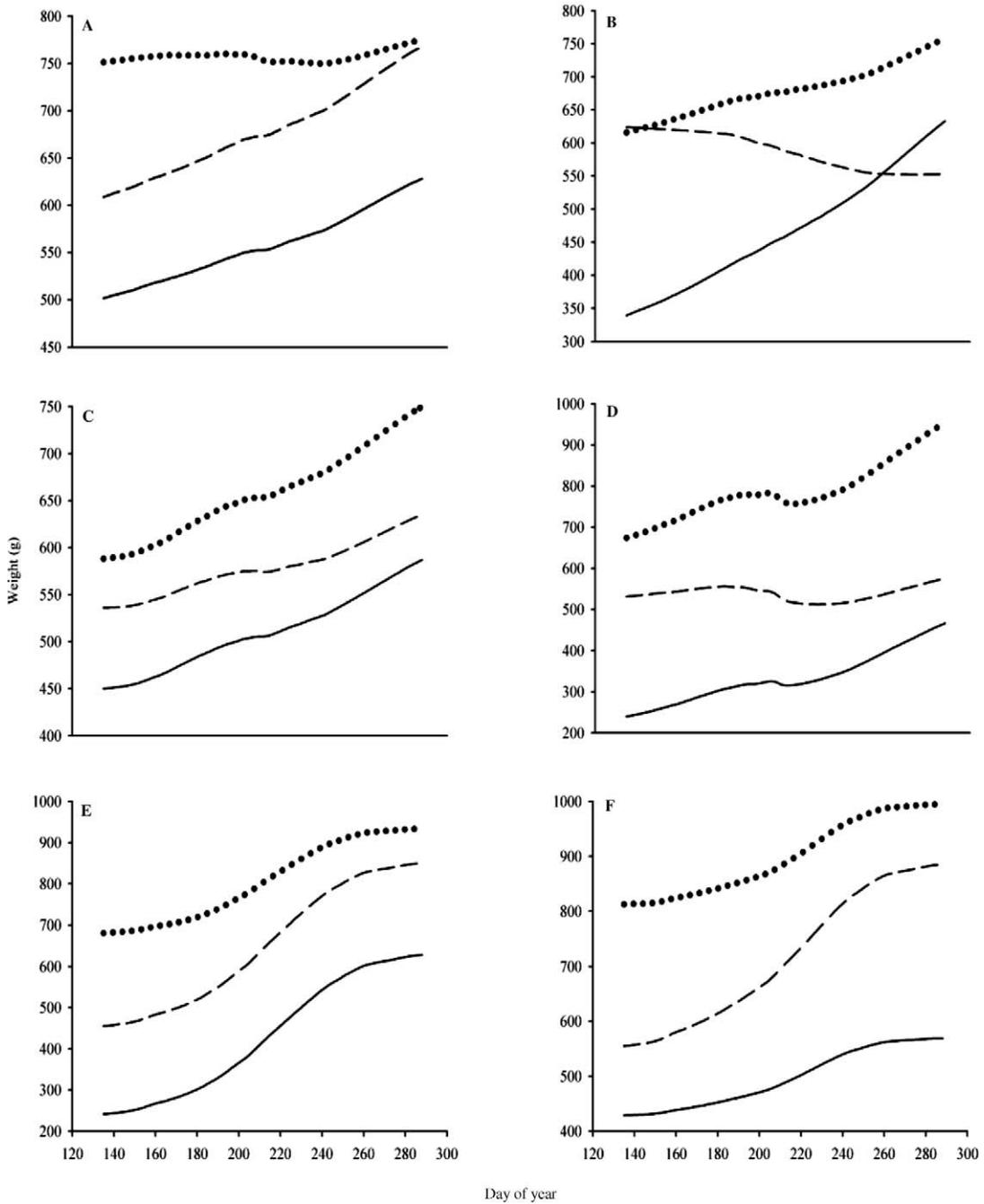


FIGURE 4.—Growth patterns of different-aged walleyes in (A)–(B) lower Lake Sharpe and (C)–(D) upper Lake Sharpe and (E)–(F) smallmouth bass in lower Lake Sharpe in 2006 and 2007, respectively (left and right columns). The solid lines denote age-3 fish, the dashed lines age-4 fish, and the dotted lines age-5 fish. Day 135 corresponds to June 15 and day 288 to October 15.

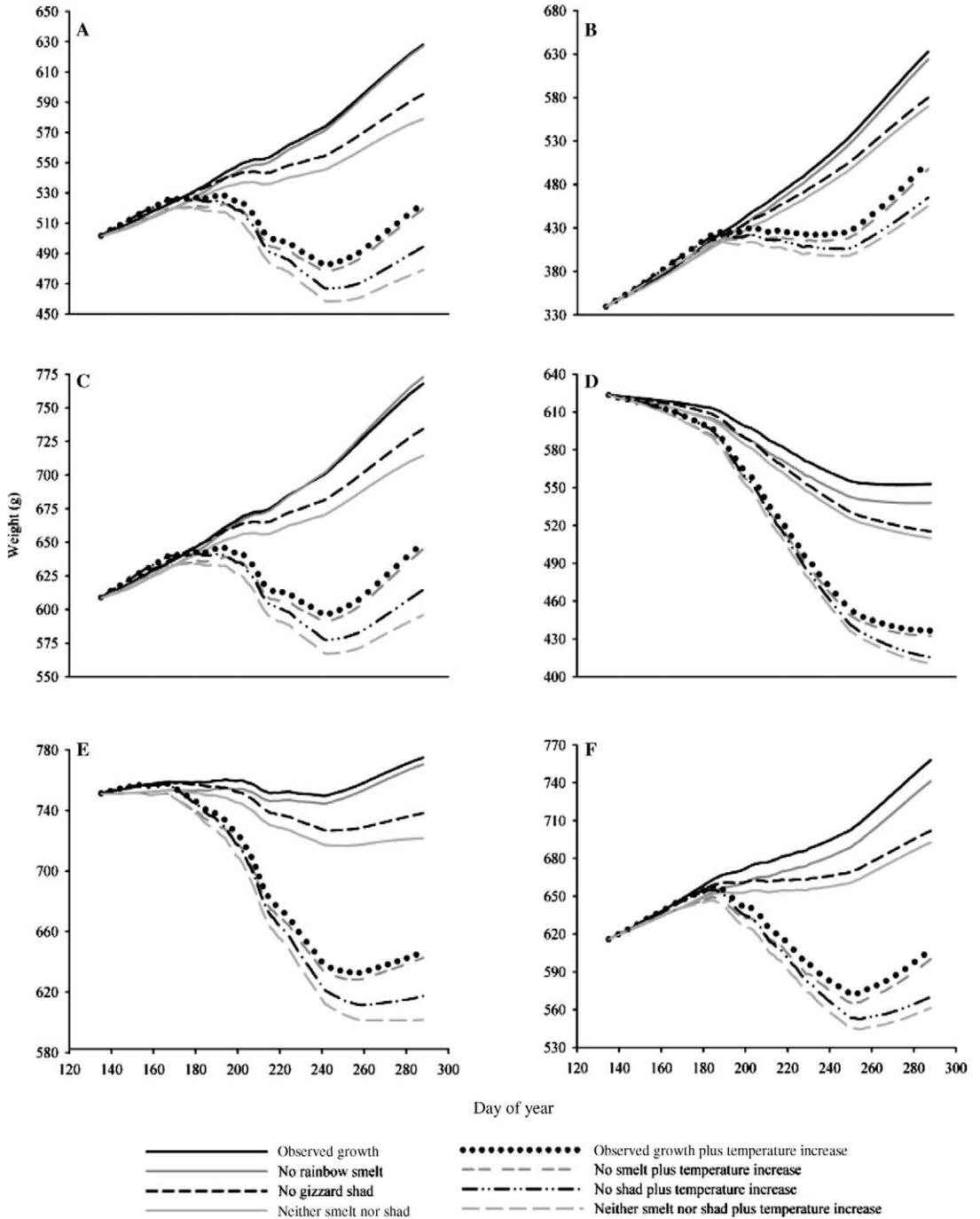


FIGURE 5.—Growth simulations of (A)–(B) age-3, (C)–(D) age-4, and (E)–(F) age-5 walleyes in upper Lake Sharpe in 2006 and 2007, respectively (left and right columns), under various conditions (see text). All simulations assume the same maximum consumption rate.

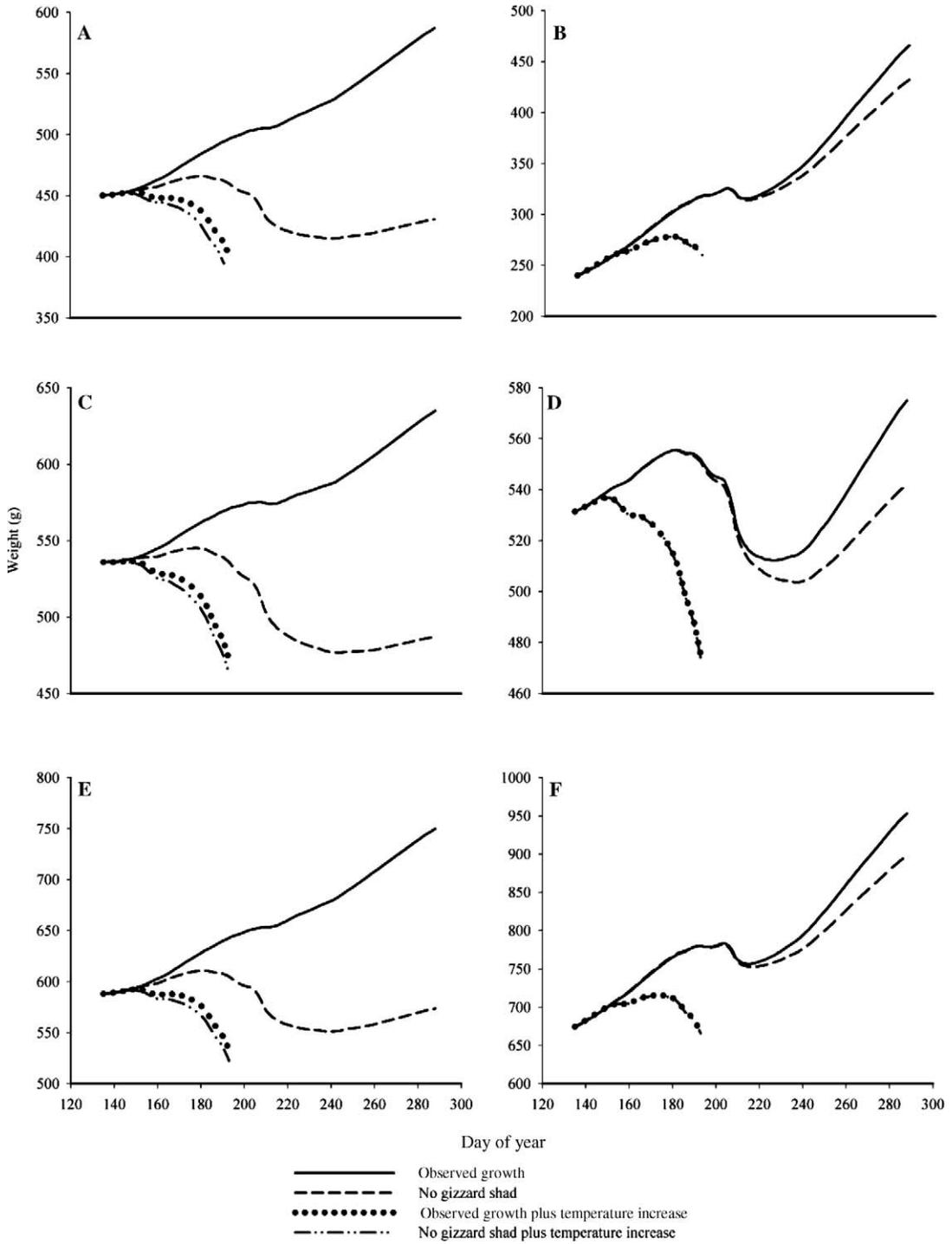


FIGURE 6.—Growth simulations of (A)–(B) age-3, (C)–(D) age-4, and (E)–(F) age-5 walleyes in lower Lake Sharpe in 2006 and 2007, respectively (left and right columns), under various conditions (see text). All simulations assume the same maximum consumption rate.

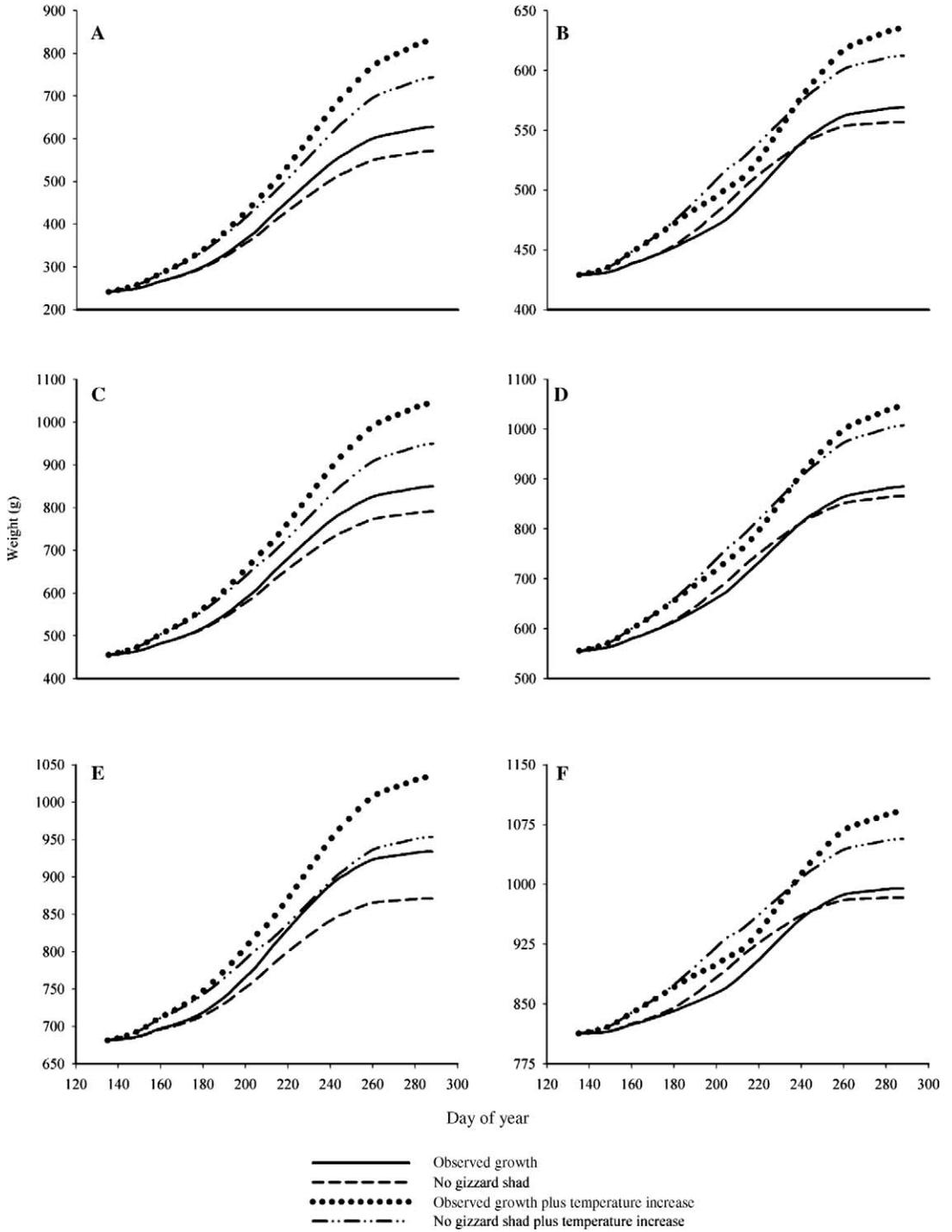


FIGURE 7.—Growth simulations of (A)–(B) age-3, (C)–(D) age-4, and (E)–(F) age-5 smallmouth bass in lower Lake Sharpe in 2006 and 2007, respectively (left and right columns), under various conditions (see text). All simulations assume the same maximum consumption rate.

collected over sandy substrates. Lower Lake Sharpe is largely characterized by flats of sand and silt substrates with limited littoral area; thus, invertebrate production is low and smallmouth bass may consume more fish owing to the greater relative availability of fish prey.

This study documented the consumption of *Sander* spp. by smallmouth bass and found that consumption was higher in months before gizzard shad became vulnerable. Bacula (2009) also documented a very low occurrence of walleye consumption by smallmouth bass in four South Dakota glacial lakes. Johnson and Hale (1977) found very few walleyes in smallmouth bass stomachs in one northeastern Minnesota lake but suggested that the large population of smallmouth bass could have had a detrimental effect on walleye recruitment via consumption. Given the low incidence of *Sander* consumption, the seeming abundance of gizzard shad in Lake Sharpe, and the consistent recruitment of walleyes in the reservoir (Adams et al. 2009), smallmouth bass probably do not consume walleyes in sufficient numbers to limit their recruitment. However, population estimates for smallmouth bass in Lake Sharpe are currently unavailable; this information is necessary to estimate overall consumption at the population level.

The patterns in diet overlap between lower reservoir walleyes and smallmouth bass are probably driven by the patterns in age-0 gizzard shad vulnerability. Diet overlap between the two species was typically low before the recruitment of gizzard shad to the Lake Sharpe prey base, probably owing to the greater diversity of prey types in smallmouth bass diets. Prey diversity can increase the stability of predator dynamics in simple food webs, in part because of reductions in competition (Petchey 2000). After age-0 gizzard shad became vulnerable, the diet overlap between walleyes and smallmouth bass was complete or nearly so for the remainder of the growing season. High consumption levels of gizzard shad by both predators relative to other prey items may result from the numerical availability (Lyons 1987; Sih and Moore 1990; Raborn et al. 2004) and vulnerability of shad (Einfalt and Wahl 1997). However, evidence of shared resources alone does not indicate competition (Matthews et al. 1982); rather, resources must be limiting and fitness-related factors (e.g., growth, condition, and fecundity) must be negatively affected (Crowder 1990). Quantifying age-0 gizzard shad availability on an annual basis would be challenging given the large size of Lake Sharpe; thus, information regarding potential prey limitations is not available at this time. Nonetheless, both walleyes and smallmouth bass consumed numerous gizzard shad on an individual basis, and no negative relationship has been observed between the growth and size structure of

walleyes and smallmouth bass dynamics (Lott et al. 2006). Further, other Lake Sharpe predators (white bass and sauger) were also observed consuming several age-0 gizzard shad per individual. Thus, it is likely that age-0 gizzard shad are presently not limiting in the reservoir once they recruit to the prey base of Lake Sharpe.

Prey resources may also be partitioned among potential competitors based on prey size. Smallmouth bass consumed a smaller range of gizzard shad sizes than did walleyes; this type of resource partitioning may allow these two species to coexist (Olson et al. 2007). While the potential for competition between walleyes and smallmouth bass is high during most of the growing season in Lake Sharpe, it is unlikely that competition is actually occurring.

Bioenergetics simulations for Lake Sharpe walleyes and smallmouth bass provided insights into the potential effects of prey limitation and increased water temperatures on predator growth. For upper reservoir walleyes, simulating the absence of rainbow smelt from predator diets reduced growth, but the absence of gizzard shad from walleye diets had a more marked effect on projected growth. As the energy densities between rainbow smelt and gizzard shad are similar (~4,800 [Lantry and Stewart 1993] and ~5,100 joules/g wet weight [Miranda and Muncy 1991], respectively), the differing effects were probably due to differences in consumption rates. However, the presence of rainbow smelt in upper Lake Sharpe may be one factor that influences the greater weights and growth rates observed in these fish than in lower Lake Sharpe walleyes. The abundance of rainbow smelt in Lake Sharpe may vary, depending on when the thermocline is established in Lake Oahe and its depth (Unkenholz 1998; Smith 2000; Hamel et al. 2008). Thus, rainbow smelt will have different effects on walleye growth, depending on the extent of entrainment in a given year. If the sensory deterrent systems described by Hamel et al. (2008) are implemented at Oahe Dam and the abundance of rainbow smelt is reduced or the species is extirpated at Lake Sharpe, the growth of upper Lake Sharpe walleyes may fall below that observed in this study.

The absence of gizzard shad had a marked effect on the modeled growth of both walleyes and smallmouth bass in Lake Sharpe, although effects were smaller for the latter species, probably because of the greater diversity of their prey and their higher observed maximum consumption values. The reduction of gizzard shad within the food web of Lake Sharpe may be a possibility in the future (Wuellner et al. 2008). Certainly, the Lake Sharpe simulations only provide a worst-case scenario. Gizzard shad could

remain vulnerable to predation, but the window of availability may occur earlier or for a shorter time (Vatland and Budy 2007). Walleyes and smallmouth bass could switch to alternative prey or increase their consumption rates to maintain body weight (Biro et al. 2007). Growth may still occur in the absence of gizzard shad under various scenarios; however, Stewart et al. (1981) demonstrated that random fluctuations in a single prey species may create instability in entire predator assemblages in simple prey–predator systems.

The simulated increases in water temperature had different but expected effects on the growth of walleyes and smallmouth bass. Walleyes were projected to lose considerable amounts of weight beginning in late spring; in fact, those in lower Lake Sharpe lost such large amounts of weight in such a short period of time that the models failed to project weight after mid-July. Water temperatures in the lower reservoir are generally greater than those in the upper reservoir because the latter reach is affected by hypolimnetic discharges from Oahe Dam. Thus, lower reservoir walleye are probably more vulnerable to the negative effects on growth associated with higher water temperatures. Lake Sharpe walleyes could find thermal refugia, subsist on energy reserves (Quist et al. 2002), or increase their consumption (Biro et al. 2007) to mitigate the negative effects of higher water temperatures. How the consumption rates of Lake Sharpe walleyes might change in response to changes in temperature is currently unknown; this study assumed constant consumption rates across all temperature scenarios, which is probably unrealistic. Quist et al. (2002) modeled the growth of walleyes in Glen Elder Reservoir, Kansas, over four summers assuming higher water temperatures and various consumption rates. In most of these scenarios, the walleyes lost weight during the summer. The consumption rates of Lake Sharpe walleyes would probably respond in a similar manner.

One issue not addressed in this study is the influence of higher water temperatures on the productivity of Lake Sharpe. Higher temperatures could have bottom-up effects on productivity (e.g., George et al. 1990; Porter et al. 1996; Müller-Navarra and von Storch 1997; Petchey et al. 1999), resulting in greater availability of other prey fishes (e.g., cyprinids). If consumption of those fish provided energetic benefits similar to those of the diets observed in this study, Lake Sharpe walleyes might not be negatively affected by higher water temperatures. Modeling these effects would be of interest, but information on prey availability, the responses of prey to higher water temperatures (e.g., in terms of growth, mortality, and spatial distribution), and the responses of walleyes to such changes is currently lacking.

In contrast, simulated increases in water temperature, whether coupled with the absence of gizzard shad in diets or not, led to greater smallmouth bass growth than currently observed. The growth of smallmouth bass has been strongly linked with air temperature (Dunlop and Shuter 2006), and climate change is expected to increase the growth rates of adults at the northern edge of their range (King et al. 1999; Jackson and Mandrak 2002). Higher water temperatures will probably increase the consumption rates of smallmouth bass, and greater feeding activity and prey exploitation may increase the risk of competition with walleyes in Lake Sharpe by reducing prey resources. The observed increases in water temperature have been linked to the colonization and establishment of smallmouth bass in new areas, which has negatively affected native aquatic communities via food web alterations (Power et al. 1985; Vander Zanden et al. 1999; Jackson and Mandrak 2002).

Information about shared prey resources and the influence of prey and water temperature on predator growth could guide management decisions for walleyes and smallmouth bass now and in the future. High diet overlap between a native predator (walleyes) and an introduced predator (smallmouth bass) was documented. However, the probability that competition is actually occurring is low given that the availability of age-0 gizzard shad (an important prey item for both predators) does not appear to be limiting in Lake Sharpe, at least for most of the growing season. The potential reduction of gizzard shad, whether through competition or lower reproduction associated with higher water temperatures, would probably affect future predator growth in this reservoir food web. To prevent future competition between predators, water level manipulations could be implemented to enhance the prey base, particularly for gizzard shad, cyprinids, and other age-0 fish such as yellow perch, as well as to provide thermal refugia for walleyes. Finally, global climate change has the potential to affect one reservoir fishery negatively but another positively. Under current prey and temperature conditions, native walleyes and introduced smallmouth bass may coexist and provide quality fisheries in this reservoir, but managers may one day have to decide whether to employ strategies that favor walleye growth and survival or allow the fishery to be dominated by smallmouth bass.

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