

Overwinter Survival of Age-0 Gizzard Shad in Missouri Reservoirs Spanning a Productivity Gradient: Roles of Body Size and Winter Severity

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Abstract.—Survival through the first winter of life can be an important bottleneck in the recruitment of fishes and is commonly size dependent, with larger fish exhibiting higher survival than smaller fish. Body size and density of age-0 gizzard shad *Dorosoma cepedianum*, an ecologically important prey species, are reportedly influenced by reservoir productivity. These differences in age-0 demographics across a productivity gradient may influence overwinter survival and subsequent year-class strength of adults. I examined fall age-0 demographics (fall mean total length, mean density, and energy density), overwinter changes in these demographics, and factors that influenced overwinter survival among five age-0 cohorts in five Missouri reservoirs spanning a productivity gradient. I specifically wanted to determine whether (1) fall age-0 demographics varied along a reservoir productivity gradient, (2) fall age-0 demographics and winter severity were related to overwinter survival, and (3) variation in the abundance of overwinter survivors among years decreased with increasing reservoir productivity. Fall demographics did not consistently vary along a productivity gradient. Fall total length was typically larger in more productive reservoirs and was the most variable in the least productive reservoir, with large fish being present during 1 year. Likewise, fall density did not vary with reservoir productivity; the highest overall density occurred in one slightly eutrophic reservoir and one highly eutrophic reservoir, and fall density was lowest and most variable in the least productive reservoir. However, energy density was higher in the more productive reservoirs than in the less productive ones. Overwinter survival ranged from 0% to 100% and increased with increasing fall total length and winter temperatures among all cohorts and reservoirs. Variation in overwinter survivor abundance did not consistently decrease along a reservoir productivity gradient. Unique characteristics of individual reservoirs and changing climatic conditions apparently obscured overall patterns in age-0 demographics and overwinter survival across reservoir productivity.

Survival through the first winter of life can be an important bottleneck in the recruitment of fishes (Ludsin and DeVries 1997; Hurst and Conover 1998; McCollum et al. 2003). Overwinter mortality of juvenile fishes can vary substantially among years because of differences in juvenile body size (Post and Evans 1989; Post et al. 1998), winter severity (Hurst and Conover 1998; Lankford and Targett 2001; McCollum et al. 2003), prey availability (Johnson and Evans 1990; Fullerton et al. 2000), predation rates (Santucci and Wahl 2003; Shoup and Wahl 2008), and complex interactions among these and other variables. Hence, the relative strength of a year-class may change during winter, resulting in poor correlation between fall age-0 abundance and spring age-1 abundance (Hurst and Conover 1998; Wiedenmann and Essington 2006). Events during the juvenile stage, such as the overwinter period, may be just as important in regulating year-class strength as events during the larval period (Ludsin

and DeVries 1997; Hurst and Conover 1998; Wiedenmann and Essington 2006).

Numerous studies have shown that smaller fish suffered higher overwinter mortality than larger fish (reviewed by Hurst 2007). In many cases, smaller fish experience higher overwinter mortality than larger ones because they contain smaller energy reserves (Miranda and Hubbard 1994a; Schultz and Conover 1997; Sutton and Ney 2001) and exhaust energy reserves more quickly due to higher mass-specific metabolic rates (Paloheimo and Dickie 1966; Miranda and Hubbard 1994a; Sutton and Ney 2001), making them more susceptible to starvation (Post and Evans 1989; Shuter et al. 1989), predation (Jonas and Wahl 1998; Chick and Van Den Avyle 2000), and other stressors (e.g., disease, cold temperatures, and osmoregulatory failure; Adams et al. 1982; Johnson and Evans 1991; Fullerton et al. 2000; Hurst 2007). The degree of size-dependent overwinter mortality may vary with latitude (Schultz et al. 1998; Fullerton et al. 2000), winter severity (Post and Evans 1989; Hurst and Conover 1998; Post et al. 1998), and fall juvenile size (Hurst and Conover 1998; Post et al. 1998).

Mortality during the first winter of life may be

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density dependent or density independent (Hurst 2007). Because growth of age-0 fishes is commonly density dependent, members of numerically strong age-0 cohorts are frequently smaller in size prior to winter than those in numerically weak cohorts (Ludsin and DeVries 1997; Matthews et al. 2001). Consequently, these strong cohorts may experience higher overwinter mortality than weak cohorts because of size-dependent mortality (Ludsin and DeVries 1997; Matthews et al. 2001; Wiedenmann and Essington 2006). Overwinter mortality can also be density independent when winters are severe, causing high mortality of the cohort, regardless of body size (O'Gorman and Schneider 1986; McCollum et al. 2003; Hurst 2007). Thus, we might expect less size dependence at extremes of a species' geographic range.

The gizzard shad *Dorosoma cepedianum*, an ecologically important species as prey (Storck 1986; Michaletz 1997b), competitor (Kirk and Davies 1987; DeVries and Stein 1992), and nutrient recycler (Schaus et al. 1997), probably experiences both density-dependent and density-independent overwinter mortality, depending on winter severity. Growth of age-0 gizzard shad is commonly density dependent (Michaletz 1997a, 1999; Bremigan and Stein 1999), and members of strong age-0 cohorts may not attain sizes large enough to survive the winter. During severe winters, mass mortalities of gizzard shad occur and the entire annual cohort may be eliminated, regardless of body size, resulting in density-independent mortality (June 1987; Wuellner et al. 2008). Most reports of mass winter mortalities have been at locations near the northern edge of the range of gizzard shad; however, they can also occur at middle and southern latitudes (Adams et al. 1982; Heidinger 1983; Storck 1986). Although winter mortality of age-0 gizzard shad is known to be variable and important to recruitment (Storck et al. 1982; Heidinger 1983), it has rarely been quantified. Previous studies of gizzard shad have focused on recruitment dynamics during the larval to fall juvenile stages of the age-0 cohort (Bremigan and Stein 1994, 1999, 2001; Michaletz 1997a, 1999). I am aware of only one study that attempted to quantify overwinter survival of age-0 gizzard shad: White et al. (1986) estimated that 100% of age-0 gizzard shad at 40–85 mm standard length and more than 99% of individuals at 90–140 mm died during winter in Lake Erie, which is located near the northern edge of the species' range.

Consistency in gizzard shad recruitment appears to vary along a productivity gradient in Missouri's large reservoirs (Michaletz 1998b). Adult year-class strength becomes more variable and first-year growth becomes slower as reservoir productivity decreases (Michaletz

1998b, 1999). Michaletz (1998b) suggested that size-dependent overwinter survival of age-0 cohorts may be responsible for this pattern, wherein smaller age-0 fish that occur in mesotrophic to slightly eutrophic reservoirs may more commonly experience higher overwinter mortality than the larger age-0 fish that occur in moderately to highly eutrophic reservoirs. As a result of these differences, adult populations in more productive reservoirs are usually more abundant, slower growing, and shorter lived than those in less productive reservoirs because of density-dependent effects (DiCenzo et al. 1996; Michaletz 1998b).

Because the roles of gizzard shad demographics, winter severity, and reservoir productivity on overwinter survival of young gizzard shad are largely unknown, I examined these potential influences among five annual cohorts of gizzard shad in five Missouri reservoirs spanning a productivity gradient. Specifically, I wanted to address three main questions: (1) do fall age-0 demographics vary across a reservoir productivity gradient, (2) do fall age-0 demographics and winter severity affect overwinter survival, and (3) does variability in the abundance of overwinter survivors among years decrease with increasing reservoir productivity, thereby accounting for the pattern described by Michaletz (1998b)? Previous studies have indicated that reservoir productivity does influence both first-year growth and density of age-0 gizzard shad (Bremigan and Stein 1999; Michaletz 1999). However, how these differences in cohort demographics interact with winter temperatures to affect overwinter survival has not been studied. Although mass mortalities during severe winters have been reported (White et al. 1986), the influence of more moderate temperatures at mid-latitudes is unknown. My findings document the importance of the winter period in the recruitment process of gizzard shad populations in reservoirs.

Methods

Study areas.—I examined factors influencing first-winter survival of five annual cohorts (2003–2007) of gizzard shad in Long Branch, Mark Twain, Thomas Hill, Pomme de Terre, and Stockton lakes (Table 1). Long Branch, Mark Twain, and Thomas Hill lakes are highly eutrophic reservoirs located in the fertile Glacial Plains physiographic section of northern Missouri, whereas the less productive Pomme de Terre and Stockton lakes are located in the Ozark Highlands physiographic section in the southwestern portion of the state (Jones et al. 2008). Land use in the watersheds varies from primarily cropland for the northern reservoirs to pasture and forest for the southern reservoirs. The reservoirs also vary in depth and

TABLE 1.—Latitude, surface area, mean depth, Secchi depth, seasonal mean total phosphorus (TP) and chlorophyll-*a* (Chl *a*) concentrations, fall age-0 gizzard shad mean total length (TL), and the mean recruitment variability index (RVI) for gizzard shad populations from five Missouri reservoirs. The RVI ranged from -1 to 1 , with larger values indicating more stable recruitment (Guy and Willis 1995). Water quality data are long-term averages (≥ 18 years) from samples taken at sites near the dams.

Reservoir	Latitude	Area (ha)	Depth (m)	Secchi depth (m) ^a	TP ($\mu\text{g/L}$) ^a	Chl <i>a</i> ($\mu\text{g/L}$) ^a	TL (mm)	RVI ^d
Long Branch	39°45'N	980	4.4	0.7	45	11.7	108 ^b	0.80
Mark Twain	39°32'N	7,530	8.9	0.9	54	14.6	106 ^c	0.87
Thomas Hill	39°34'N	2,000	4.9	0.6	46	12.8	94 ^b	0.81
Pomme de Terre	37°54'N	3,170	9.3	1.8	24	12.9	68 ^b	0.64
Stockton	37°41'N	10,080	10.9	2.9	11	5.7	69 ^b	0.56

^a Jones et al. (2008).

^b Michaletz (1998a).

^c Michaletz, unpublished data.

^d Michaletz (1998b).

surface area, with Long Branch and Thomas Hill lakes being shallower and smaller than the other lakes. Gizzard shad first-year growth was slower and adult (age-3 and older) year-class strength was more variable (based on the recruitment variability index) in Pomme de Terre and Stockton lakes than in the other reservoirs (Michaletz 1998b; Table 1). All reservoirs except Thomas Hill Lake are operated by the U.S. Army Corps of Engineers for flood control (Long Branch and Pomme de Terre lakes) or for both flood control and hydropower generation (Mark Twain and Stockton lakes). Thomas Hill Lake is owned by Associated Electric Company and is used as a cooling reservoir for a coal-fired power plant. I expected winter severity to vary not only among winters but also among reservoirs because of differences in latitude, and in the case of Thomas Hill Lake, artificial heating related to power plant operations.

Fish sampling.—I collected age-0 gizzard shad in late October to early November and yearlings in early April of the subsequent year to examine overwinter changes in cohort demographics. I chose sampling dates that minimized the likelihood that growth of gizzard shad would occur between sampling periods. Because of their more southerly location, I always sampled Pomme de Terre and Stockton lakes last in the fall and first in the spring. Water temperature averaged 16.2°C (range = 11.5–20.3°C) during fall sampling and 12.8°C (8–17.5°C) during spring sampling. It is doubtful that measureable growth occurred between sampling periods because feeding activity (and presumably growth) of gizzard shad declines rapidly as water temperatures fall below about 15°C (Salvatore et al. 1987). Water temperatures during fall and spring sampling were commonly near or below this temperature. When water temperature exceeded 15°C, it fell below this temperature within several days after fall sampling or had only exceeded this temperature for a

few days before spring sampling. In addition to rapidly declining temperatures, decreasing photoperiod during the fall probably reduced the potential for growth (Woiwode and Adelman 1991).

I sampled gizzard shad with paired trawls (1-m² frame, 6-mm mesh) towed at night in a stair-stepped fashion from the surface to near the bottom of the reservoir in shallow areas or to a maximum depth of 9 m in deep areas. Tow duration depended on water depth and ranged from about 2.0–5.5 min. Tow speed was 1.6 m/s, and flowmeters were placed in the mouth of each trawl to estimate the volume of water filtered by each trawl. Tows were made at six fixed limnetic sites in upper and lower sections of each reservoir to account for potential spatial differences in gizzard shad abundance and size structure (Bremigan and Stein 1999; Michaletz and Gale 1999). Gizzard shad collected in trawls were immediately placed on ice and stored in a freezer within a few hours of collection. Samples taken simultaneously with each of the two trawls were pooled for processing and analysis. In some cases when large numbers of gizzard shad were collected in one tow, the entire sample was weighed and a subsample was then weighed and retained for processing. Trawl samples were usually processed the next day by counting all of the gizzard shad in each sample to estimate density (number/1,000 m³). For subsamples, numbers of gizzard shad were extrapolated to the entire sample before density was estimated. I developed length-frequency distributions for each section of each reservoir by measuring about 200 individuals for total length (TL, nearest mm), and a subsample of these fish were weighed (wet weight, nearest 0.01 g). Some of the measured and weighed fish were returned to the freezer for subsequent energy content analysis (see below).

Because energy content may vary with fish size and influence overwinter survival, I estimated energy

density (ED, J/g wet weight) for fish collected in the fall and spring. I measured ED using two methods. For fish collected before 2006, I estimated ED for 10 fish that spanned the size range for each section of each reservoir (using methods of Wuenschel et al. 2006). Dry weight (DW) was determined by freeze-drying to a constant weight, and lipid content (g, DW) was estimated by acid hydrolysis (AOAC International 2002) conducted by the Agricultural Experiment Station Chemical Laboratories of the University of Missouri, Columbia. I calculated total energy content of each fish by the amounts of lipid and lean tissue (DW minus lipid content) using energy equivalent values of 39,538.8 J/g for lipid and 20,082.2 J/g for lean tissue (converted from caloric values reported by Brett and Groves 1979, assuming 1 cal = 4.184 J). I then divided total energy content by wet weight to estimate ED. Excluding fish collected in fall 2005, I used these fish to develop a linear relationship between percent DW (%DW) and ED—a relationship that commonly exists within fish species (Hartman and Brandt 1995). I used fish from fall 2005 to assess the accuracy of the %DW–ED relation in predicting ED. Percent error was estimated by subtracting the observed ED from the ED predicted from the %DW–ED relationship, dividing this difference by the observed ED, and multiplying by 100. For fish that were collected, measured, and weighed (wet weight) in 2006–2008, DWs were estimated for 25 fish/section by placing the fish on previously weighed aluminum pans and drying to a constant weight at 60°C. I then estimated ED using the previously developed %DW–ED relationship.

When examining percent lipid content (DW basis) of fish of increasing size from collections made in fall 2003 and 2004, I noticed an abrupt change in percent lipids between about 85 and 95 mm TL (Figure 1). Percent lipids changed from mostly less than 20% to mostly greater than 20% over this length range. This abrupt increase made it necessary to develop two %DW–ED relationships, one for smaller fish and one for larger fish. To determine at which length to separate the two size-classes, I used logistic regression to estimate the length at which 50% of the fish had a lipid content of 20% or more, similar to methods used to obtain 50% sexual maturity (Quinn and Deriso 1999). Fish were coded as 0 if percent lipid was less than 20% and were coded as 1 if percent lipid was 20% or more. I repeated this procedure for lipid contents of 18% and 22%. I then averaged the predicted lengths for these three lipid contents to estimate the length used to separate the two size-classes.

Winter severity.—To account for differences in winter severity among the five winters and reservoirs,

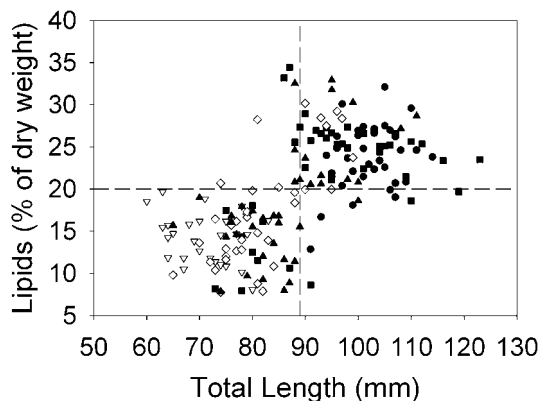


FIGURE 1.—Relationship between percent lipids and total length (TL) for age-0 gizzard shad in five Missouri reservoirs during fall 2003 and 2004. The horizontal dashed line indicates 20% lipid content, and the vertical dashed line indicates 89 mm TL, the length used to separate the two fish size-classes. Filled symbols indicate the highly eutrophic reservoirs (filled circles = Long Branch Lake; filled squares = Mark Twain Lake; filled triangles = Thomas Hill Lake), and open symbols indicate the mesotrophic to slightly eutrophic reservoirs (open inverted triangles = Pomme de Terre Lake; open diamonds = Stockton Lake).

I used recording thermographs to record water temperatures (measured every 4 h) throughout the winter at a depth of 1 m. Temperatures measured at this depth should adequately characterize the thermal regimes that juvenile gizzard shad experienced because these fish remain near the surface of the water throughout the winter (White et al. 1986). I placed thermographs in each section of each reservoir, except during the winter of 2003–2004, when all reservoirs except Thomas Hill Lake received a thermograph in only one section. Four winter severity variables were examined: (1) the rate of temperature decline in late fall to early winter, (2) the mean winter temperature, (3) the winter duration (i.e., the number of days when the temperature was < 10°C), and (4) the number of days when the temperature was less than 4°C. Rapidly falling temperatures can cause mortality to fish that fail to acclimate quickly enough to the changing conditions (Griffith 1978; White et al. 1986; Graham et al. 1990). Thus, I estimated the rate of temperature decline (°C per day) as the slope of the regression relating mean daily water temperature to dates from late October or early November to the time when water temperatures leveled off in early winter (usually December). I calculated mean winter temperature for a 142-d period from November 9 or 10 to the subsequent March 30 or 31 (depending on whether it was a leap year or not). I chose this period because (1) temperature data were

available for all reservoirs and years during this period and (2) it encompassed most of the time between fall and spring sampling. I also calculated the number of days at less than 4°C because these colder temperatures may be especially stressful to clupeids and young of other species (Griffith 1978; White et al. 1986; Lankford and Targett 2001; McCollum et al. 2003). In addition to the winter of 2003–2004, when not all sections received thermographs, winter temperature data were unavailable in several instances because of missing or malfunctioning thermographs. However, water temperature data were always available for at least one section for each reservoir and year.

Data analysis.—I examined fall age-0 demographics and overwinter changes in these demographics among the five reservoirs. These demographics included density, TL, and ED. I also related overwinter survival to fall age-0 demographics and winter temperature. Because preliminary analyses revealed that TL, ED, and survival of age-0 gizzard shad and winter temperatures were generally similar between sections (lower and upper) within a reservoir and fall–spring period, I pooled fish and averaged water temperature data from the sections for analyses. To determine whether growth of age-0 gizzard shad could be density dependent, I correlated fall density with fall mean TL for all reservoirs combined and for each reservoir separately. I also used correlation to relate fall and spring density for gizzard shad cohorts to determine whether relative year-class strength was consistent from fall to spring. I used bootstrapping to resample fall and spring density data sets to generate 1,000 survival estimates that were used to calculate mean survival and associated 95% confidence intervals (Manly 1997). Survival estimates were compared with fall density via correlation analysis to determine whether survival was density dependent. Because plots of fall density versus spring density and fall density versus survival indicated a threshold effect of fall density, I also analyzed these relationships with a two-dimensional (2D) Kolmogorov–Smirnov (KS) test (Garvey et al. 1998a). This test is appropriate when the strength of a relationship between two variables varies across the range of observed values.

To determine whether fall ED of age-0 gizzard shad varied among reservoirs, I conducted a repeated-measures linear mixed model (MIXED procedure; SAS Institute 2005) using reservoir, TL (the covariate), and their interaction as fixed effects and year as a random variable. I used the first-order autoregressive covariance structure for this model. If the model was found to be significant ($P \leq 0.05$), I used pairwise comparisons of least-squares means (using Tukey–Kramer-adjusted P -values for multiple comparisons) to

determine which reservoirs differed from each other. To assess overwinter changes in ED, I used analysis of covariance (ANCOVA) with season (fall or spring), TL (the covariate), and their interaction as independent variables. If the interaction term was not significant, it was dropped from the final model. For significant season effects, I calculated the percent change in ED for the average-size fish in the fall (fall mean TL).

To determine whether overwinter survival was size dependent within a reservoir and cohort, I compared fall and spring length distributions (5-mm TL bins) using the KS test. If the KS test was significant, I calculated a departure index described by Menning et al. (2007) to determine whether size-selective mortality occurred. This index measures the magnitude and direction of change in ordered distributions by comparing a test distribution (i.e., spring length distribution) with a reference distribution (i.e., fall length distribution). The range of this index always has an absolute value of 2. For normal or uniform distributions, the index will range from -1 to 1 , but the range will change with departures from these distributions. For this study, negative values (left shift) would indicate higher mortality of larger individuals, whereas positive values (right shift) would indicate higher mortality of smaller individuals, assuming that individuals did not grow between fall and spring samples.

I used logistic regression to model the effects of fall age-0 demographics and winter temperature variables on overwinter survival of gizzard shad cohorts. Fall cohort demographics included mean TL and the estimated ED for a fish of mean TL (calculated from previously described models). Survival (S) estimates were logit-transformed ($\log_e\{S/[1 - S]\}$) before using linear regression (REG procedure; SAS Institute 2005) to determine which variables potentially influenced survival. Because the \log_e of zero is undefined, I added 0.0001 to all survival estimates. In one case, when the survival estimate exceeded 1.00 ($>100\%$ survival), I set the survival estimate to 0.99. I compared linear regression models using the information-theoretic approach (Burnham and Anderson 2002). I calculated (1) Akaike's information criterion corrected for small-sample bias (AIC_c) to assess the fit of each candidate model, (2) the AIC_c difference (Δ_i) between the candidate model and the model with the lowest AIC_c value, and (3) Akaike weights (w_i ; i.e., the weight of evidence for each model given the data set and the set of candidate models). Models with the lowest AIC_c and the highest values of w_i have the most support. Models with AIC_c that differed by less than 2 units were assumed to be similarly supported. I compared the relative fit of 23 models for explaining variation in

TABLE 2.—Mean (\pm SE) fall total length (TL, mm), fall density (number/1,000 m³), and spring density and mean (95% confidence interval [CI]) percent survival for 2003–2007 cohorts of gizzard shad in five Missouri reservoirs. Grand means (GM; with coefficient of variation [CV] in parentheses) of these variables across all cohorts are listed for each reservoir.

Reservoir	Cohort	Mean \pm SE			Survival mean (95% CI)
		Fall TL	Fall density	Spring density	
Long Branch	2003	100 \pm 0.3	230 \pm 101	8 \pm 6	4.8 (0.3–17.5)
	2004	107 \pm 0.4	47 \pm 27	22 \pm 6	69.4 (17.7–100)
	2005	111 \pm 0.4	144 \pm 74	19 \pm 4	18.1 (5.5–55.7)
	2006	110 \pm 0.4	120 \pm 33	26 \pm 4	23.2 (11.9–41.4)
	2007	116 \pm 0.4	40 \pm 13	2 \pm 1	6.1 (1.3–14.6)
Mark Twain	GM (CV)	109 (5)	116 (67)	15 (65)	24 (109)
	2003	84 \pm 0.3	73 \pm 22	3 \pm 1	5.0 (2.2–9.9)
	2004	100 \pm 0.4	47 \pm 18	78 \pm 23	100 (71.8–100)
	2005	94 \pm 0.4	120 \pm 54	20 \pm 7	21.8 (4.9–66.4)
	2006	83 \pm 0.3	104 \pm 40	1 \pm 0.2	1.1 (1.4–2.3)
Thomas Hill	2007	89 \pm 0.3	313 \pm 156	0.1 \pm 0.1	0.03 (0–0.1)
	GM (CV)	90 (8)	131 (80)	20 (163)	26 (166)
	2003	86 \pm 0.2	171 \pm 59	51 \pm 17	33.9 (10.9–77.6)
	2004	81 \pm 0.2	378 \pm 119	15 \pm 4	4.6 (1.8–10.0)
	2005	82 \pm 0.3	482 \pm 383	6 \pm 2	3.1 (0.4–12.9)
Pomme de Terre	2006	87 \pm 0.3	662 \pm 327	25 \pm 9	5.1 (1.2–16.8)
	2007	75 \pm 0.2	1,396 \pm 813	0	0 (0)
	GM (CV)	82 (6)	618 (76)	19 (103)	9 (149)
	2003	70 \pm 0.2 ^a	46 \pm 27 ^a	4 \pm 2	0 (0) ^b
	2004	71 \pm 0.2	334 \pm 187	16 \pm 4	7.3 (1.8–28.1)
Stockton	2005	68 \pm 0.3	192 \pm 87	28 \pm 15	18.7 (4.1–62.8)
	2006	60 \pm 0.3	373 \pm 210	0.1 \pm 0.1	0.03 (0–0.2)
	2007	55 \pm 0.2	851 \pm 517	6 \pm 1	1.2 (0.3–4.5)
	GM (CV)	65 (11)	438 (66) ^c	10 (120)	5 (147) ^b
	2003	83 \pm 0.8	5 \pm 2	0.1 \pm 0.1	2.0 (0–9.9)
	2004	75 \pm 0.3	37 \pm 24	0	0 (0)
	2005	107 \pm 1.9	2 \pm 1	0.4 \pm 0.2	19.6 (0–51.4)
	2006	66 \pm 0.4	87 \pm 34	0	0 (0)
	2007	78 \pm 0.4	135 \pm 56	55 \pm 28	49.2 (9.7–100)
	GM (CV)	82 (19)	53 (107)	11 (221)	14 (150)

^a Data were available from the lower section only; the upper section was not sampled because of equipment malfunction.

^b Survival for the 2003 cohort was calculated for the lower section only.

^c Data from fall 2003 were not included.

survival. Because fall age-0 mean TL and ED were highly correlated ($r = 0.79$, $P < 0.0001$), as were the three winter temperature variables other than the rate of temperature decline ($r < -0.90$ or $r = 0.80$; all $P < 0.0001$), I restricted the models to include only one of the fall age-0 variables and one of the temperature variables other than the rate of temperature decline. After the final model was developed, the equation was transformed back into the original units:

$$P_s = \frac{\exp(\beta_0 + \beta_1 X_1 + \beta_2 X_2 + \cdots \beta_i X_i)}{1 + (\exp\beta_0 + \beta_1 X_1 + \beta_2 X_2 + \cdots \beta_i X_i)},$$

where P_s is the probability of survival, β_0 is the regression intercept, $\beta_{1...i}$ are regression coefficients, and $X_{1...i}$ are independent variables.

Results

Fall Cohort Demographics

Fall age-0 gizzard shad demographics varied among reservoirs and cohorts but did not vary consistently

across a reservoir productivity gradient. Fall mean TL was larger in the more productive Long Branch, Mark Twain, and Thomas Hill lakes than in the less productive Pomme de Terre Lake, as expected (Table 2). However, fall mean TL in the least productive reservoir, Stockton Lake, was the most annually variable, and its overall average was the same as for Thomas Hill Lake. Likewise, fall density did not vary consistently with reservoir productivity, with Pomme de Terre and Thomas Hill lakes containing the greatest densities and Stockton Lake containing the least. Similar to fall mean TL, fall density was the most variable in Stockton Lake. Fall mean TL was weakly correlated with fall density across all reservoirs and years (Figure 2). Although nonsignificant because of small sample size ($N = 5$ years), correlation coefficients for fall mean TL versus density ranged from -0.59 to -0.85 within reservoirs, except for Mark Twain Lake ($r = -0.18$). Fall ED varied with reservoir ($F = 24.53$; $df = 4$, 755 ; $P < 0.0001$) and increased with increasing age-0 fall TL ($F = 60.68$; $df = 1$, 755 ; $P < 0.0001$). The

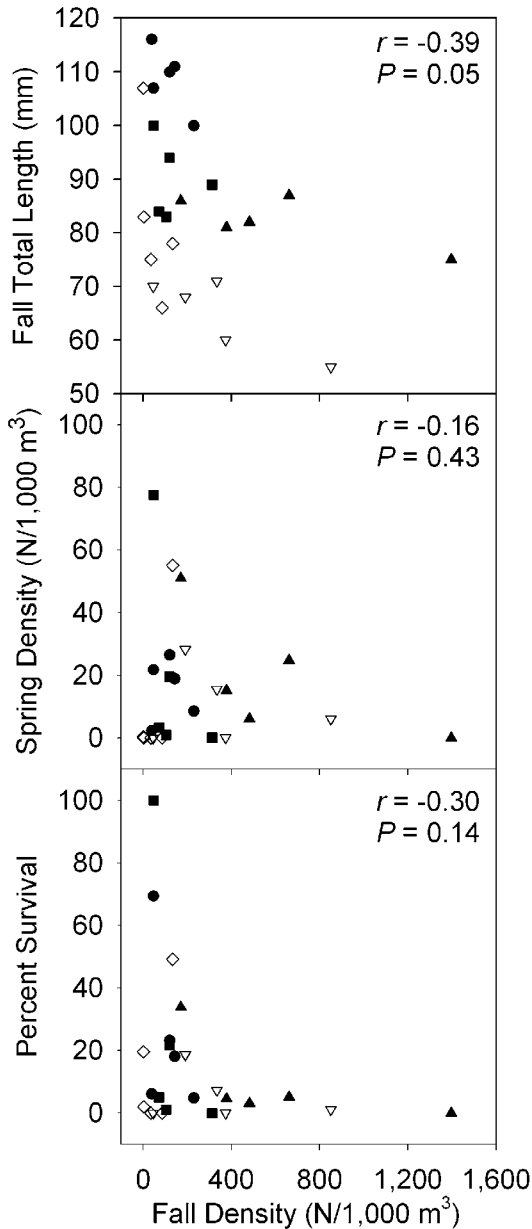


FIGURE 2.—Relationships between fall mean density (number/1,000 m³) and fall mean total length (mm), fall mean density and spring density, and fall mean density and survival (%) of gizzard shad cohorts in five Missouri reservoirs (reservoirs and associated symbols are listed in Figure 1).

interaction term between reservoir and age-0 TL in the preliminary model was not significant ($P = 0.07$) and was not included in the final model. Pairwise comparisons of least-squares means revealed that fall ED was lowest in the least productive Stockton and Pomme de Terre lakes, intermediate in Mark Twain

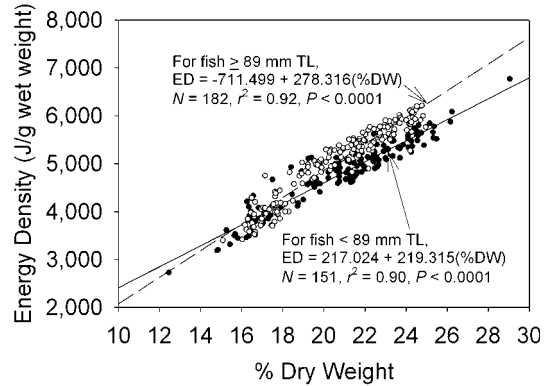


FIGURE 3.—Relationships between energy density (ED) and percent dry weight (%DW) for two size-classes of gizzard shad collected from five Missouri reservoirs in fall 2003, spring and fall 2004, and spring 2005. Filled circles indicate observations for the 151 fish less than 89 mm total length (TL), and open circles indicate observations for the 182 fish of 89 mm TL and larger.

Lake, and greatest in Long Branch and Thomas Hill lakes (all Tukey–Kramer adjusted $P < 0.02$). Energy density for fish collected in 2006–2008 was computed from %DW–ED regression equations (Figure 3). A TL of 89 mm was used to separate the two size-classes (Figures 1, 3) based on the average TL estimated from the three logistic equations. The %DW–ED regression equations accurately predicted ED for fish collected in fall 2005 (mean percent error = 1.0%, SE = 0.6%, range = -11.1 to 11.1%, $N = 87$).

Winter Severity

Mean winter water temperature ranged from 2.7°C to 8.0°C and winter duration lasted from 101 to 147 d across reservoirs and winters (Table 3). Mean winter temperatures averaged about 3°C warmer, winter duration was about 20 d shorter, and the number of days less than 4°C was about two to four times less in Pomme de Terre, Stockton, and Thomas Hill lakes than in Long Branch and Mark Twain lakes. However, the rate of temperature decline in late fall to early winter was similar among reservoirs, averaging from 0.21°C to 0.24°C per day.

Overwinter Changes in Cohort Demographics

Cohort demographics frequently changed substantially from fall to spring samples. Cohort density in the spring was usually much lower than that in the previous fall (Table 2). Annual variation in spring density did not vary consistently with reservoir productivity. Spring density varied the most in Stockton Lake, as expected, but spring density variation in

TABLE 3.—Mean (range in parentheses) winter water temperature variables for five Missouri reservoirs during the winters of 2003–2004 through 2007–2008 based on temperatures at 1-m depth. Rate of decline indicates the rate at which water temperatures fell in late fall to early winter. Mean temperature is the average during November 9 or 10 to March 30 or 31, depending on whether it was leap year or not.

Reservoir	Rate of decline (°C/d)	Mean temperature (°C)	Winter duration (d at <10°C)	Number of days at < 4°C
Long Branch	0.24 (0.17–0.29)	3.9 (2.7–4.8)	138 (134–147)	85 (69–102)
Mark Twain	0.21 (0.14–0.26)	4.6 (3.0–5.3)	131 (121–139)	76 (59–100)
Thomas Hill	0.23 (0.17–0.30)	7.2 (5.3–7.9)	106 (101–123)	33 (16–70)
Pomme de Terre	0.21 (0.16–0.29)	7.1 (6.5–7.8)	115 (111–120)	21 (0–42)
Stockton	0.22 (0.16–0.31)	6.9 (5.9–8.0)	115 (112–120)	24 (1–45)

Mark Twain Lake exceeded that in Pomme de Terre Lake. Spring density was most consistent in Long Branch Lake. Across all reservoirs and cohorts, spring density was not correlated with fall density (Figure 2) and the 2DKS test was also nonsignificant (maximum

difference in integrated probabilities for the two observed bivariate distributions [D_{BKS}] = 0.09, P = 0.27). Spring density was not significantly correlated with fall density within reservoirs, although all correlations were negative (r = –0.70 to –0.03; all P

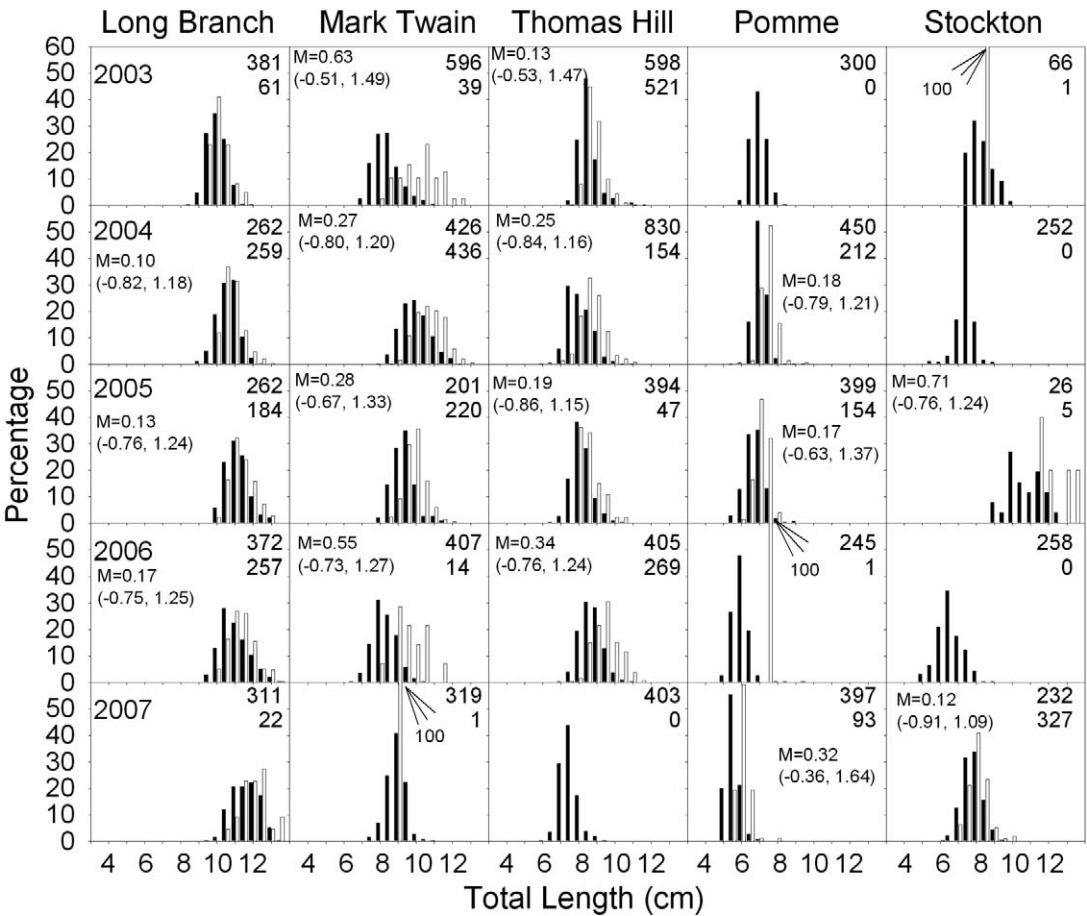


FIGURE 4.—Length frequencies (5-mm total length bins) for 2003–2007 cohorts of gizzard shad sampled in the fall (age 0; filled bars) and subsequent spring (age 1; open bars) in five Missouri reservoirs (Pomme = Pomme De Terre Lake). In the upper right corner of each graph, the numbers indicate sample sizes for the fall (top number) and spring (bottom number). A departure index (M ; Menning et al. 2007) was calculated when there was a significant difference (Kolmogorov–Smirnov test: $P \leq 0.05$) between fall and spring length frequencies; the range of possible M -values is in parentheses.

TABLE 4.—Summary of analysis of covariance for total length (TL, mm) and seasonal effects on energy density (ED; J/g wet weight) from fall to spring for the 2003–2007 cohorts of gizzard shad in five Missouri reservoirs. Numerator df equaled 1 for TL and season; denominator df are listed. Percent change in ED from fall to spring is listed for fish of mean fall TL. The interaction terms between season and TL are not included in the models and were nonsignificant except where indicated.

Reservoir	Source of variation	2003				2004				2005				2006				2007			
		df	F	P	%	df	F	P	%	df	F	P	%	df	F	P	%	df	F	P	%
Long Branch	TL	31	0.01	0.92		36	1.55	0.22		67	0.17	0.68		97	0.91	0.34		68	0	0.99	
	Season		0.09	0.77	0		146.96	<0.0001	–27		130.72	<0.0001	–17		463.32	<0.0001	–21 ^a		126.14	<0.0001	–23
Mark Twain	TL	37	6.25	0.02		38	0.96	0.33		49	5.67	0.02		60	3.94	0.05					
	Season		1.48	0.23	0		318.79	<0.0001	–31		27.36	<0.0001	–14 ^a		4.78	0.03	–10				
Thomas Hill	TL	37	0	0.99		37	0.70	0.38		63	6.92	0.01		97	21.30	<0.0001					
	Season		3.01	0.09	0		46.40	<0.0001	–19		9.01	0.004	–7		32.11	<0.0001	–9 ^b				
Pomme de Terre	TL					39	7.96	0.008		68	1.23	0.27						95	13.42	0.0004	
	Season						101.71	<0.0001	–27		9.12	0.004	–8						111.31	<0.0001	–21
Stockton	TL									12	4.32	0.06						95	7.40	0.008	
	Season										3.89	0.04	0						83.32	<0.0001	–11

^a Significant interaction term revealed that larger fish lost less ED than smaller fish.

^b Significant interaction term revealed that smaller fish lost less ED than larger fish.

> 0.19), except for Stockton Lake, where there was a marginal positive correlation ($r = 0.80$, $P = 0.10$). Overwinter survival estimates ranged from 0% to 100% and averaged 16% among reservoirs and cohorts (Table 2). There was no trend in variability of survival estimates with reservoir productivity, but survival tended to be higher in Long Branch and Mark Twain lakes than in the other reservoirs. The grand mean survival estimate of 14% for Stockton Lake (Table 2) is somewhat misleading given that survival was 2% or less for three of the five cohorts. Across all reservoirs and cohorts, survival was not correlated with fall density (Figure 2); neither were these variables correlated within reservoirs ($r = -0.63$ to 0.60 ; all $P > 0.25$). For all reservoirs and cohorts combined, there appeared to be a threshold effect of fall density, where

survival was highly variable at low fall densities but was always low at high fall densities ($D_{BKS} = 0.11$, $P = 0.10$).

Comparisons of fall and spring length frequencies revealed that size-dependent overwinter mortality commonly occurred within cohorts for all reservoirs (Figure 4). Length frequency distributions commonly shifted to the right from fall to spring samples, and all departure index values were positive, indicating that smaller fish suffered higher mortality than larger fish. Small sample sizes in the spring frequently prevented comparisons of fall and spring length frequencies, especially for Stockton Lake.

Cohorts that survived the winter usually lost ED. Energy density was significantly lower in the spring than in the previous fall for most reservoirs and cohorts except the 2003 cohort, for which no significant differences occurred (Table 4). Fish length was only significant in about one-third of the ANCOVAs. The interaction between season and fish length was significant in only 3 of 18 tests (not included in Table 4). Two of these significant interactions indicated that smaller fish lost a greater proportion of ED than larger fish, and the other indicated that larger fish suffered greater losses. Overwinter losses of ED ranged from 0% to 31% for a fish of average fall size. For cohorts that survived the winter, percent change in ED was marginally negatively correlated with percent survival ($r = -0.42$, $P = 0.08$, $N = 18$) but was not related to fall mean TL ($r = -0.11$, $P = 0.66$, $N = 18$).

Factors Affecting Overwinter Survival

Both fall age-0 demographics and winter severity were correlated with overwinter survival of gizzard shad cohorts. The three best models had AIC_c values within 1.5 units of each other and w_i values of 0.14 or

TABLE 5.—Top-nine regression models explaining variability in overwinter survival (logit-transformed) of gizzard shad cohorts in five Missouri reservoirs. Explanatory variables are fall mean total length (TL; mm), energy density (ED; J/g wet weight) for a fish of mean TL, mean winter water temperature (WT; °C), number of days at less than 4°C (T4), winter duration (WD; days at < 10°C), and rate of temperature decline in the fall (TR; °C/d). Akaike's information criterion corrected for small-sample bias (AIC_c), AIC_c difference (Δ_i), and Akaike weights (w_i) are reported for each model. All other models had w_i of 0.01 or less and are not reported here.

Model	r^2 or R^2	AIC_c	Δ_i	w_i
TL	0.296	69.25	0	0.30
TL, WT	0.344	70.33	1.08	0.17
TL, T4	0.334	70.73	1.48	0.14
TL, WD	0.313	71.52	2.27	0.10
TL, TR	0.297	72.10	2.85	0.07
ED	0.180	73.06	3.81	0.04
TL, WT, TR	0.346	73.44	4.19	0.04
TL, T4, TR	0.337	73.79	4.54	0.03
TL, WD, TR	0.313	74.66	5.41	0.02

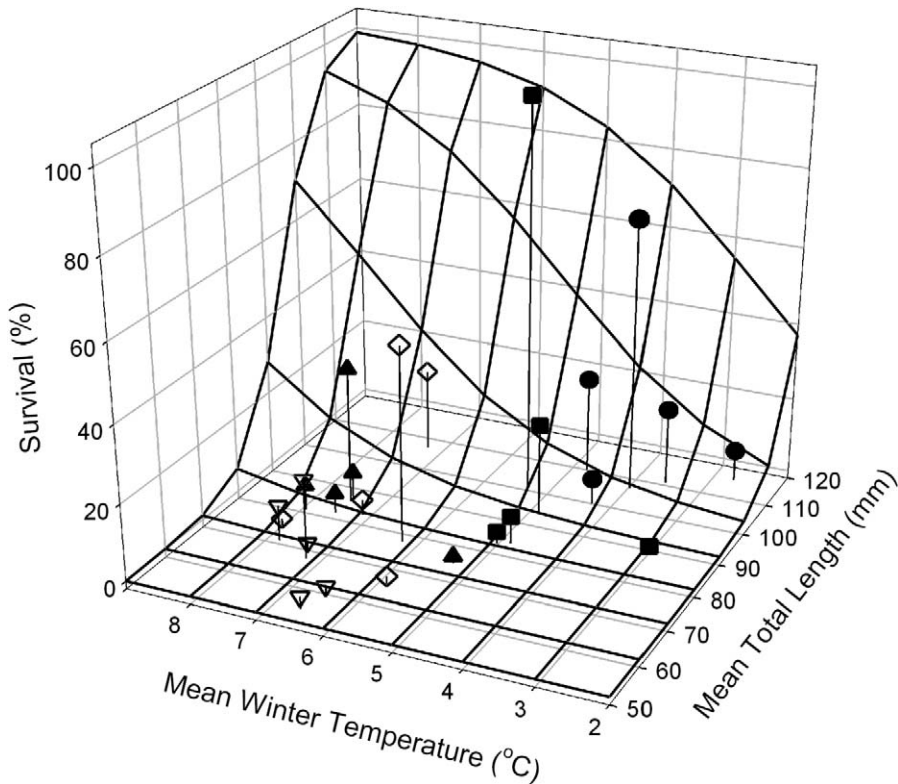


FIGURE 5.—Scatter plot showing the relationship between fall mean total length of age-0 gizzard shad, mean winter temperature, and percent survival in five Missouri reservoirs; and a mesh graph showing the predicted relationship from the logistic regression equation given in the text. Reservoirs and associated symbols are listed in Figure 1.

more (Table 5). All three models contained mean fall TL, and two of the models included a temperature variable. Mean fall TL alone explained most of the variation ($r^2 = 0.296$); inclusion of temperature variables explained less than 5% of additional variation in survival. However, the importance of temperature may have been underestimated in this analysis because of the confounding relationship between mean fall TL and winter temperature ($r = -0.60$, $P = 0.002$). Cohorts with the largest body size occurred in the northern reservoirs, where winter temperatures were colder. Thus, I chose the model that included both mean fall TL and mean winter temperature as the final model. The final model in logistic form was

$$P_s = \frac{\exp(-23.411 + 0.179\text{TL} + 0.709\text{WT})}{1 + \exp(-23.411 + 0.179\text{TL} + 0.709\text{WT})},$$

where TL represents mean fall TL of the cohort and WT represents mean winter temperature. Cohort survival increased with increases in mean TL and mean winter temperature (Figure 5). The model predicted that even at the warmest mean winter

temperature (9°C), survival of fish less than 80 mm TL never exceeded 10%. However, at this same temperature, survival rapidly increased to 28% for 90-mm fish. At the coldest winter temperature (2°C), survival was less than 10% for all but the largest fish (120 mm TL).

Discussion

The first winter of life was an important bottleneck in the recruitment process of gizzard shad, similar to findings for other species (Ludsin and DeVries 1997; Hurst and Conover 1998; McCollum et al. 2003). Variable overwinter survival significantly altered the relative year-class strength of age-0 gizzard shad; spring yearling densities were uncorrelated with fall age-0 densities, similar to results of other studies (Hurst and Conover 1998; Wiedenmann and Essington 2006). For many cohorts, overwinter mortality was high and rivaled mortality rates of the larval period (Michaletz 1997a). In other cases, overwinter mortality was quite low, especially for cohorts with large body size. Thus,

year-class strength of adults was clearly not established until sometime after the first winter of life.

This study represents one of only a few studies that have attempted to quantify overwinter survival in the field. Estimating fish overwinter survival with field studies is very challenging. Seasonal differences in catchability and distribution of fish may cause biases in survival estimates. Catchability may have been greater in the spring than in the fall because temperatures were usually colder and fish were in poorer condition, which reduces the ability of the fish to escape the trawls. Hence, survival may have been overestimated. Distributional differences from fall to spring may also have caused biases in survival estimates. For example, during the winter, gizzard shad may have been attracted to the warmwater discharge created by the power plant at Thomas Hill Lake (Cox and Coutant 1975; White et al. 1986). I attempted to minimize this possibility by ensuring that sampling sites were distant (>1.7 km) from this discharge. Perhaps, fish could have moved into waters deeper than I trawled. Water deeper than 9 m was present in portions of all reservoirs except Long Branch and Thomas Hill lakes. However, White et al. (1986) reported that age-0 gizzard shad remained in surface waters throughout the winter; thus, the fish should have been vulnerable to the trawl sampling in both the fall and spring. Finally, young gizzard shad are patchily distributed (Van Den Avyle et al. 1995), which resulted in some imprecise estimates of survival. Although I could have possibly increased precision by increasing the number of trawl sites, acquiring the required number of samples would have been impractical in some cases. Although survival estimates are not without potential biases, I documented that overwinter survival was remarkably variable across reservoirs and cohorts and that it was frequently negligible. In the next sections, I address the three questions that I posed in the Introduction.

Do Fall Age-0 Demographics Vary Across a Reservoir Productivity Gradient?

Fall age-0 demographics did not vary consistently across a reservoir productivity gradient. I expected fall age-0 TL to increase with increasing reservoir productivity, as was found by Michaletz (1998b, 1999). Overall, the largest age-0 fish occurred in the most productive reservoirs and the smallest age-0 fish occurred in the least productive reservoirs, as expected. However, fall age-0 size was most variable in Stockton Lake, the least productive reservoir, where large age-0 fish also occurred during 1 year. Density of age-0 gizzard shad reportedly increases with increasing reservoir productivity (Hoxmeier and DeVries 1998; Allen et al. 1999; Bremigan and Stein 1999), a pattern

that was not found for age-0 fish in the fall in my study or for juveniles in a previous study of Missouri reservoirs (Michaletz 1999). Densities were highest in Thomas Hill Lake, a highly eutrophic reservoir, and in Pomme de Terre Lake, a slightly eutrophic reservoir. Densities were lowest and most variable in Stockton Lake. Perhaps more consistent with expectations, ED was higher in the more productive reservoirs than in the less productive reservoirs.

Inconsistencies in age-0 demographics in relation to reservoir trophic status are probably a consequence of complex interactions among climatic influences, density-dependent relationships, and reservoir-specific differences in hydrology, morphology, and other hydrogeomorphic features (Michaletz 1997a; Bremigan and Stein 1999; Bremigan et al. 2008). A drought occurred in Missouri during the first 3 years of the study and was most severe in the southwestern portion of the state, where Stockton and Pomme de Terre lakes are located. Spring (mid-April to late June) inflows into these two reservoirs were especially low during 2005, when inflows averaged 50–80% less than inflows measured during other years (U.S. Geological Survey, unpublished data). These inflows are probably especially important sources of nutrients for enhancing the prey resources necessary for growth and survival of age-0 gizzard shad in oligotrophic to mesotrophic reservoirs (e.g., Stockton Lake), where internal sources and recycling of nutrients are much less than in highly eutrophic systems (Vanni et al. 2006). Densities of small-bodied zooplankton prey, important for growth and survival of larval gizzard shad, tend to increase with increasing nutrient concentrations (Bremigan and Stein 1999; Bremigan et al. 2008). With reduced nutrient input, prey resources in Stockton Lake may have been inadequate to promote high survival of larval gizzard shad, resulting in fewer but larger juveniles in 2005. A similar scenario occurred in Stockton Lake during 1987, when spring inflows were exceptionally low (Michaletz 1997a). Annual variation in fall density and TL of age-0 gizzard shad was greatest in Stockton Lake, possibly in response to differences in nutrient inputs resulting from varying precipitation patterns. Fall age-0 gizzard shad demographics in Pomme de Terre Lake did not vary as much as in Stockton Lake, but mean TL was smaller and mean density was greater in 2006 and 2007, when spring inflows were higher than in the previous 3 years.

Density-dependent growth complicated the relationship between mean fall TL of gizzard shad and reservoir productivity. At high densities, mean fall TL tended to be smaller across all reservoirs than when densities were low. Why fall densities were highest in Thomas Hill and Pomme de Terre lakes is unclear.

These reservoirs differ substantially in watershed characteristics, productivity, and morphology. Long Branch Lake has watershed and reservoir characteristics that are very similar to those of Thomas Hill Lake, yet fall densities were usually much lower and mean fall TL was much higher in Long Branch Lake. The most apparent difference between these two reservoirs is their differing thermal regimes due to power plant operations at Thomas Hill Lake. Apparently, the unique characteristics of individual reservoirs obscure the broad relationship between fish densities and reservoir productivity, especially when examining a small set of reservoirs such as in this study. Despite the confounding influence of age-0 density, reservoir productivity did influence first-year growth. Fish were larger in the more productive reservoirs than in the less productive reservoirs at similar densities (Figure 2). Apparently, food quality, food quantity, or both were greater per capita in more productive reservoirs, resulting in faster growth. Higher ED in fish in the more productive reservoirs supports this conclusion (Malzahn et al. 2007).

Do Fall Age-0 Demographics and Winter Severity Affect Overwinter Survival?

Overwinter survival of age-0 gizzard shad was related to both fall age-0 demographics and winter severity. Survival increased with larger body size and warmer winter temperatures, similar to findings for several other species (Post and Evans 1989; Johnson and Evans 1991; Post et al. 1998). Survival was highly variable at low fall age-0 densities but was consistently low at high densities, probably because fall body size was usually smaller at high densities. Size-dependent survival occurred both among and within winters. Among winters, age-0 cohorts with small fall body size usually experienced higher overwinter mortality than cohorts with large fall size. Within winters, comparisons of fall and spring length frequencies revealed that smaller members of the cohort frequently did not survive the winter. Similar size-dependent overwinter survival has been observed for many fish species (Hurst 2007). Winter severity strongly affects overwinter survival (Post and Evans 1989; Johnson and Evans 1991; Lankford and Targett 2001; McCollum et al. 2003). In this study, survival during colder winters was usually less than that during warmer winters for fish of similar size. Survival was less than 10%, even for the relatively large fish in Long Branch and Mark Twain lakes, during the cold winter of 2007–2008.

Larger age-0 gizzard shad not only contained more total energy due to their larger size but also had higher EDs than smaller fish, which is consistent with studies of gizzard shad (Kim et al. 2007) and other species

(Miranda and Hubbard 1994a; Schultz and Conover 1997; Sutton and Ney 2001; McCollum et al. 2003). Higher EDs for larger fish were at least partially due to an abrupt increase in lipid content as fish grew from 85 to 95 mm TL. Similar abrupt ontogenetic changes in lipid content have been reported for other fish species (Pothoven et al. 2006; Wuenschel et al. 2006) and may be related to maturation. Although smaller fish contained less energy, it is uncertain whether they used more of their energy reserves overwinter than did larger fish. Within a reservoir and cohort, significant interaction terms between fish size and season were uncommon among models explaining overwinter changes in ED, suggesting that energy loss or gain was unrelated to fish size. Among reservoirs and cohorts, overwinter changes in ED were unrelated to mean fall TL for surviving cohorts. Unfortunately, only fish that survived the winter could be analyzed for ED, but perhaps smaller fish had depleted their energy reserves and died before the spring collections.

This study was not designed to specifically identify various overwinter mortality mechanisms for gizzard shad. However, mechanisms probably included starvation, osmoregulatory or physiological failure, and predation. Gizzard shad probably starved throughout the winter because feeding activity is nearly nonexistent when water temperatures fall below about 10°C (Salvatore et al. 1987; Mundahl 1991). Overwinter losses in ED approached 30% for survivors in some cases. It is unknown how much energy can be lost by age-0 gizzard shad before mortality occurs. However, studies of other fish species suggest that energy losses of about 50–60% can result in starvation mortality (Savitz 1971; Shuter et al. 1980; Johnson and Evans 1991), and mortality of small fish can occur at proportionally lower energy losses than for large fish (Pangle et al. 2004). In many cases, fish in this study not only lost ED but also body weight, which together resulted in total energy losses approaching 40% in some instances. This suggests that starvation mortality quite possibly occurred, especially for small fish.

Osmoregulatory or physiological failure may also cause mortality in overwintering fishes, especially during drastic temperature changes or severe winters (White et al. 1986; Johnson and Evans 1991; McCollum et al. 2003). Gizzard shad are susceptible to cold shock when temperatures fall rapidly (Cox and Coutant 1975). White et al. (1986) found that age-0 gizzard shad in Lake Erie experienced high mortality due to enzymatic failure during periods of rapidly falling temperatures. Average temperature declines of about 0.1–0.3°C per day in the study reservoirs were much less severe than the values greater than 3–5°C per day reported by Cox and Coutant (1975) and White et

al. (1986). Temperatures rarely declined more than 1°C per day in any reservoir, but declines did exceed 3°C per day on two occasions during the winter of 2003–2004 in Thomas Hill Lake. However, survival of fish that winter was fairly high at 34%, suggesting that these temperature drops did not cause high mortality. White et al. (1986) also found that age-0 gizzard shad suffered from several other physiological malfunctions during the winter period, including the inability to use lipid reserves. Fish in this study typically lost energy reserves; however, survivors of the 2003–2004 winter in Long Branch and Mark Twain lakes had a lipid content (about 22–27%) similar to that of fish collected during the previous fall (about 21–23%). However, survival of this cohort was substantially lower in both reservoirs (about 5%) than for the winter of 2004–2005, when fish had higher survival (69–100%) but lost about 40% or more of their lipid content. Possibly, fish during the winter of 2003–2004 suffered from the same malfunction as those in Lake Erie, although thermal regimes did not appear to be substantially different between the winters of 2003–2004 and 2004–2005. Hence, it is unclear what caused the difference in the use of lipid reserves between these winters.

Predation probably also influenced overwinter survival of fish in the study reservoirs. Predation can be a major source of overwinter mortality and may act in a size-dependent manner, with smaller fish suffering higher mortality than larger fish (Miranda and Hubbard 1994b; Garvey et al. 1998b; Shoup and Wahl 2008; but see Santucci and Wahl 2003). Smaller fish are more vulnerable to predators than larger fish because they are usually in poorer energetic condition, which impairs their ability to escape predators (Jonas and Wahl 1998; Chick and Van Den Avyle 2000), and smaller fish can be consumed by a broader size range of gape-limited predators (Hambright et al. 1991; Michaletz 1997b). Juvenile gizzard shad are especially susceptible to overwinter predation because they become stressed during periods of cold temperatures (Cox and Coutant 1975; White et al. 1986), making them highly vulnerable to predators (Minton and McLean 1982; Wahl and Nielsen 1985). All study reservoirs contained black bass *Micropterus* spp., crappies *Pomoxis* spp., and other predators that are known to feed during the winter at middle and southern latitudes (Miranda and Hubbard 1994b; McCollum et al. 2003; Santucci and Wahl 2003; Shoup and Wahl 2008).

There is probably no single mortality factor; rather, multiple stressors probably interact to affect overwinter mortality of gizzard shad. These interactions are likely to operate through both density-independent and density-dependent processes. During severe winters,

mortality probably operates in a density-independent fashion, whereas in more moderate winters density-dependent processes may be more important. Although the relative importance of various mortality factors is difficult to ascertain, it is evident that both fall body size and winter severity are influential in mortality processes.

Does Variability in the Abundance of Overwinter Survivors among Years Decrease with Increasing Reservoir Productivity?

The variability in overwinter survivors among cohorts did not consistently decrease with increasing reservoir productivity. Although variation in overwinter survivors was highest in the least productive reservoir, Stockton Lake, variation in more productive Mark Twain Lake was higher than in less productive Pomme de Terre Lake. Therefore, the observed variability in overwinter survivors may not entirely explain the recruitment patterns described by Michaletz (1998b). It is possible that the abundance of spring survivors does not strongly correlate to the abundances of adults used by Michaletz (1998b) to estimate recruitment variability because of differential survival between spring yearlings and age-3 and older fish. However, the recruitment variability index used by Michaletz (1998b) is sensitive to missing year-classes and may not accurately quantify the degree of variation among existing year-classes (Isermann et al. 2002). Perhaps, the lower recruitment variability index values reported by Michaletz (1998b) for Stockton and Pomme de Terre lakes were a consequence of more frequent missing year-classes than for the more productive reservoirs. In this study, I also observed more frequent missing spring cohorts and cohorts with extremely low spring abundance (which may not be detected as adults) in Stockton and Pomme de Terre lakes than in the other reservoirs. As Michaletz (1998b) suggested, overwinter mortality was size dependent, with larger fish usually experiencing higher survival. However, fall sizes did not consistently vary along a productivity gradient and differed from those previously reported for the study reservoirs. Grand mean fall TL was about 10–15 mm smaller in Mark Twain and Thomas Hill lakes and 13 mm larger in Stockton Lake than in past studies. These size differences may also explain why there was not a consistent pattern in recruitment variability across a productivity gradient. Differences in size between previous work and the present study emphasize the dynamic nature of reservoir gizzard shad populations. Fluctuating abundances and sizes of young gizzard shad due to annual differences in fish production and variable overwinter survival affect not only gizzard shad population

dynamics (Michaletz 1998b) but also predator–prey, nutrient recycling, and zooplankton dynamics (Adams et al. 1982; Michaletz 1997b; Schaus et al. 2002). Reservoir managers must account for these dynamics when implementing strategies to improve sport fish populations or water quality.

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