

## First-Year Growth, Condition, and Size-Selective Winter Mortality of Freshwater Drum in the Lower Missouri River

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**Abstract.**—We compared first-year growth and relative condition ( $K_n$ ) of the 1997 and 1998 year-classes of freshwater drum *Aplodinotus grunniens* among three sites in a 235-km reach of the channelized Missouri River and tested for the occurrence of size-selective overwinter mortality during the first winter. Prewinter mean length was 15 mm greater, mean weight was 8 g greater, and mean  $K_n$  was 5% greater at the upstream site than at the downstream site. The prewinter mean length of age-0 freshwater drum was significantly greater in 1997 (115 mm) than in 1998 (109 mm), but  $K_n$  was significantly greater in 1998 (107) than in 1997 (102). There was no evidence that density-dependent interactions influenced prewinter growth and  $K_n$ . Size-selective overwinter mortality of the smallest size-classes of freshwater drum occurred at two of three sites during the 1997–1998 winter, and  $K_n$  decreased 9–15%. Size-selective overwinter mortality of the 1998 cohort of freshwater drum did not occur during the 1998–1999 winter, and  $K_n$  declined 0–10%. A prolonged growing season (through early December 1998), in conjunction with less severe winter water temperature conditions, apparently minimized the incidence of size-selective overwinter mortality for the 1998 cohort of freshwater drum. We conclude that size-selective overwinter mortality of age-0 freshwater drum occurs in the lower channelized Missouri River but depends on the length of the prewinter growing season, winter duration, and the severity of winter water temperatures.

Growth during the first year of life is widely recognized as a critical factor affecting recruitment in fishes. Rapid growth of individuals increases the probability of survival during the larval life stage (Houde 1987; Uphoff 1989; Gallego and Heath 1997; Houde 1997). However, adequate growth and survival through the larval stage does not ensure successful recruitment to juvenile or adult life stages; winter is a second size-dependent critical period (Shuter et al. 1980; Hurst and Conover 1998). Several field and laboratory studies have demonstrated that overwinter mortality can reduce juvenile populations, with smaller individuals generally experiencing greater overwinter mortality than larger individuals (Hurst and Conover 1998; Post et al. 1998; Schlosser 1998;

Schultz et al. 1998). However, this pattern is not consistent among fish species in all aquatic environments (Toneys and Coble 1979; Madenjian et al. 1996; Hurst and Conover 1998). Winter duration and the severity of winter water temperatures may influence the magnitude of size-selective overwinter mortality (Bodensteiner and Lewis 1992; Hurst and Conover 1998). Despite inferences from other studies, the role of winter as a mechanism influencing mortality and the recruitment of fishes in temperate flood plain rivers has not been extensively studied (Junk et al. 1989; see Bodensteiner and Lewis 1992).

Assessments of overwinter mortality can be used to determine the extent to which recruitment is regulated by size-dependent processes, and it is important to identify how physical and biological processes during the first growing season affect growth and influence the likelihood of size-selective overwinter mortality. Within the last two decades, there has been an increasing research emphasis to examine the growth and recruitment dynamics of fishes in large rivers (e.g., Risotto and Turner 1985; Junk et al. 1989; Gutreuter et al. 1999; Braaten and Guy 2002; Pegg and Pierce 2002). Studies in large flood plain rivers have focused primarily on examining the influence of temporal variations in discharge on fish growth (e.g., the flood pulse; Junk et al. 1989; Bayley 1991;

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Rutherford et al. 1995; Gutreuter et al. 1999). Less research emphasis has been directed towards examining the spatial variation in fish growth in these systems. Gradients of physicochemical variables and productivity that occur in large rivers (Vannote et al. 1980) can influence spatial patterns of food availability, and subsequently affect fish growth during the first growing season. Similarly, anthropogenic modifications that vary spatially among river reaches can elicit differential effects on fish growth (Przybylski 1996). Competition for food during the first summer of life may affect the growth and condition of fish, and enhance the potential for size-selective overwinter mortality (Schlosser 1998).

The objectives of this study were to (1) compare first-summer growth and body condition of freshwater drum *Aplodinotus grunniens* between 2 years and among three sites in the lower channelized Missouri River; (2) test for potential density-dependent interactions on growth and body condition; and (3) test for the occurrence of size-selective overwinter mortality.

#### Study Area

The Missouri River is channelized and flow-regulated from Sioux City, Iowa, to the mouth located near St. Louis, Missouri. Construction of wing dikes on inside bends and the placement of riprap on outside bends to facilitate navigation have resulted in the near-elimination of natural off-channel areas (e.g., side channels and backwaters) and sand bar habitats (Funk and Robinson 1974). Discharge in the Missouri River is regulated by water releases through the Gavins Point Dam, the lowermost of six main-stem impoundments on the Missouri River. Water released through the Gavins Point Dam is increased from April through late November or early December to facilitate navigation in the channelized river. During the non-navigation season, flows in the channelized river are at volumes one-half to two-thirds of the navigation season discharge (Hesse and Newcomb 1982; Latka et al. 1995).

#### Methods

*Study sites.*—Three study sites were established in a 235-river kilometer (rkm) reach of the Missouri River. Study sites were located near St. Joseph, Missouri (site 1, rkm 707–737 from the mouth of the river), upstream from Kansas City, Missouri (site 2, rkm 596–618), and downstream from Kansas City near Lexington, Missouri (site 3, rkm 502–525).

*Sampling.*—Age-0 freshwater drum and other fishes were sampled during 1997 and 1998 from five, outside-bend riprap shorelines within each of the three study sites. Fish were sampled in mid-October, mid-November, and mid-December of both years. The five outside bends at each site were trisected into three subreaches representing the lower, middle, and upper thirds of the bend. One subreach on each outside bend was randomly selected for sampling in October. In November, one of the two remaining subreaches on each outside bend was randomly selected and sampled. The remaining subreach was sampled in December. This sampling protocol was used to prevent resampling subreaches. The sampling regime resulted in a total of 90 samples (3 sites  $\times$  5 outside bends  $\times$  3 sampling months  $\times$  2 years). All sites were sampled over a 3-d time period. Fishes were sampled along riprap shorelines using pulsed-DC electrofishing (400–420 V, 6–10 A, single spherical electrode). Sample duration varied between 530 s and 1,825 s depending on the length of the subreach bordered by riprap.

Age-1 freshwater drum were sampled from wing dike pools at the three sites during March 1998 (representative of the 1997 year-class) and March 1999 (representative of the 1998 year-class) to examine survival through winter. It was necessary to sample wing dike pools in March rather than outside bends because wing dike pools are the primary overwintering habitats for fishes in the channelized Missouri River (Hesse and Newcomb 1982; Newcomb 1989). A deepwater electrofishing apparatus was used to sample fish in the pools. A 6.1-m-long insulated cable attached to a spherical electrode (0.9 m circumference) was suspended from a 1.6-m-long boom at the front of the boat and lowered to the bottom. The electrode system was powered with pulsed-DC electrofishing (320–410 V, 6–13 A). The sampling protocol consisted of slowly moving the boat in reverse through all areas of the wing dike pool for 560–2,300 s depending on the pool size. Stunned fish would float to the surface 3–5 min after power was initially applied, and would remain afloat for several minutes. Fish collected from outside bend and wing dike habitats were enumerated after sampling, and the total length (mm) of all freshwater drum was measured. Freshwater drum less than 200 mm were weighed (g), placed in individual plastic bags, and immediately frozen on dry ice.

*Age determination, body condition, and food habits.*—Scales from freshwater drum measuring less than 200 mm were mounted between glass

slides and aged using a microfiche projector (42× magnification). Age-0 individuals collected from October to December and age-1 individuals collected in March (assigned a January 1 birthdate) were distinguished from older age-classes by the absence of an annulus. Bur (1984) determined that annulus formation in the scales of freshwater drum occurred between June and August. Relative condition ( $K_n$ ) was used to quantify changes in body condition among sampling periods. Relative condition was calculated as

$$K_n = (W/W') \times 100,$$

where  $W$  is the weight of an individual (g), and  $W'$  is a length-specific mean weight (g) based on the length-weight relationship of age-0 (October–December) and age-1 (March) freshwater drum collected in this study. Although a standard weight ( $W_s$ ) equation for freshwater drum is available,  $W_s$  was not calculated in this study because individuals less than 100 mm (the minimum size recommended for the  $W_s$  equation; Anderson and Neumann 1996) were collected. Therefore,  $K_n$  values calculated in this study are specific to the population of age-0 and age-1 freshwater drum in our study area. Stomach contents from age-0 and age-1 freshwater drum were excised from thawed individuals, identified, and enumerated. The primary focus of the food habit portion of the study was to qualitatively document whether age-0 and age-1 freshwater drum were feeding during the sampling periods. Therefore, food habit data from individuals at all sites were pooled by sampling period and qualitatively summarized as frequency of occurrence (i.e., the percent of individuals containing a specific food item).

*Water temperature and river discharge.*—Daily water temperature was monitored from May through November 1997 and 1998 with continuous-recording water temperature loggers located in sites 2 and 3. A temperature logger was also deployed at site 1 during 1997, but it was vandalized and not replaced in 1998. Therefore, daily water temperature data for site 1 in both years were obtained from water treatment and power generating facilities located near the site, as were water temperatures for December through March for all the three sites. Missouri River discharge data were obtained from U.S. Geological Survey gauges located near site 1 and site 3. No gauge occurs at site 2; therefore, discharge measurements from site 1 were used for site 2.

*Statistical analyses.*—Two sets of statistical anal-

yses were conducted. The first was used to examine physical and biological characteristics prior to winter. A nonparametric one-way analysis of variance (ANOVA; Kruskal–Wallis test) was used to compare daily water temperature and daily discharge among sites and between years for the period spanning the initiation of freshwater drum spawning to the October sampling date. Based on samples of larval freshwater drum, Braaten (2000) determined that spawning was initiated in mid-June of 1997 and late May of 1998. The Kruskal–Wallis test was used because errors for water temperature and discharge were not normally distributed. When significant differences ( $P \leq 0.05$ ) existed in the overall Kruskal–Wallis test, pairwise comparisons were conducted using multiple Wilcoxon two-sample tests. The critical probability level ( $\alpha = 0.05$ ) was maintained in multiple comparisons using a Bonferroni adjustment (e.g.,  $P = \alpha/\text{number of pairwise comparisons}$ ; Trippel and Hubert 1990).

A two-way ANOVA was used to compare pre-winter length, weight, and  $K_n$  of age-0 freshwater drum in October between years and among sites. Movements of age-0 freshwater drum from outside bends to wing dike pools following the October samples (see Results) reduced the sample size, and precluded statistical comparisons for November and December. Length, weight, and  $K_n$  data met the assumptions of parametric ANOVA. Correlation analyses between mean length, weight, and  $K_n$  of age-0 freshwater drum sampled in October and October catch per effort ( $C/f$ ; number/min of electrofishing) of age-0 freshwater drum were used to test for potential density-dependent interactions and their subsequent influence on the growth and condition of age-0 freshwater drum. Freshwater drum and many other Missouri River fishes feed on benthic macroinvertebrates (Hesse et al. 1982; Wahl et al. 1988; Pflieger 1997). Thus, we also used correlation analysis between mean length, weight, and  $K_n$  of age-0 freshwater drum and total  $C/f$  of these associated species that feed on aquatic macroinvertebrates to examine what effects these other species have on age-0 freshwater drum. Total  $C/f$  included age-0 and older fishes of the following species: freshwater drum, green sunfish *Lepomis cyanellus*, orangespotted sunfish *L. humilis*, bluegill *L. macrochirus*, largemouth bass *Micropterus salmoides*, channel catfish *Ictalurus punctatus*, blue catfish *I. furcatus*, flathead catfish *Pylodictis olivaris* less than 100 mm, black bullhead *Ameiurus melas*, stonecat *Noturus flavus*, river carpsucker *Carpionodes carpio*, quillback *C. cyprinus*, blue sucker *Cycleptus elongatus*, smallmouth buffalo

*Ictiobus bubalus*, bigmouth buffalo *I. cyprinellus*, goldeye *Hiodon alosoides*, common carp *Cyprinus carpio*, goldfish *Carassius auratus*, emerald shiner *Notropis atherinoides*, river shiner *N. blennioides*, sand shiner *N. stramineus*, red shiner *Cyprinella lutrensis*, fathead minnow *Pimephales promelas*, *Hybognathus* spp, and logperch *Percina caprodes*.

The second set of analyses was used to compare water temperature conditions through winter and to examine size-selective overwinter mortality of age-0 freshwater drum between October (prewinter) and March (postwinter) of the succeeding year. A Kruskal–Wallis test was used to compare winter water temperature among sites and between years. A Bonferroni adjustment as described above was applied to pairwise comparisons. To assess the potential for growth, the number of days that water temperature exceeded 9°C after the October sampling period was determined based on the finding that growth of age-0 freshwater drum ceases at 9–11°C (McInerney and Held 1995). Winter severity was indexed as the number of days that water temperatures were 5°C or less. In addition, cumulative degree-days at 5°C or less were calculated as  $\sum T - t_i$ , where  $T = 5^\circ\text{C}$  and  $t_i$  = daily water temperature less than or equal to  $T$ . Quantile–quantile plots as described by Post and Evans (1989) were used to compare prewinter (October) and postwinter (March) length–frequency distributions for each site and year, and identify pre- and postwinter changes in the length frequencies resulting from overwinter growth and size-selective mortality. In this analysis, quantiles 1, 5, 10, 25, 50, 75, 90, 95, and 99% were calculated from the pre- and postwinter length distributions. Postwinter length quantiles and changes in quantile growth increments (i.e., postwinter minus prewinter) were regressed on prewinter length quantiles to estimate the slope of the relationship. A positive slope significantly less than 1.0 between post- and prewinter length quantiles provides evidence of size-selective overwinter mortality of small size-classes (Post and Evans 1989). A significant negative slope between quantile growth increments and prewinter length quantiles also provides evidence of size-selective overwinter mortality of small individuals (Post and Evans 1989). Within each site, mean  $K_n$  was compared between October and March using  $t$ -tests to examine overwinter changes in body condition.

### Results

#### *Prewinter Water Temperature, Discharge, Fish Length, Weight, and Body Condition*

Water temperature between spawning and October samples did not differ significantly among

sites between years (Kruskal–Wallis chi-square = 8.6,  $df = 5$ ,  $P = 0.13$ ). Median water temperatures for the sites were 24.8°C to 25.0°C in 1997, and 25.6°C to 26.1°C in 1998. Missouri River discharge differed significantly among sites between years (Kruskal–Wallis chi-square = 138.9,  $df = 3$ ,  $P = 0.0001$ ). Median discharge in 1997 was similar ( $P > 0.05$ ) between site 1 (2,247 m<sup>3</sup>/s) and site 3 (2,278 m<sup>3</sup>/s), but was significantly greater ( $P = 0.0001$ ) at site 3 (2,006 m<sup>3</sup>/s) than at site 1 (1,497 m<sup>3</sup>/s) in 1998.

The mean length of age-0 freshwater drum in October differed significantly between years ( $F = 6.1$ ,  $df = 1, 24$ ,  $P = 0.021$ ) and among sites ( $F = 17.99$ ,  $df = 2, 24$ ,  $P = 0.0001$ ). The mean length of the 1997 cohort of freshwater drum was greater than the 1998 cohort, and the length was greater at site 1 than at sites 2 and 3 (Figure 1). There was no significant year-by-site interaction for length ( $F = 0.98$ ,  $df = 2, 24$ ,  $P = 0.39$ ).

Mean weight of age-0 freshwater drum in October did not differ significantly between years ( $F = 2.53$ ,  $df = 1, 23$ ,  $P = 0.13$ ), but was significantly different among sites ( $F = 18.9$ ,  $df = 2, 23$ ,  $P = 0.0001$ ). Similar to length, mean weight was greater at site 1 than at sites 2 and 3 (Figure 1). The year-by-site interaction for weight was not significant ( $F = 0.82$ ,  $df = 2, 23$ ,  $P = 0.45$ ). Freshwater drum weights were not obtained for one sample due to excessive wind. Therefore, sample size for the ANOVA involving weight and  $K_n$  (see below) was reduced by one.

Log-transformed (base 10) length and weight of the 1997 and 1998 cohorts of freshwater drum were highly correlated (Pearson  $r = 0.99$ ,  $P < 0.0001$ ,  $N = 1,397$ ). Lack of correlation between  $K_n$  and fish length ( $r = 0$ ,  $P = 0.93$ ,  $N = 1,397$ ) indicated  $K_n$  was not length-biased. Relative condition of age-0 freshwater drum in October differed significantly between years ( $F = 22.58$ ,  $df = 1, 23$ ,  $P = 0.0001$ ) and among sites ( $F = 7.57$ ,  $df = 2, 23$ ,  $P = 0.003$ ), and was greater in 1998 than in 1997 (Figure 1). Mean  $K_n$  was greater at site 1 than at sites 2 and 3 (Figure 1). The year-by-site interaction for  $K_n$  was not significant ( $F = 0.69$ ,  $df = 2, 23$ ,  $P = 0.51$ ).

There were no significant correlations between mean length ( $r = -0.33$ ,  $P = 0.24$ ), mean weight ( $r = -0.47$ ,  $P = 0.09$ ) and mean  $K_n$  ( $r = -0.52$ ,  $P = 0.06$ ), and  $C/f$  of age-0 freshwater drum sampled from outside bends in October 1997. Similarly, total  $C/f$  of fishes that feed on aquatic macroinvertebrates was not significantly correlated with mean length ( $r = -0.29$ ,  $P = 0.29$ ), mean

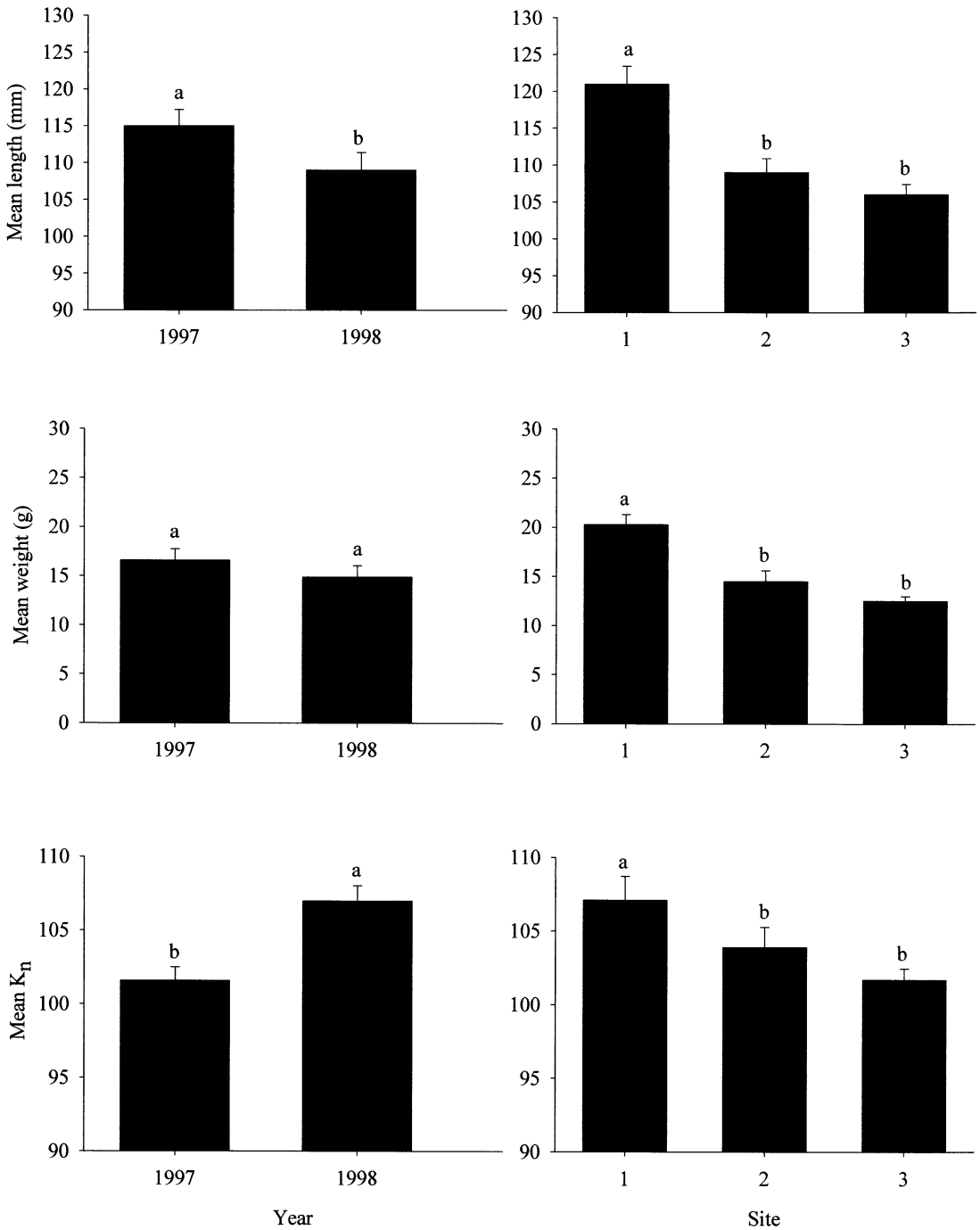


FIGURE 1.—Mean ( $\pm 1$  SE) length (top panel), weight (middle panel), and relative condition ( $K_n$ , bottom panel) of age-0 freshwater drum sampled on outside bends in October 1997 and 1998 at three sites in the lower channelized Missouri River. Bars within each graph that have the same letter are not significantly different ( $P > 0.05$ ).

TABLE 1.—Water temperature conditions for sites 1, 2, and 3 in the lower channelized Missouri River between mid-October 1997 and March 1998 and between mid-October 1998 and March 1999.

Year	Site	Number of days	Median water temperature (°C)	25–75% water temperature quartiles	Number of days $\geq 9^{\circ}\text{C}$	Number of days $\leq 5^{\circ}\text{C}$	Degree-days $\leq 5^{\circ}\text{C}$
1997–1998	1	155	3.3	1.1–6.1	25	107	293
	2	154	3.9	2.5–5.6	22	95	234
	3	141	4.4	3.3–6.1	20	84	167
1998–1999	1	157	5.6	3.3–10.0	45	72	135
	2	146	5.6	2.8–9.7	40	62	162
	3	146	5.6	3.3–8.9	36	56	148

weight ( $r = -0.51$ ,  $P = 0.06$ ), and mean  $K_n$  ( $r = -0.08$ ,  $P = 0.78$ ) of age-0 freshwater drum in October 1997. For October 1998, there were no significant correlations between  $C/f$  of age-0 freshwater drum and mean length ( $r = 0.18$ ,  $P = 0.52$ ), mean weight ( $r = 0.17$ ,  $P = 0.55$ ), and mean  $K_n$  ( $r = 0.19$ ,  $P = 0.50$ ). Total  $C/f$  in October 1998 was not significantly correlated with mean length ( $r = -0.21$ ,  $P = 0.45$ ), mean weight ( $r = -0.22$ ,  $P = 0.43$ ), and mean  $K_n$  ( $r = -0.12$ ,  $P = 0.68$ ) of age-0 freshwater drum.

#### *Overwinter Water Temperature, Feeding, and Assessment of Mortality*

Duration of the growing season and winter water temperature conditions varied between years. Following October samples, water temperature remained at or above  $9^{\circ}\text{C}$  for 20–25 d in 1997 and 36–45 d in 1998 (Table 1). Significant differences in winter water temperature were detected in 3-site  $\times$  2-year Kruskal–Wallis test ( $P < 0.0001$ ). However, the differences resulted primarily from between-year comparisons within sites. The median water temperature was significantly colder ( $P < 0.05$ ) during the 1997–1998 than the 1998–1999 winters at site 1 and site 2, but was similar ( $P > 0.05$ ) at site 3 between years (Table 1). No significant differences ( $P > 0.05$ ) in winter water temperatures occurred among sites within years (Table 1). The severity of winter conditions was greater during the 1997–1998 winter than during the 1998–1999 winter. There were 84–107 d that water temperature was less than or equal to  $5^{\circ}\text{C}$  during the 1997–1998 winter, but there were only 56–72 d during the 1998–1999 winter that water temperature was less than or equal to  $5^{\circ}\text{C}$ . Similarly, the number of degree-days that water temperature was less than or equal to  $5^{\circ}\text{C}$  was greater during the 1997–1998 winter (167–293) than the 1998–1999 winter (148–162).

Stomachs from age-0 freshwater drum during all sampling periods (except December 1997 when

no freshwater drum were sampled) contained identifiable food organisms (Table 2). Frequency of occurrence was highest for Diptera and Ephemeroptera in October 1997, but age-0 freshwater drum also consumed Trichoptera, Pelecypoda, and Amphipoda. During November 1997, stomachs from age-0 freshwater drum contained Ephemeroptera, Trichoptera, and Diptera. Recent feeding by the 1997 cohort of freshwater drum sampled from wing dikes in March 1998 was evident, as indicated by the presence Ephemeroptera, Trichoptera, Diptera, Cladocera, and Copepoda taxa. The 1998 cohort of freshwater drum was actively feeding during all sampling periods. In October 1998, Trichoptera and Ephemeroptera taxa had the highest frequency of occurrence in the diet of age-0 freshwater drum, but Diptera, Oligochaeta, Orthoptera, and fish taxa were also present. The diet of age-0 freshwater drum sampled in November and December 1998 was composed primarily of Trichoptera, Ephemeroptera, and Diptera taxa, but Copepoda taxa were also present in the diet during November 1998. Individuals of the 1998 cohort sampled from wing dikes in March 1999 were actively feeding, as indicated by the presence of Cladocera, Trichoptera, Ephemeroptera, Diptera, Collembola, and Copepoda taxa in the diet. The proportion of age-0 freshwater drum with empty stomachs generally increased among October, November, and December samples. Empty stomachs were observed in 52.9% (1998) and 27.8% (1999) of the age-1 freshwater drum sampled from wing dikes in March.

Age-0 freshwater drum on outside bends moved to overwintering habitats, and shifts in size structure occurred between October and December samples in both years. The number of age-0 freshwater drum sampled on outside bends declined between October and November samples (Table 3). Additional declines in the number of age-0 freshwater drum sampled on outside bends occurred between November and December samples. The

TABLE 2.—Number of stomachs examined, percentage of stomachs containing no food items (percent empty), and frequency of occurrence of food taxa found in the stomachs of age-0 freshwater drum sampled during October, November, and December and age-1 freshwater drum sampled during March in the lower channelized Missouri River. No age-0 freshwater drum were sampled in December 1997.

Variable or food item	October		November		December	March	
	1997	1998	1997	1998	1998	1998	1999
Number of stomachs	18	18	17	20	12	17	18
Percent empty	5.6	22.2	70.6	45.0	50.0	52.9	27.8
Frequency of occurrence (%)							
Trichoptera	18	57	20	64	67	24	47
Ephemeroptera	47	57	60	36	67	35	53
Diptera	100	29	20	27	50	12	35
Collembola							41
Cladocera						94	94
Copepoda				27		6	18
Amphipoda	6						
Pelecypoda	18						
Oligochaeta		7					
Orthoptera		7					
Fish		7					

prolonged duration of water temperatures exceeding 9°C in both years, in conjunction with active feeding (Table 2), had an influence on the growth and prewinter size structure of age-0 freshwater drum. Between October and November 1997, mean length decreased 2–27 mm and maximum length decreased 24–37 mm at all sites. However, the minimum length of age-0 freshwater drum sampled between October and November 1997 in-

creased 6–10 mm at all sites. These results suggest that the movement of age-0 freshwater drum from outside bends to overwintering habitats was size-related, and that the growth of smaller individuals occurred between the October and November sampling periods. A similar pattern of size-related movement and growth was observed between October and November 1998 as maximum length decreased 14–22 mm and minimum length increased

TABLE 3.—Sample size and summary statistics for total length of age-0 freshwater drum sampled in the lower channelized Missouri River from outside bends in October, November, and December (1997 and 1998) and age-1 freshwater drum sampled from wing dike pools in March (1998 and 1999).

Site	Year	Month	N	Length (mm)		
				Mean	Minimum	Maximum
1	1997	October	76	123	66	175
		November	26	96	72	138
	1998	March	114	128	91	173
		October	192	119	67	164
		November	32	112	89	150
	December	4	76	63	105	
March	66	146	73	186		
2	1997	October	104	114	61	168
		November	9	103	71	144
	1998	March	19	114	77	153
		October	208	105	59	176
		November	47	113	93	161
	December	11	106	80	148	
March	79	119	88	164		
3	1997	October	146	108	69	181
		November	48	106	78	151
	1998	March	100	111	65	168
		October	99	105	66	154
		November	12	106	83	132
	December	5	90	81	102	
March	6	109	87	148		

17–34 mm. Age-0 freshwater drum during December were either absent from outside bends (1997) or collected in low abundance (1998), and mean length, minimum length, and maximum length decreased between November and December samples.

Assessments of overwinter mortality were restricted to comparisons between October and March samples. The mean length of age-0 freshwater drum between October and March increased 0 to 5 mm during the 1997–1998 winter, and 4 to 27 mm during the 1998–1999 winter (Table 3). The quantile-quantile plots and increment plots suggested that the occurrence of size-selective overwinter mortality varied among sites and between years. Evidence of size-selective overwinter mortality for small individuals occurred at sites 1 and 2 between October 1997 and March 1998 as pre- and postwinter quantiles were significantly related and the slopes were significantly less than 1.0 (Figure 2). Quantile length increments for sites 1 and 2 were inversely related to prewinter length quantiles (Figure 2), with the smallest prewinter quantile length-groups exhibiting the greatest length increases through the winter. There was no evidence of size-selective overwinter mortality of small individuals at site 3 between October 1997 and March 1998 (Figure 2). Pre- and postwinter quantiles for site 3 were significantly related, but the slope of the relationship was significantly greater than 1.0. Quantile length increments for site 3 were positively related to prewinter quantile length-groups (Figure 2).

There was little evidence for size-selective overwinter mortality of small individuals between October 1998 and March 1999. Pre- and postwinter quantile length-groups at sites 1 and 2 were significantly related (Figure 3); however, the slopes were not significantly different from 1.0. There were no significant relationships between quantile length increments and prewinter length quantiles at sites 1 and 2 (Figure 3). The low number ( $N = 6$ ) of age-0 freshwater drum sampled at site 3 in March 1999 precluded assessments of size-selective overwinter mortality at this site.

Relative condition of freshwater drum declined significantly between October and March samples at nearly all sites during both years (Table 4). Mean  $K_n$  decreased 15% (site 1), 9% (site 2), and 9% (site 3) during the 1997–1998 winter. During the 1998–1999 winter, mean  $K_n$  declined 9% (site 1) and 10% (site 2), but was similar at site 3.

## Discussion

### *Prewinter Growth and Condition*

Age-0 freshwater drum exhibited discernable patterns in prewinter growth and condition across the spatial scale studied as evidenced by the consistent pattern of decreasing length, weight, and  $K_n$  of age-0 freshwater drum in October among sites. The lack of significant site-by-year interactions in the growth and condition analyses indicated the trends were consistent among sites between years. These results suggest that prewinter growth and condition of age-0 freshwater drum are influenced by factors that consistently differ among sites. Differences in food production and availability among sites may account for spatially consistent differences in growth. Poulton et al. (2003) found that the mean density of aquatic invertebrates on rock basket artificial substrates declined significantly from upstream to downstream sites in the Missouri River and was 1,802 organisms/L at St. Joseph, Missouri (near site 1), 1,713 organisms/L at Parkville, Missouri (within site 2), and 237 organisms/L at Lexington, Missouri (within site 3). Poulton et al. (2003) suggested that toxicants and pollutants from Kansas City, Missouri, may negatively impact downstream aquatic macroinvertebrate communities. Thus, anthropogenic river modifications and their subsequent impact on food resources provide a possible explanation for the pattern of decreasing growth and  $K_n$  of age-0 freshwater drum among sites. Similarly, the increasing trend in turbidity from upstream to downstream in the Missouri River (Galat et al. 2001) may negatively influence aquatic productivity and macroinvertebrate densities, and consequently suppress growth and condition of age-0 freshwater drum. Rutherford et al. (1995) suggested that growth of freshwater drum in the Mississippi River was enhanced during low turbidity conditions because the macroinvertebrate production and foraging efficiency of freshwater drum were greater under low than high turbidity.

In addition to spatial variations in growth and condition, age-0 freshwater drum exhibited between-year differences in mean length and  $K_n$ ; however, greater mean lengths of the 1997 cohort but higher  $K_n$  of the 1998 cohort suggest differential growth responses of freshwater drum between years. Several factors may account for differences in growth between years. First, Missouri River discharge was 1.1–1.5 times greater in 1997 than in 1998. Therefore, freshwater drum during the 1997 growing season were likely exposed to

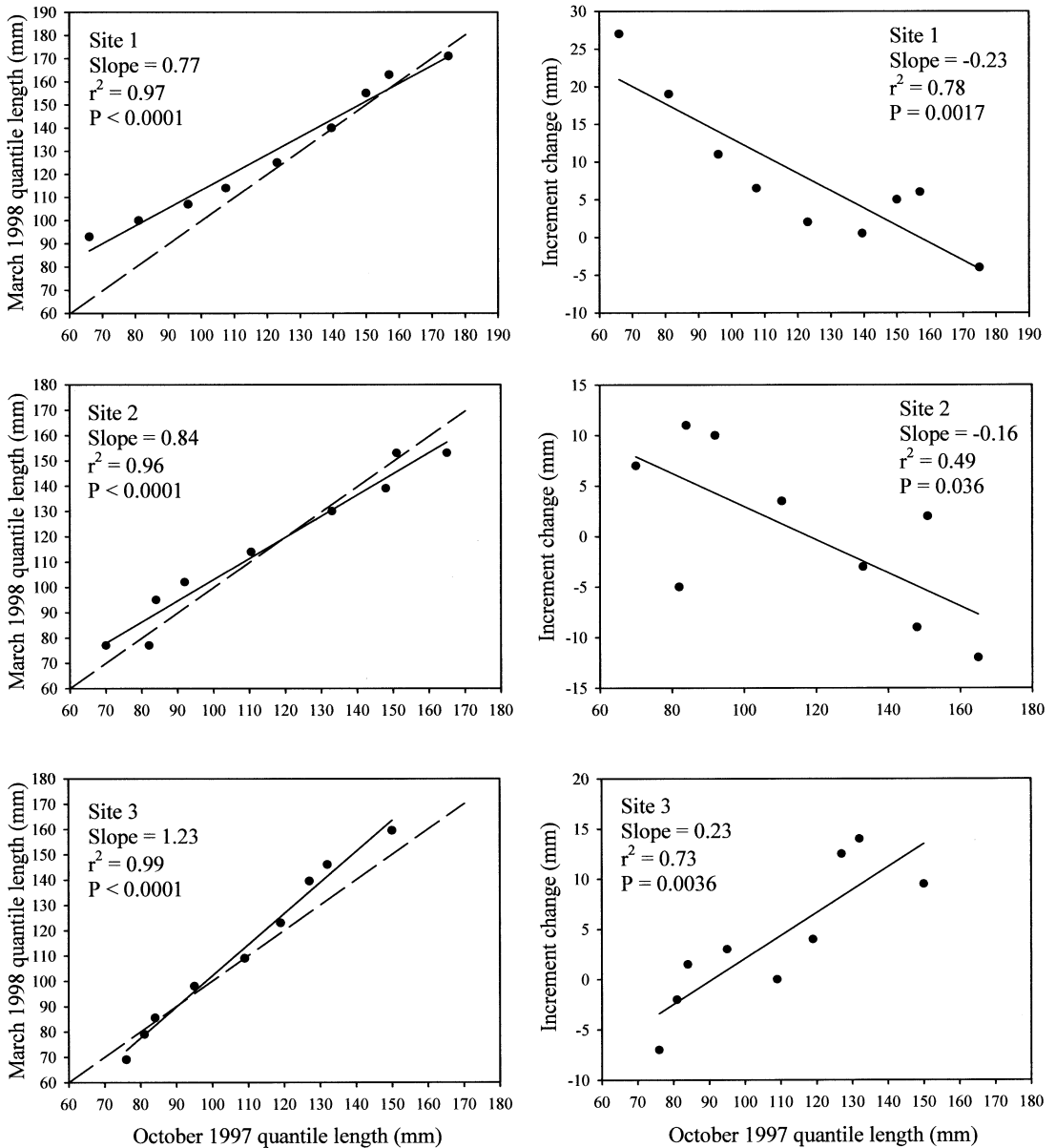


FIGURE 2.—Prewinter (October 1997) and postwinter (March 1998) quantile-quantile plots and growth increment-quantile plots for age-0 and age-1 freshwater drum sampled at sites 1, 2, and 3 in the lower channelized Missouri River. The dashed line on the quantile-quantile plots shows the 1:1 relationship.

higher velocity conditions because velocity increases with increasing discharge in the Missouri River (Slizeski et al. 1982). High velocities may select for larger individuals and inflate mean length (i.e., 1997 year-class) due to selective mortality of smaller individuals (Torralva et al. 1997). A second explanation for the greater length but reduced  $K_n$  of the 1997 cohort of freshwater drum

is differential growth allocation between years. This possibility is supported by the finding that mean weight did not differ between years. One mechanism used by fishes to offset greater energetic demands and an increased frictional drag associated with high velocities is to modify body morphology by increasing length (Gordon et al. 1992). The finding that age-0 freshwater drum in

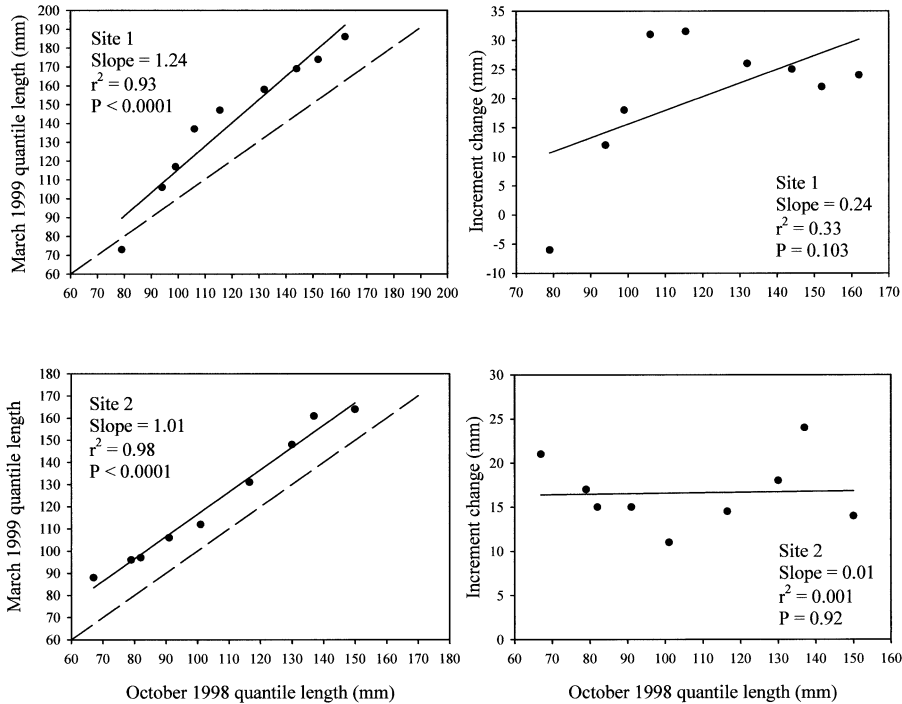


FIGURE 3.—Prewinter (October 1998) and postwinter (March 1999) quantile-quantile plots and growth increment-quantile plots for age-0 and age-1 freshwater drum sampled at sites 1 and 2 in the lower channelized Missouri River. The dashed line on the quantile-quantile plots shows the 1:1 relationship.

1997 were more streamlined (i.e., longer) than in 1998 and weighed less for a given length (i.e., lower  $K_n$ ) supports this explanation. Several studies have documented phenotypic plasticity in fishes in response to gradients of environmental conditions (Beacham et al. 1988; Beacham et al. 1989; Holopainen et al. 1997; Torralva et al. 1997). The labile nature of phenotypic plasticity (as in Scheiner 1993) supports the hypothesis that the body

morphology of age-0 freshwater drum may respond fairly quickly (e.g., within a growing season) to changes in Missouri River discharge and velocity. For example, Holopainen et al. (1997) demonstrated that changes in the body morphology of crucian carp *Carassius carassius* could be environmentally induced, with complete phenotypic change occurring in 3 months.

TABLE 4.—Mean (relative condition ( $K_n$ ; SD in parentheses) for the 1997 and 1998 cohorts of freshwater drum sampled at sites 1, 2, and 3 in the lower channelized Missouri River during October and March. Mean  $K_n$  between months within cohorts differed significantly ( $t$ -tests,  $P < 0.05$ ) at all sites, except the 1998 cohort at site 3. Values in brackets are sample sizes.

Site	1997 cohort		1998 cohort	
	October 1997	March 1998	October 1998	March 1999
1	103 (7.4) [76]	88 (6.5) [114]	110 (9.0) [192]	100 (7.9) [66]
2	101 (8.3) [103]	92 (4.4) [19]	107 (8.5) [208]	96 (10.4) [79]
3	100 (7.5) [141]	91 (9.7) [100]	103 (7.5) [99]	103 (7.3) [6]

There was little correlative evidence to suggest that the growth and condition metrics of age-0 freshwater drum in October were influenced by density-dependent factors. Other studies have reported that density-dependent factors can influence growth in fishes (Michaletz 1997; Post et al. 1998; Schlosser 1998), but Bayley (1988) presented little evidence that density-dependent factors influenced growth of fishes in flood plain environments. Our results are somewhat surprising given the fact that unlike unmodified flood plain rivers, feeding by fishes in the channelized Missouri River is restricted to main channel habitats, thereby increasing the likelihood for competition.

*Size-Selective Winter Mortality*

Results from this study indicate that the incidence of overwinter mortality of age-0 freshwater

drum varied between years, and that the pattern of overwinter mortality was size-selective. Sites 1 and 2 during the 1997–1998 winter exhibited the strongest evidence for the occurrence of size-selective overwinter mortality of small age-0 freshwater drum. Although size-selective predation has been implicated as a mechanism of size-selective overwinter mortality (Miranda and Hubbard 1994), it is unlikely that piscivores in the lower Missouri River (e.g., flathead catfish, sauger *Sander canadensis* [formerly *Stizostedion canadense*]) could account for the loss of small freshwater drum during winter because piscivory would likely exhibit a consistent size-dependent effect at all sites between years. Conversely, interacting mechanisms related to the length of the prewinter growing season and winter water temperature conditions contributed to the incidence of size-selective overwinter mortality of small freshwater drum. First, the growing season persisted 16–20 d longer in 1998. The longer growing season resulted in greater prewinter  $K_n$  and higher energy reserves based on the positive correlation between body condition and fat content (Anderson and Neumann 1996). Second, winter duration was greater and water temperatures were colder during the 1997–1998 winter than the 1998–1999 winter. Other studies have also indicated that winter severity and winter duration increase the likelihood for size-selective overwinter mortality (e.g., Post and Evans 1989; Hurst and Conover 1998; Fullerton et al. 2000) through one or a combination of factors. Exhaustion of prewinter energy reserves during the longer and colder winter of 1997–1998 is a mechanism that could directly or indirectly contribute to the pattern of size-dependent mortality observed in this study. Although the diet data indicated that freshwater drum were actively feeding during all sampling occasions, feeding during both winters was insufficient to maintain  $K_n$  values at prewinter levels as evidenced by a decline in  $K_n$  through both winters. However, age-0 freshwater drum from the 1997 cohort had lower pre- and postwinter  $K_n$  than the 1998 cohort. Although the use of energy reserves is reduced at cold relative to warm water temperatures (Schultz and Conover 1999), rates of decline in  $K_n$  were similar between the colder 1997–1998 winter (9–15%) and warmer 1998–1999 winter (9–10%, excluding site 3 which had a low sample size). Despite colder temperatures and the reduced use of energy reserves, the longer duration of the 1997–1998 winter necessitated prolonged utilization of stored energy reserves. Hurst et al. (2000) also found that striped

bass *Morone saxatilis* depleted similar amounts of energy reserves during cold (15.8%) and warm (14.9%) winters, but the former occurred over a 100-d period and the latter occurred over a 26-d period in late winter. In a related study, Bodensteiner and Lewis (1992) concluded that energy depletion through winter was not the cause of incapacitation (and presumably death) of freshwater drum in the Mississippi River. This conclusion was based on the finding that dead freshwater drum sampled in March from the main-stem Mississippi River and healthy individuals from backwater habitats had similar condition values, liver somatic index values, and percent body fat in late winter (i.e., March); however, Bodensteiner and Lewis (1992) did not quantify changes in body condition and energy reserves between fall and winter samples.

A third mechanism that can contribute to overwinter mortality in fishes is the impairment of osmoregulatory processes. The severity of osmoregulatory impairment in freshwater drum (Bodensteiner and Lewis 1992) and other fishes (Johnson and Evans 1996) is greater at colder than warmer water temperatures. For example, osmoregulatory impairment was implicated as the cause of winter mortality in freshwater drum by Bodensteiner and Lewis (1992) who found that mortality of freshwater drum in simulated winter conditions for 0–45 d and 91–135 d was greater at 1°C than at 5°C and 10°C. Although Bodensteiner and Lewis (1992) did not elaborate on size-dependent mortality related to osmoregulatory impairment, small individuals can be more susceptible to osmoregulatory dysfunction and ultimately death compared with larger individuals (Johnson and Evans 1996).

In contrast to sites 1 and 2, there was a lack of evidence for size-selective overwinter mortality of small freshwater drum at site 3 during the 1997–1998 winter. Given that winter duration and severity at this site were similar to conditions at sites 1 and 2, one would expect a similar incidence of size-selective overwinter mortality of small freshwater drum at site 3. Two factors may account for the inconsistency. First, wing dike pools at site 3 may provide more suitable overwinter habitat for freshwater drum. For example, Newcomb (1989) found that depth, velocity, and substrate were important factors influencing the suitability of wing dikes as overwinter habitat for channel catfish in the channelized Missouri River. We did not collect detailed habitat data in the wing dikes to further elaborate on this hypothesis. A second explanation

for the lack of size-selective overwinter mortality at site 3 relates to differences in the date of sampling. Wing dikes at site 3 in March 1998 were sampled 13–14 d earlier than at site 1 and site 2. Therefore, samples of overwintering freshwater drum from site 3 did not reflect the same cumulative exposure to winter duration and severity as exhibited by samples of freshwater drum at site 1 and site 2. Although studies indicate that mortality can occur throughout the winter period (e.g., Hurst and Conover 1998), there is also evidence to suggest that overwinter mortality may be episodic and occur primarily near the end of winter. For example, Kirjasniemi and Valtonen (1997) found age-0 roach *Rutilus rutilus* maintained under simulated winter conditions exhibited minimal mortality between late November and February, but incurred increased rates of size-dependent mortality between late February and late March. Hurst et al. (2000) found striped bass depleted energy reserves over a 26-d period only during late winter.

The cold water temperatures that occurred through the 1997–1998 winter were more characteristic of typical overwinter conditions than the warmer water temperatures that occurred during the 1998–1999 winter. For example, in the five winters preceding this study, 60–78% of the days between mid-October and mid-March at site 1 were represented by water temperatures less than or equal to 5°C. Comparatively, 69% of the daily water temperatures at site 1 during the 1997–1998 winter were less than or equal to 5°C. In contrast, only 46% of the daily water temperatures at site 1 during the 1998–1999 winter were less than or equal to 5°C. These results suggest that age-0 freshwater drum in the lower channelized Missouri River are regularly exposed to severe winter water temperatures that enhance the likelihood for size-selective overwinter mortality. Thus, these results cumulatively imply that recruitment of freshwater drum in the lower channelized Missouri River is influenced by size-selective overwinter mortality during some years.

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