

Influence of Cladoceran Composition and Abundance on Survival of Age-0 Paddlefish

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Abstract.—We evaluated the influence of prey composition and abundance on survival and growth of age-0 paddlefish *Polyodon spathula* in 0.5-ha rearing ponds. Cladoceran abundance was measured in the spring of 1999 ($n =$ four ponds), 2000 ($n =$ six ponds) and 2005 ($n =$ five ponds) at Gavin's Point National Fish Hatchery, South Dakota. Using an information theoretic approach, we found that density of small cladocerans (e.g., *Bosmina*) at the time of larval stocking was the best supported model in explaining paddlefish survival. In contrast, estimates of *Daphnia* abundance (initial, mean, and maximum density) were poor predictors of paddlefish survival. Neither the magnitude of *Daphnia* abundance nor whether abundance was increasing or decreasing in the ponds after stocking appeared to influence paddlefish survival. Paddlefish growth, however, was positively related to mean *Daphnia* abundance in ponds. These patterns highlight the need to better understand larval feeding ecology of paddlefish and the role of electrosensory detection as it relates to prey composition and abundance.

Introduction

The larval stage of fishes represents a critical period in their life history and significant mortality at this stage can ultimately determine fish production (Zaret 1980). For paddlefish *Polyodon spathula* larvae, high mortality generally coincides with the transition to exogenous feeding, a period lasting from about 12–20 d after hatching (Kroll et al. 1994). Because energy acquisition can influence larval survival, it follows that prey availability during this critical period can have strong effects on paddle-

fish survival and production. In natural settings, a mismatch in the timing between larvae and their prey can lead to reduced survival and recruitment (Cushing 1990).

As particulate feeders, small paddlefish (<120 mm total length [TL]) rely on the rostrum and associated ampullae to detect and locate prey (Wilkens et al. 2002; Wilkens and Hofmann 2007). Unlike large, filter feeding paddlefish that exhibit little selectivity for crustacean zooplankton (but see Rosen and Hales 1981; Kozfkay and Scarnecchia 2002), small paddlefish (<120 mm TL) are highly selective for cladoceran prey (Michaletz et al. 1982). In rearing ponds, growth rate of small paddlefish is often

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positively associated with *Daphnia* density (Michaletz et al. 1982; Mims and Shelton 2005).

Relationships among paddlefish growth, survival, and zooplankton abundance can be complex. In Missouri ponds, total survival of age-0 paddlefish measured from May to September was positively related to larval growth rates (May to June; Michaletz et al. 1982). However, total survival (May to September) was inversely related to total growth for the same time period (May to September), implying that survival of paddlefish larvae is set shortly after stocking. Thus, the composition and abundance of prey during early exogenous feeding stages (i.e., larval stocking) likely has an important influence on growth and survival of age-0 paddlefish.

In this study, we explore the influence of prey composition and abundance on survival and growth of age-0 paddlefish. Given the importance of cladoceran zooplankton, we evaluate several hypotheses related to the timing, abundance, and composition of cladoceran prey in paddlefish rearing ponds. We discuss implications of prey availability for larval paddlefish and highlight the need for additional work on larval feeding ecology.

Methods

Paddlefish Source

Age-0 paddlefish are annually produced at the U.S. Fish and Wildlife Service's Gavin's Point National Fish Hatchery in Yankton, South Dakota and stocked into the Missouri River as part of paddlefish restoration efforts. In May of 1999, 2000, and 2005, paddlefish eggs and milt were obtained from broodstock collected from Lewis and Clark Reservoir and/or Lake Francis Case, South Dakota (Stancill et al. 2002). Eggs and milt were transported to the hatchery where eggs were fertilized and incubated indoors. After hatching, larvae were then

acclimated to pond water for 2–3 d prior to stocking into rearing ponds.

Paddlefish Survival and Growth

A total of twelve 0.5-ha ponds were used to rear age-0 paddlefish in all 3 years. Three of these ponds were used in both 1999 and 2000. Prior to stocking paddlefish larvae, ponds were filled with water from Lewis and Clark Reservoir and allowed to establish natural algae and zooplankton populations for 7–12 d (Graham 1986; Mims et al. 1995). Paddlefish were stocked at a density of 56,600 larvae/ha during the first week of June 1999 ($n =$ four ponds) and 2000 ($n =$ six ponds). Stocking protocols in 2005 differed from those in 1999 and 2000. In 2005, paddlefish were stocked in five ponds at a density of 58,390 larvae/ha and larvae were held in net pens for 5-d poststocking. Each year, ponds were fertilized twice a week with alfalfa meal and/or chopped hay (Graham et al. 1986). In 1999, each pond received a total of about 298 kg of alfalfa meal. In 2000, each pond was fertilized with a total of 136 kg of alfalfa meal and 310 kg of chopped hay, and in 2005, ponds each received about 230 kg of alfalfa meal.

After 5 weeks, all ponds were drained and paddlefish fingerlings were enumerated and weighed to estimate survival (%) and yield (kg/ha). Fifty to 70 paddlefish from each pond were also measured for total length (mm) and body mass (g). We compared paddlefish survival and yield among years using analysis of variance (ANOVA). Survival estimates were transformed ($\arcsin \sqrt{\text{survival}}$) prior to analysis (Krebs 1989) and Tukey's multiple comparison test was used to detect year-to-year differences in survival and yield (SAS Institute Inc. 1999). Relationships among paddlefish growth (final mass, g), survival, and yield were evaluated using correlation analysis (SAS Institute Inc. 1999).

Zooplankton Composition and Abundance

Initial prey availability.—To evaluate initial zooplankton composition and abundance, we sampled crustacean zooplankton within 24 h of stocking paddlefish larvae in 1999, 2000, and 2005. In each pond, we selected three sampling sites (~15 m apart) from open water areas with water depths greater than 2 m. Zooplankton were collected from each pond ($n =$ three sites per pond) between 1300 and 1500 hours using a conical-shaped plankton net (18 cm diameter, 150 μm mesh) that was pulled vertically from the pond bottom to the surface. Zooplankton were then rinsed into specimen containers and preserved in 5% Lugol's solution. In the laboratory, zooplankton were identified to genus and enumerated. Only cladoceran zooplankton were included in analyses because of their importance to young paddlefish (Rosen and Hales 1981; Michaletz et al. 1982; Mims and Schmittou 1989). Density of cladoceran zooplankton was averaged from samples ($n = 3$) taken from each pond and expressed as number per liter.

Temporal patterns in prey availability.—Temporal patterns in cladoceran abundance and composition were evaluated in 1999 ($n =$ four ponds) and 2000 ($n =$ six ponds). In both years, we collected zooplankton once a week during the 5-week rearing phase. Each week, zooplankton were collected from three sampling sites per pond, as previously described. In the laboratory, all cladoceran zooplankton were identified and enumerated. We compared patterns in cladoceran abundance using a two-factor repeated measures ANOVA, with zooplankton taxa (i.e., *Daphnia* or *Bosmina*) and sampling week as grouping factors.

Model Development and Analysis

Initial prey availability.—We developed a set of four candidate models to evalu-

ate the relative influence of zooplankton composition and abundance on paddlefish survival. Zooplankton data collected within 24 h of stocking larval paddlefish were used to quantify initial prey availability in 1999 ($n = 4$), 2000 ($n = 6$), and 2005 ($n =$ five ponds). Measures of initial prey availability included (1) the abundance of large cladocerans (primarily *Daphnia*, length = 1.30 mm, SE = 0.07), (2) the abundance of small cladocerans (primarily *Bosmina*, length = 0.35 mm, SE = 0.01), (3) total cladoceran abundance, and (4) an index of foraging potential (IFP). The IFP was calculated as *Bosmina* density divided by the sum of *Bosmina* plus *Daphnia* abundance and is based on the planktivory index of Kitchell and Kitchell (1980). When size-selective predation occurs via foraging on larger cladocerans (i.e., *Daphnia*), IFP values generally increase (Amsinck et al. 2003). In our study, we calculated zooplankton abundance within 24 h of stocking paddlefish larvae, when effects of size-dependent planktivory would likely be negligible. Hence, we postulated that lower IFP values represented greater foraging potential for paddlefish at the time of stocking if size-selective predation is important.

Temporal patterns in prey availability.—To evaluate patterns in zooplankton abundance and their effects on paddlefish survival, we evaluated five candidate models that included mean and maximum densities of both large (*Daphnia*) and small (*Bosmina*) cladocerans during the 5-week rearing phase. We also estimated the change in *Daphnia* density during the first 2 weeks of rearing (i.e., week 2 – week 1), to evaluate the influence of increasing or decreasing *Daphnia* abundance on paddlefish survival. Weekly zooplankton data collected in 1999 ($n = 4$) and 2000 ($n =$ six ponds) were used to quantify temporal patterns in cladoceran abundance over the 5-week rearing phase.

Model selection.—We used an information theoretic approach (Akaike 1973;

Burnham and Anderson 1998) to evaluate the relative support among competing models given our observations for each data set. Akaike's information criterion (AIC values) was used to calculate Akaike weights. Evidence ratios, calculated as the ratio of Akaike weights (i.e., w_i for model i/w_j for model j) were then used to select the best model for explaining variation in paddlefish survival (Burnham and Anderson 1998). AIC values were computed as

$$\text{AIC} = N \log(\hat{\sigma}^2) + 2K,$$

where N is the number of observations, $\hat{\sigma}^2$ is the residual sums of squares from least square regression, and K is the number of estimable parameters in the model (including the intercept and σ^2). We adjusted the AIC value to account for small sample size (AIC_c value) using the equation

$$\text{AIC}_c = \text{AIC} + \frac{2K(K+1)}{N-K-1}.$$

Because two data sets were used to evaluate the influence of zooplankton abundance on paddlefish survival (e.g., initial versus temporal), it was not possible to compare or rank models from the different analyses. Inference from each analysis was conditional on the data used as input.

Results

Paddlefish Survival and Growth

Survival of age-0 paddlefish ranged from 0% to 55% and varied significantly among years ($F_{2,12} = 4.32$, $P = 0.03$). Mean survival was higher in 1999 than in 2000 ($P < 0.05$; Table 1). Similarly, paddlefish yield varied significantly among years ($F_{2,12} = 4.82$, $P = 0.03$) ranging from 0 to 388 kg/ha and was lower in 2000 than in 1999 and 2005 ($P < 0.05$; Table 1). Although variable, paddlefish yield was strongly related to fish survival ($n = 15$, $r = 0.77$, $P < 0.001$; Figure 1). In contrast, yield was not related to mean growth of age-0 fish ($n = 15$, $r = -0.28$, $P = 0.30$). However, growth was inversely related to total survival ($n = 15$, $r = -0.71$, $P = 0.005$), implying that fish production was influenced more by survival than by mean growth of age-0 paddlefish.

Zooplankton Composition and Abundance

Initial prey availability.—*Daphnia* spp. and *Bosmina* spp. represented more than 90% of total cladoceran abundance in rearing ponds. Other cladocerans included *Ce-*

Table 1. Estimates of mean survival, yield, and mass of age-0 paddlefish reared in 0.5-ha ponds at Gavin's Point National Fish Hatchery, Yankton, South Dakota in 1999, 2000, and 2005. Density of *Bosmina* and *Daphnia* are included for each year and represent mean densities within 24 h of stocking paddlefish larvae. For each column, values with the same letter(s) are not significantly different (Tukey's multiple comparison test, $P > 0.05$). Values in parentheses represent 1 SE.

Year	<i>n</i>	Age-0 paddlefish			Initial zooplankton abundance	
		Mean survival (%)	Mean yield (kg/ha)	Mean fish mass (g)	Mean <i>Bosmina</i> density (no./L)	Mean <i>Daphnia</i> density (no./L)
1999	4	32 (9) a	185.4 (62.5) a	13.3 (4.1) a	93.1 (18.7) a	14.3 (5.3) a
2000	6	5 (2) a	30.2 (13.1) b	19.6 (3.9) a	28.3 (5.3) b	48.3 (12.7) b
2005	5	18 (8) ab	189.6 (54.3) a	20.7 (5.5) a	90.5 (15.5) a	18.4 (6.4) a

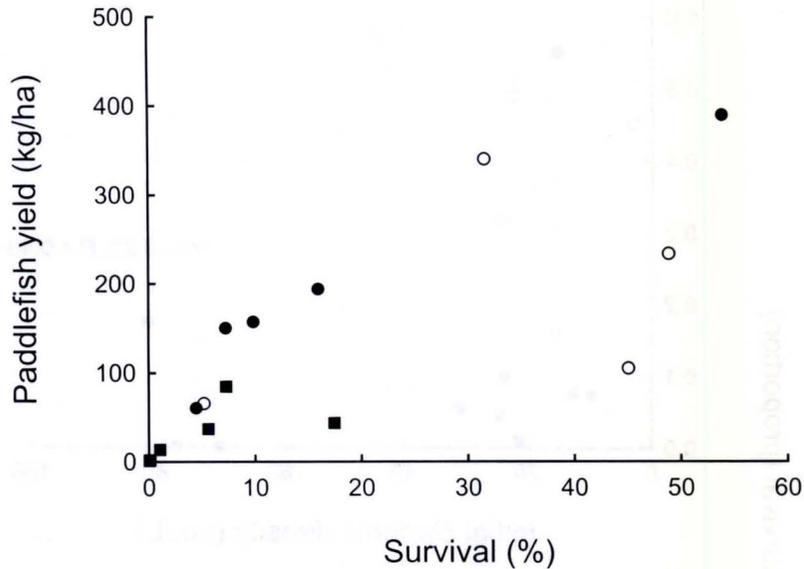


Figure 1. Relationship between yield (kg/ha) and survival (%) for age-0 paddlefish reared in 0.5-ha ponds at Gavin's Point National Fish Hatchery, Yankton, South Dakota ($r = 0.77$, $P < 0.001$; $\circ = 1999$, $\blacksquare = 2000$, $\bullet = 2005$).

riodaphnia spp. (9%) and *Moina* spp. (<1%). Mean initial *Daphnia* abundance in the ponds varied significantly among years (ANOVA; $F_{2,12} = 4.1$, $P = 0.04$) and was higher in the spring of 2000 than in 1999 or 2005. Similarly, mean initial *Bosmina* density varied significantly among years ($F_{2,12} = 8.29$, $P = 0.005$) but was lower in 2000 than in 1999 or 2005 ($P < 0.05$; Table 1).

Modeling results revealed that *Bosmina*

density and total cladoceran abundance at the time of larval stocking were the best supported models in predicting age-0 paddlefish survival (Table 2). The IFP and *Daphnia* abundance at the time of stocking were not well supported. The evidence ratio for the best model (*Bosmina*) versus *Daphnia* was 70, implying that initial *Daphnia* density in the ponds was a poor estimator of paddlefish survival (Figure 2).

Table 2. Models used to explore variation in paddlefish survival for fish reared in 0.5 ha-ponds in 1999 ($n = 4$), 2000 ($n = 6$), and 2005 ($n = 5$) at Gavin's Point National Fish Hatchery, Yankton, South Dakota. Initial density of small (*Bosmina*) and large (*Daphnia*) cladocera was estimated within 24 h of stocking paddlefish larvae into rearing ponds ($n = 15$). The index of foraging potential (IFP) was calculated as *Bosmina* density divided by the sum of *Bosmina* plus *Daphnia* density in each pond. K = the number of estimable parameters in the model. AIC_c = adjusted Akaike's Information Criterion to account for small sample size. ΔAIC_c = the change in AIC_c . w_i = Akaike weight, model i .

Model	n	K	AIC_c	ΔAIC_c	w_i
<i>Bosmina</i>	15	3	-22.50	0	0.70
<i>Bosmina</i> + <i>Daphnia</i>	15	4	-20.56	1.95	0.26
IFP	15	3	-16.03	6.48	0.03
<i>Daphnia</i>	15	3	-14.78	7.73	0.01
Global	15	5	-11.84	10.66	0.00

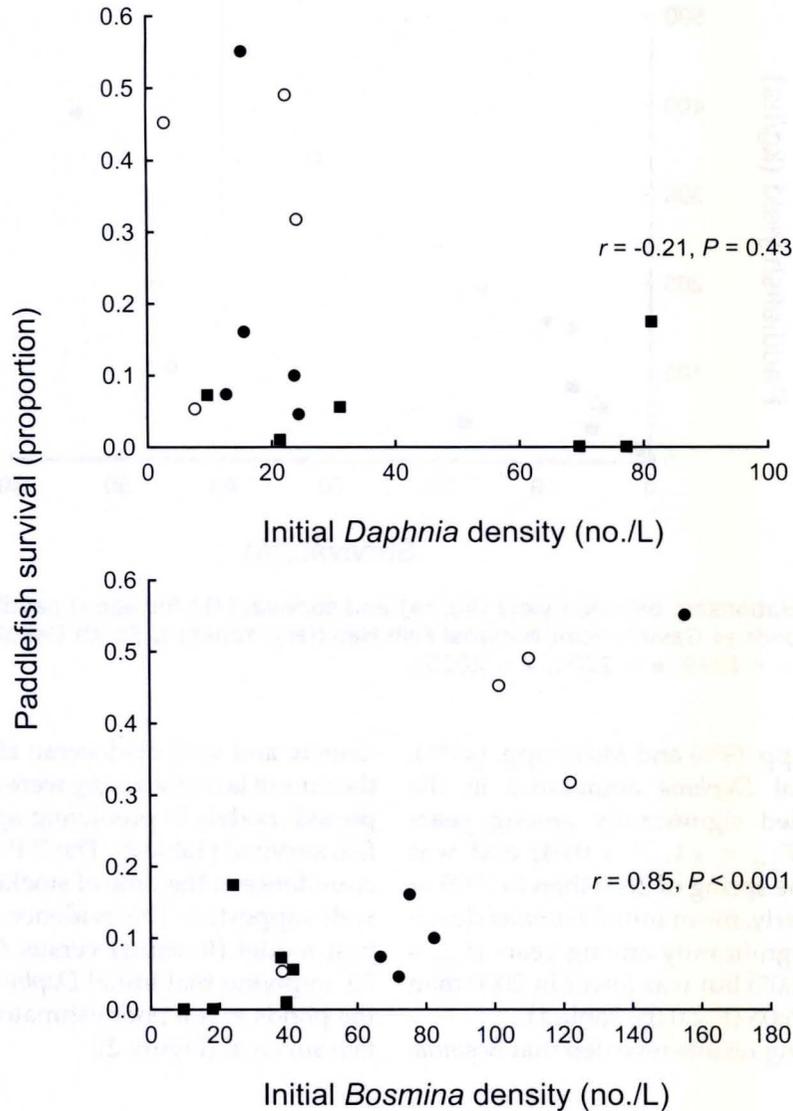


Figure 2. Relationship between age-0 paddlefish survival and initial density of *Daphnia* (top) or *Bosmina* (bottom) in 0.5-ha rearing ponds at Gavin's Point National Fish Hatchery, Yankton, South Dakota. Paddlefish larvae were stocked in June 1999, 2000, and 2005 (\circ = 1999; \blacksquare = 2000; \bullet = 2005). Pearson's correlation coefficient and significance level are given.

Temporal patterns in prey availability.— Mean weekly density of cladoceran zooplankton varied significantly in 1999 ($F_{4,20} = 6.46$, $P = 0.001$) and 2000 ($F_{4,40} = 14.4$, $P < 0.0001$). In 1999, mean *Daphnia* abundance in the ponds ($\bar{x} = 20.1/L$) was similar to that observed for *Bosmina* ($\bar{x} = 22.8/L$;

$F_{1,6} = 0.09$, $P = 0.77$). However, densities of each taxa varied differently with time (taxa \times week interaction, $F_{4,20} = 7.61$, $P = 0.007$); *Bosmina* density was highest at the time of larvae stocking (93.1/L) and declined to less than 0.5/L by the end of the rearing phase. Over the same time period, mean

Daphnia density peaked (52.4/L) during the second week of rearing and declined to 2.5/L after 5 weeks (Figure 3). In 2000, we observed similar trends for *Bosmina* as in 1999, with highest abundance (mean = 28.3/L) observed at the time of stocking and decreasing to less than 0.2/L by the second week. On the average, *Bosmina* abundance was appreciably lower in 2000 (6.1/L) than in 1999 (22.8/L). In contrast, temporal patterns in *Daphnia* abundance differed from those observed in 1999. In

2000, *Daphnia* abundance was highest at the time of stocking (48.4/L) and declined to 5.2/L after 5 weeks. Moreover, mean *Daphnia* abundance (24.3/L) was significantly higher than *Bosmina* abundance in 2000 ($F_{1,10} = 55.7, P < 0.0001$; Figure 3).

Estimates of both maximum and mean *Bosmina* abundance were the best supported models for explaining variation in paddlefish survival (Table 3). Because maximum *Bosmina* density was observed at the time of larval stocking, this finding corroborated

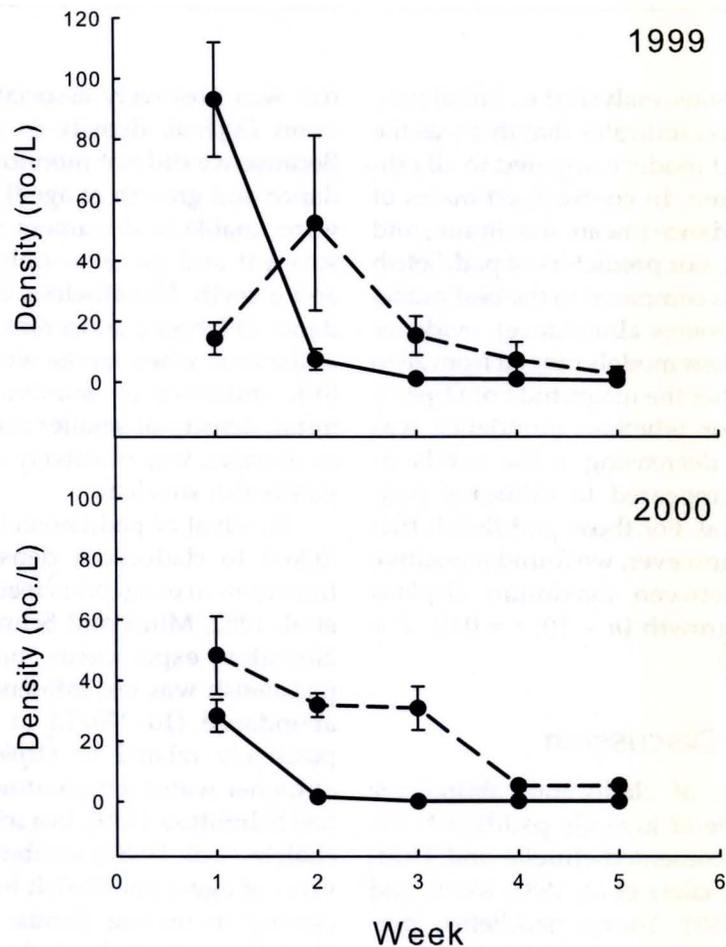


Figure 3. Patterns in *Bosmina* (solid line) and *Daphnia* (dashed line) abundance in paddlefish rearing ponds sampled in 1999 (top, $n = 4$) and 2000 (bottom, $n = 6$) at Gavin's Point National Fish Hatchery, Yankton, South Dakota. Ponds were stocked with paddlefish larvae on June 4, 1999 or June 7, 2000, corresponding to week 1. Error bars represent ± 1 standard error.

Table 3. Models used to explore variation in paddlefish survival for fish reared in 0.5-ha ponds in 1999 ($n = 4$) and 2005 ($n = 5$) at Gavin's Point National Fish Hatchery, Yankton, South Dakota. Maximum and mean densities for *Bosmina* and *Daphnia* were estimated from weekly samples ($n = 5$) collected from rearing ponds ($n = 10$). Change in *Daphnia* abundance ($\Delta Daphnia$) represents the difference in *Daphnia* density from week 1 to week 2 (i.e., week 2 - week 1). K = the number of estimable parameters in the model. AIC_c = adjusted Akaike's Information Criterion to account for small sample size. ΔAIC_c = the change in AIC_c . w_i = Akaike weight, model i .

Model	n	K	AIC_c	ΔAIC_c	w_i
Maximum <i>Bosmina</i> density	10	3	-13.25	0	0.57
Mean <i>Bosmina</i> density	10	3	-12.44	0.81	0.38
Mean <i>Daphnia</i> density	10	3	-6.70	6.56	0.02
Maximum <i>Daphnia</i> density	10	3	-6.13	7.13	0.02
$\Delta Daphnia$	10	3	-4.98	8.28	0.01
Global	10	6	16.41	29.67	0.00

rates our previous analysis (i.e., initial prey availability) and indicates that this was the best supported model compared to all other models tested. In contrast, estimates of *Daphnia* abundance (mean, maximum, and change) were poor predictors of paddlefish survival; when compared to the best model (maximum *Bosmina* abundance), evidence ratios for *Daphnia* models ranged from 28 to 57. Thus, neither the magnitude of *Daphnia* abundance nor whether abundance was increasing or decreasing in the ponds after stocking appeared to influence paddlefish survival. For those paddlefish that did survive, however, we found a positive correlation between maximum *Daphnia* density and growth ($n = 10$, $r = 0.61$, $P = 0.05$; Figure 4).

Discussion

The influence of cladoceran abundance on growth rate of juvenile paddlefish has been well documented (Ruelle and Hudson 1977; Michaletz et al. 1982; Mims and Schmittou 1989). Young paddlefish prefer cladoceran prey and exhibit increased growth in ponds where cladoceran abundance is high (Michaletz et al. 1982; Mims and Shelton 2005). Similarly, we found that total growth of young-of-the-year paddle-

fish was positively associated with maximum *Daphnia* density in rearing ponds. Because we did not monitor weekly abundance and growth of age-0 paddlefish, we were unable to document size-dependent survival and growth—only total survival and growth. Nonetheless, the initial abundance of larger cladocerans (e.g., *Daphnia*), at the time when larvae were stocked, had little influence on survival, whereas the initial density of smaller cladocerans, such as *Bosmina*, was positively associated with paddlefish survival.

Survival of paddlefish larvae has been linked to cladoceran density during the transition to exogenous feeding (Michaletz et al. 1982; Mims and Schmittou 1989). In laboratory experiments, survival of larval paddlefish was not influenced by *Daphnia* abundance (10–270/L) at 15°C but was positively related to *Daphnia* abundance at higher water temperatures (21°C; Mims and Schmittou 1989). In a related study, Michaletz et al. (1982) attributed higher survival of age-0 paddlefish to mean *Daphnia* density in rearing ponds. Initial *Daphnia* abundance in their study, however, was noticeably higher (70–140/L) than that observed in our study (14–48/L). In contrast, the composition of smaller cladocerans was higher in our study (72% of total

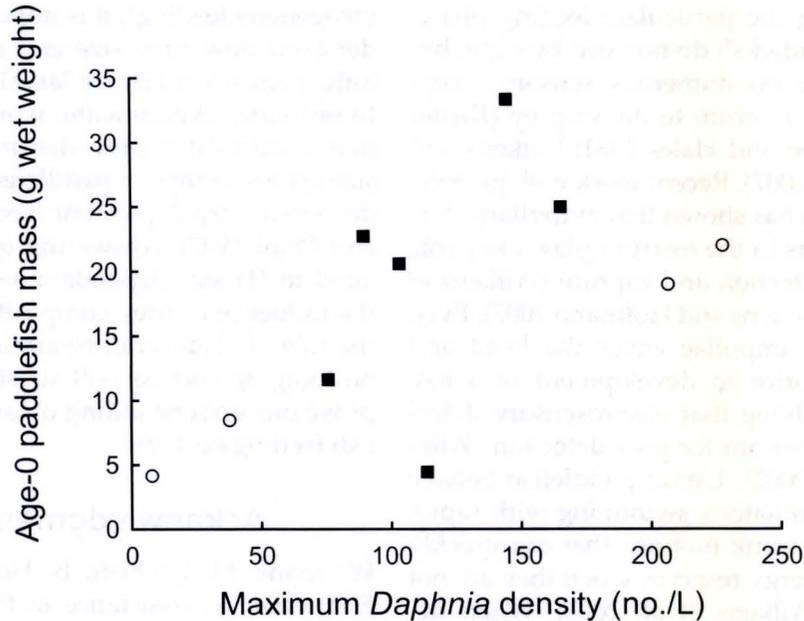


Figure 4. Relationship between paddlefish growth (mean mass, g) and maximum *Daphnia* density observed in 0.5-ha rearing ponds at Gavin's Point National Fish Hatchery, Yankton, South Dakota (○ = 1999, ■ = 2000; $r = 0.61$, $P = 0.05$).

cladoceran abundance) compared to that (43%) reported by Michaletz et al. (1982). The abundance of *Daphnia* and *Bosmina* often vary inversely owing to seasonal succession and/or size-selective predation by fishes (DeMott and Kerfoot 1982). Because the relative abundance of different prey can influence prey selection (Mills et al. 1986), consumption of either *Daphnia* or *Bosmina* by larval paddlefish may vary depending on the density of each taxa. Moreover, high density *Daphnia* populations likely contain a broad size range of individuals that would provide an opportunity for larval paddlefish to consume smaller individuals. To our knowledge, this has not been evaluated in studies of larval paddlefish diets.

The importance of small cladocerans to growth and survival of paddlefish larvae is not well documented. Like larger cladocerans, small cladocerans are frequently reported in the diet of young paddlefish (Ros-

en and Hales 1981; Hoxmeier and DeVries 1997). In the Alabama River, *Bosmina* dominated the diets of juvenile paddlefish (Hoxmeier and DeVries 1997). In many young fishes, prey selectivity changes as fish grow from larvae to early juveniles (Keast 1980; Miller et al. 1990; Schael et al. 1991; Graeb et al. 2004). Experimental work with walleye *Sander vitreus* showed that larvae (<17 mm) selected intermediate-sized cladocerans (0.4–0.9 mm) and avoided consuming larger cladocerans (>1 mm) until they reached a length greater than 17 mm (Mayer and Wahl 1997). Empirical data suggest that diets of young paddlefish vary with body size. In the Missouri River, *Daphnia* were found in about 50% of larval paddlefish diets (15–20 mm) but increased in frequency to 100% as fish attained lengths greater than 30 mm (Ruelle and Hudson 1977). Changes in body size, although small (~10 mm), can have important implications for prey selection by young fishes.

During the particulate feeding phase, young paddlefish do not feed by sight, but rather rely on numerous sensory receptors in the rostrum to detect prey (Kistler 1906; Rosen and Hales 1981; Wilkens and Hofmann 2007). Recent work with juvenile paddlefish has shown that ampullary electroreceptors in the rostrum play a key role in prey detection and capture (Wilkens et al. 2002; Wilkens and Hofmann 2007). Even as larvae, ampullae cover the head and opercula prior to development of a rostrum, implying that electrosensory detection is important for prey detection (Wilkens et al. 2002). Larval paddlefish behave as ram ventilators, swimming with rapid, inefficient trunk motions that can quickly deplete energy reserves when they are not feeding (Wilkens et al. 2002). When deprived of food for short durations (several hours), larval paddlefish become emaciated and eventually die (Mims and Schmittou 1989; Wilkens et al. 2002).

Zooplankton density has direct implications for passive electrosensory detection by particulate feeding paddlefish. Zooplankton are known to emit weak electrical signals from muscular activities associated with swimming and feeding (Freund et al. 2002). Dense swarms of zooplankton produce electrical "noise" that presumably enhance prey detection by young paddlefish (Freund et al. 2002). As a result, the swarming behavior of cladocerans (Jakobsen and Johnsen 1988) may enhance electrosensory detection by paddlefish and influence their foraging efficiency. In 1999, when survival rates were highest, *Bosmina* density in rearing ponds was more than three times higher than that observed in 2000.

Although diet studies frequently document the importance of cladoceran zooplankton to young paddlefish, little attention has been paid to the mean size of prey consumed by larval (<20 mm) versus early juvenile (>20 mm) fish. Because most mortality occurs during the early larval stage

(exogenous feeding), it is important to understand how prey size and composition influences selectivity by larval paddlefish. In our view, experimental work is needed that manipulates prey density and prey size across a range of paddlefish lengths to document size-dependent feeding (Mayer and Wahl 1997). Answering questions related to (1) size-dependent selectivity, (2) the influence of prey composition, and (3) the role of cladoceran swarming behavior on foraging success will substantially improve our understanding of larval paddlefish feeding ecology.

Acknowledgments

We thank M. Drobish, B. Holcomb, and E. Themm for assistance in the field and laboratory. C. Paukert, M. Brown, and two anonymous reviewers provided helpful comments that improved the manuscript. This work was supported in part through research funding and technical assistance provided by the U.S. Fish and Wildlife Service, Gavins Point National Fish Hatchery and the U.S. Geological Survey Cooperative Research Unit, South Dakota State University. The U.S. Geological Survey South Dakota Cooperative Fish & Wildlife Research Unit is jointly sponsored by the U.S. Geological Survey, South Dakota State University, the South Dakota Department of Game, Fish & Parks, the Wildlife Management Institute, and the U.S. Fish and Wildlife Service.

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