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Effect of Size-Grading and Feeding Frequency on Growth and Size Variation of Paddlefish, *Polyodon spathula,* Juveniles Reared in Ponds

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Paddlefish, *Polyodon spathula*, are commercially important as a source of black caviar and boneless meat. Currently, wild capture accounts for most of the production in the United States; however, state agencies are increasingly regulating the wild harvest, while market acceptance and demand are increasing. An opportunity exists for the development of paddlefish aquaculture, which requires production of Phase II juveniles ($\geq$150 g), for stocking in ponds and reservoirs (Mims et al. 2009).

Production of juvenile paddlefish in tanks or ponds results in hierarchic size structures. Gershanovich (1983) reported that growth of individual paddlefish in flow-through tanks was determined by their position in the hierarchy, and size variability increased with increasing density. Size variability is a common problem in intensive fish culture, and both grading and feeding frequency have been studied as methods of amelioration for various species. A study of yellow perch, *Perca flavescens*, showed a decrease in coefficient of variation (CV) and an increase in the number of fish reaching market size in the second year when larger fish were cultured separately from smaller or ungraded groups (Wallat et al. 2005). However, Carmichael (1994) reported that size-graded channel catfish, *Ictalurus punctatus*, repartitioned the size variation within groups, either increasing variation when tightly graded, or decreasing variation from an artificially set higher level, when reared under controlled conditions in tanks. In a study of age-0 hybrid sunfish, F_1: female green sunfish, *Lepomis cyanellus*, $\times$ male bluegill, *Lepomis machrochirus*, Wang et al. (1998) found that increased feeding frequency decreased interindividual size variation among treatments. However, a study of juvenile gibel carp, *Carassius auratus gibelio*, by Zhou et al. (2003) found no such effect. Paddlefish have not been studied for either the effects of size-grading or feeding frequency.

Amelioration of the size variation in groups of pond-reared paddlefish juveniles could reduce feed and, other production costs, as well as the culture period. In this study, the effects of size-grading and increased feeding frequency on growth and size variation in pond-reared juvenile paddlefish were tested.

Methods and Materials

The results of two separate experiments conducted in consecutive years were combined for this study. In both experiments, paddlefish fingerlings were propagated according to Mims and Shelton (2005) from wild broodstock captured in the Ohio River near Louisville, Kentucky, USA.

The paddlefish were fed live zooplankton from the onset of exogenous feeding until reaching average total length of 6 cm, and then trained to accept a 1.6-mm floating trout feed (Rangen EXT 450, 45% protein, 16% lipid, Rangen, Inc., Buhl, ID, USA). Ponds used for both experiments were 0.02 ha research ponds covered with netting and aerated with a 0.37 kW surface aerator. Water quality was maintained within the limits recommended by Mims and Shelton (2005) during both experiments. Water quality monitoring included twice daily measurement of dissolved oxygen and temperature and twice weekly measurement of pH, nitrite, and total ammonia nitrogen.

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Sodium chloride was added to the ponds to maintain chloride concentration above 15 mg/L for protection from nitrite toxicity (Tucker et al. 1989).

In the first experiment, paddlefish from a single cohort, average weight (±SD) 25.1 ± 7.8 g, were graded using an adjustable bar grader into two groups: large and small grade, and stocked into six ponds at 500 paddlefish/pond (24,710/ha), three ponds for each grade. In addition, three ponds were stocked with ungraded paddlefish from the same cohort. The bulk weights and individual weights of 100 randomly selected paddlefish stocked into each pond were recorded. Feeding was begun immediately with a 35% protein 6% lipid floating feed (Rangen EXTR 350, 3.2 mm) at 10% of body weight per day (BWD), fed once per day at 0800 h. Aeration was continuous except for 2 h after feeding. After 35 d, the paddlefish were sampled for weight and the feeding rate was readjusted to 10% BWD. This rate was unchanged until the end of the experiment at 76 d in order to maintain adequate water quality. However, throughout the experiment, sufficient feed remained on the pond surface after cessation of feeding to make an assumption of satiation.

At harvest, the paddlefish from each pond were counted, and 100 randomly selected fish from each pond were weighed individually and recorded. Survival, CV at stocking and harvest, and relative growth were calculated for each group. Survival and relative growth were compared by ANOVA. The data from each group were pooled and tested for normality at time of stocking and harvest using Kolmogorov's goodness of fit test. Miller's jackknife method was used to compare variation between groups. The Kruskal–Wallace test ($n_1 = n_2 = n_3 = 150$) was used to test equality of the probability distributions of each group. Dunn's procedure was used for multiple comparisons under the Kruskal–Wallace Test. Differences were considered significant at Type I probability of 5%.

In the second experiment, paddlefish of average weight (±SD) 8.5 ± 0.2 g were stocked into six ponds, also at the rate of 24,710 paddlefish/ha. The individual weights of 30 randomly selected paddlefish stocked into each pond were recorded. Three replicate ponds were randomly assigned to each of two treatments. Fish in the first treatment were fed once per day (1T/d) at 1400 h. Fish in the second treatment were fed three times per day (3T/d) at 0800, 1400, and 2000 h with the total daily ration equal to the 1T/d treatment. The presence of uneaten feed after feeding activity had stopped, and in the morning of the following day, was assumed to indicate satiation feeding. Aeration was continuous except during a 1-h period at each feeding. The paddlefish were acclimated to the ponds for 6 d, during which time they were fed the 1.6-mm floating trout feed at 4% BWD once per day. The feeding rate was then increased to 25% BWD and the treatment regimen was initiated.

After 22 d, a 3.2-mm floating catfish feed was added to the ration (Rangen Production 35, 35% protein, 6% lipid) at a ratio of 25% catfish feed to 75% trout feed, while the total ration remained unchanged. After 9 d, the paddlefish were sampled for weight and the feeding rate was adjusted to 10% BWD, while the ratio of catfish to trout feed was adjusted to 50% each. After 6 d, the ratio was adjusted to 25% trout feed to 75% catfish feed without changing the total ration. After 3 d, it was decided that the paddlefish were large enough to eliminate the trout feed from the ration.

After 78 d on the regimen, the paddlefish were harvested. The total number of paddlefish harvested from each pond was recorded, along with the individual weights and total lengths (TL) of 30 randomly selected paddlefish from each pond. Survival and relative growth (RG) were calculated for each replicate pond. Fulton's condition factor (FCF) was calculated for each paddlefish measured for individual weight and TL. The sample data were pooled by treatment and tested for conformance to the normal distribution at stocking and harvest, using Kolmogorov's goodness of fit test. Coefficient of variation was also calculated from the pooled data at stocking and harvest. Miller's jackknife method was used to test equality of variances between treatments. The Wilcoxon rank-sum

TABLE 1. *Distribution, average weight, variance, coefficient of variation (CV), survival and relative growth (RG) at stocking, and/or harvest for graded paddlefish juveniles stocked in 0.02 ha ponds.*[1]

Group	Distribution	Average weight[2] (g) (±SD)	Variance (g)	CV[3]	Survival %	RG[4]
Stocking						
Large grade	Asymmetric	28.0 ± 5.2	27.4a	19	—	—
Small grade	Asymmetric	17.4 ± 4.6	21.6b	27	—	—
Ungraded	Symmetric*	25.1 ± 7.8	60.6c	31	—	—
Harvest						
Large grade	Asymmetric	288.8 ± 96.9a	9392a	31	98.8a	7.22a
Small grade	Asymmetric	223.7 ± 76.3b	5815b	35	92.3b	8.46a
Ungraded	Asymmetric	277.7 ± 80.8c	6521b	42	95.7a	9.66a

[1]Values in a column with same letters are not significantly different ($P > 0.05$).

[2]Average weight is listed for reference. The Kruskal–Wallace procedure tests the probability that a randomly selected observation from one group is equal to, greater than, or less than randomly selected observations from the other groups.

[3]CV (coefficient of variation) = (100) SD/mean of replicate final weights.

[4]RG (relative growth) = (mean final weight − mean initial weight)/mean initial weight.

*P value is 0.09, indicating weak conformance to a normal (symmetric) distribution.

test ($n_1 = n_2 = 90$) was used to verify if the paddlefish weights and FCF for each treatment were from equal probability distributions. Survival and RG were compared by t-test. In all statistical tests, treatment differences were considered to be significant at Type I probability of 5%.

Results

In the grading experiment, Kolmogorov's goodness of fit test showed that the size distributions of paddlefish were non-normal (asymmetric) at stocking with one exception; the small-grade group ($P = 0.09$) indicated weak conformance to the normal distribution (symmetric). Variances of the three groups at stocking were significantly different ($P < 0.05$). Variances for the large-grade, small-grade, and ungraded groups were 27.4, 21.6, and 60.6 g, respectively. Average weights at stocking were (±SD) 28.0 ± 5.2 g, 17.4 ± 4.6 g, and 25.1 ± 7.8 g for the large-grade, small-grade and ungraded paddlefish, respectively. Coefficients of variation at stocking were 19, 27, and 31 for the same respective groups (Table 1).

At harvest, survival for the large grade (98.8%) was higher than that of the small grade (92.3%; $P < 0.05$), but not different from the ungraded group (95.7%; $P > 0.05$), which was also higher than the small-grade group ($P < 0.05$). Relative growth was not significantly different between groups, averaging 8.4 ($P > 0.5$; Table 1). Kolmogorov's goodness of fit test found that all distributions at harvest were non-normal ($P = 0$). Variance of the large-grade group (9392 g) was significantly higher than that of the small-grade (5815 g) or ungraded (6521 g) groups ($P < 0.05$), although the small-grade and ungraded groups were not significantly different ($P > 0.05$; Table 1). Average weights at harvest were 288.8, 223.7, and 277.7 g for the large-grade, small-grade and ungraded groups, respectively. The Kruskal–Wallace test and Dunn's procedure verified that all three groups were from different distributions ($P < 0.05$) and that paddlefish body weights in the large-grade group tended to be greater than in the ungraded group, which tended to be greater than in the small-grade group ($P < 0.05$). Coefficients of variation at harvest were 31, 35, and 42 for the large-grade, small-grade, and ungraded groups, respectively (Table 1).

In the feeding frequency experiment, size distributions at stocking were normal ($P = 0.86$) for 1T/d and log-normal for 3T/d ($P = 0.56$) and of questionable similarity ($P = 0.07$). This error in obtaining equal samples from the cohort of available paddlefish cannot be explained. Variances at stocking were not different ($P > 0.05$), averaging 4.8. Coefficients of variation at stocking were 25 and 27 for the 1T/d and 3T/d treatments, respectively (Table 2).

TABLE 2. *Distribution, average weight, variance, coefficient of variation (CV), survival, relative growth (RG), and Fulton's condition factor (FCF) at stocking and/or harvest for paddlefish juveniles stocked in 0.02 ha ponds and fed one time or three times per day.*[1]

Group	Distribution	Average weight[2] (g)	Variance (g)	CV[3]	Survival %	RG[4]	FCF[5]
Stocking							
1T/d	Symmetric	8.5 ± 0.2	4.7a	25	—	—	—
3T/d	Asymmetric	8.5 ± 0.2	4.9a	27	—	—	—
Harvest							
1T/d	Asymmetric	192.5 ± 29.5a	5276a	36	52.1 ± 17.3a	21.5 ± 4.1a	265 ± 15a
3T/d	Symmetric	223.0 ± 20.8b	6210a	35	60.7 ± 9.7a	25.9 ± 2.8a	270 ± 7a

TL = total length.

[1]Values except variance and CV are ±SD. Values in a column with same letters are not significantly different ($P > 0.05$).

[2]Average weight is listed for reference. The Wilcoxon rank-sum procedure tests the probability that a randomly selected observation from one group is equal to, greater than, or less than a randomly selected observation from the other group.

[3]CV (coefficient of variation) = (100) SD/mean of replicate final weights.

[4]RG (relative growth) = (mean final weight − mean initial weight)/mean initial weight.

[5]FCF (Fulton's condition factor) = (individual final weight/TL^3) × 10^5.

At harvest, survival between treatments was not significantly different ($P > 0.05$) and averaged 56.4%. Relative growth was also not significantly different ($P > 0.05$), averaging 23.6.

Size distribution in the 1T/d treatment shifted to log-normal at harvest ($P = 0.28$), whereas in the 3T/d treatment, the size distribution shifted to normal ($P = 0.58$). Treatment variances at harvest were not significantly different ($P > 0.05$), averaging 5743 g. The Wilcoxon rank-sum test verified that FCFs for the two treatments were from the same distribution, averaging 268. However, paddlefish body weights were from different distributions with weights in the 3T/d treatment (average 223 g) tending to be greater than that in the 1T/d treatment (average 193 g). Coefficients of variation at harvest were 36 and 35 for the 1T/d and 3T/d treatments, respectively (Table 2).

Discussion

Size grading had mixed effects on size variation and growth. Relative growth was similar for all three groups, and the Kruskal–Wallace test indicated that when individuals from each group were randomly selected and compared, that which was selected from the large-grade group was likely to be of highest weight, followed by the ungraded and small-grade groups, respectively (the non-parametric Kruskal–Wallace test is not a comparison of means). This is the same order as at stocking. Therefore, growth of all three groups was similar in a relative manner, and not affected by grading. However, interindividual size variation was affected by grading. Although the variances of the graded groups were similar at stocking (Table 1; Table 2), at harvest, the variance of the large-grade group was significantly greater than either of the other two groups, which were not significantly different from each other. In addition, increase in CV was highest in the large-grade group (+12) while lower and of similar magnitude (+8 and +9) in the small-grade and ungraded groups. These results indicate that some factor existed in the large-grade group of fish that facilitated reemergence of a size hierarchy with greater interindividual size variation than in the other groups.

In the feeding frequency experiment, no treatment effect was detected except the shift to a log-normal (asymmetric) (1T/d) and a normal (symmetric) distribution (3T/d) from normal and log-normal distributions at stocking for the two respective treatments. This result correlates with the outcome of probable greater weight for a randomly selected fish from the 3T/d treatment when compared to a fish selected from the 1T/d treatment (the Wilcoxon rank-sum test is not a comparison of means). Thus, the data indicate a growth advantage for the fish fed 3T/d. The data indicate that size hierarchies were established in both treatments over the course of the experiment with corresponding increases in variance and CV. It is also notable that both groups of fish were in good condition (Mims and Knaub 1993) at harvest (FCF average 268) indicating that neither group was food limited, at least with respect to maintenance.

When the two experiments are compared, the difference in survival is apparent. Survival in the grading experiment was much higher (average 95.6%) than in the feeding frequency experiment (average 54.6%). One possible explanation is the difference in average weight at stocking (25.1 vs. 8.5 g). Predation is another possible cause. Although birds were excluded by netting, predation at night by raccoons, *Procyon lotor*, was problematic during the feeding frequency experiment because of a large local population and drought conditions, which caused these animals to leave their natural habitats to forage. Paddlefish typically congregate at the surface to feed after dark and the vertically sided concrete aprons surrounding the research ponds used in this study provided easy access for foraging raccoons.

It is difficult to predict the outcome of pond experiments with paddlefish from literature on other species because they are obligate filter feeders on zooplankton in nature. In intensive culture, best practice is to train paddlefish to accept floating feed in tanks, followed by stocking into ponds for further grow out, also on floating feed (Mims and Shelton 2005). Once stocked in ponds, feeding activity is not vigorous and can be highly variable between ponds stocked at equal numbers (Onders et al. 2005). Therefore, it was necessary for this study to assume that the presence of floating feed on the pond surface after feeding activity had ceased indicated satiation feeding, even though the actual causes for cessation of feeding are speculative. In addition, unlike other species commonly cultured in ponds, paddlefish are ram-ventilators and must swim continuously, but not necessarily in schooling form; resulting in random collisions, which have further effects on feeding, energy expenditure, and growth (Gershanovich 1983). The common density-dependent mechanisms affecting growth of fish (Backiel and Le Cren 1978) certainly apply to fed paddlefish juveniles on the population level, as evidenced by the difference in relative growth between the two experiments in the present study. Specifically, the smaller fish in the feeding frequency study, with lower effective density at harvest because of lower survival, exhibited higher relative growth than the fish in the grading experiment, which were larger at stocking, had higher survival, and therefore, higher effective density.

The degree of interindividual size variation within a cultured fish population can affect yield; however, it is known that when food is not limiting, as in fed ponds, the number of fish contained within the available space determines yield and not the growth of individual fish until physiological, genetic, water quality, or other related factors become critical (Hepher 1978). Population parameters such as carrying capacity or critical standing crop, which is the point at which population growth rate declines from the potential physiological rate as food becomes limiting (Hepher and Pruginin 1981), may have spatial components; but these parameters are more related to food supply, which is not usually a factor when supplemental feeding is present. Further, these density-dependent mechanisms do not explain the source of interindividual size variation, although it is known that interindividual variation in paddlefish increases with increasing density, whether in flow-through tanks (Gershanovich 1983) or ponds (Onders et al. 2008).

Wohlfarth (1977) summarized the results of several Japanese publications concerning the frequency distributions of pond-cultured common carp, *Cyprinus carpio*. Right-skewed size distributions (toward smaller individuals) were commonly observed in these studies along with the occurrence of small numbers of large fish termed *Tobi koi* or Shoot carp by the Japanese authors. In one of the Japanese studies, carp fry from a single cohort were reared in separate chambers with no shooting observed, while fry from the same cohort reared communally resulted in skewed size distributions; indicating the effects of interaction. The conclusions of these studies indicated that competition for food (interaction) resulted in right-skewed frequency distributions with the most successful individuals appearing as Shoot carp, whereas the remainder of the population grew more slowly or not at all. When competition for food was not present, either because the fish were grown separately or food was present in abundance, Shoot carp did not appear. However, Carmichael (1994) concluded that competition for food was not the reason for interindividual size variation in fed channel catfish, and pointed to the building of social hierarchies as the likely cause without discussing the basis for the hierarchies.

Wohlfarth also discussed a genetic component, citing a study by Hulata et al. (1976) in which groups of common carp with faster growing genotypes exhibited the shooting phenomenon, whereas slower growing genotypes produced more symmetric distributions. This may explain the greater variance at harvest of the large-grade group in the grading experiment, when compared to the small-grade and ungraded groups, if an assumption is made that the largest individuals in the cohort were larger because of an inherited faster growth rate.

Wohlfarth's analysis also included discussion of a study by Lewis and Heidinger (1971) in which hybrid sunfish; female green sunfish, *Lepomis cyanellus*, × male redear sunfish, *Lepomis microlophus*, were either fed trout pellets or reared on natural food alone, with those fed supplemental feed displaying greater asymmetry in size distribution. The authors concluded that the greater asymmetry was the result of some individuals not utilizing the supplemental feed. It is possible that variation in utilizing feed also affects interindividual size variation in groups of fed paddlefish. However, the question arises: what factors transform uniformly sized feed-trained paddlefish at stocking to highly variable size groups at harvest when continuously presented with excess feed? Excess feeding has been shown to have no effect on interindividual size variation in paddlefish (Onders et al. 2008), unlike the carp in the Japanese studies. Therefore, to merely state that (inheritance of growth rate aside), competitive interaction, or utilization of feed explains the variation, without examining the basis for these factors seems an over-simplification.

Competitive social interactions and resultant dominance hierarchies are commonly cited as the cause of size heterogeneity in groups of teleost fish (Wang et al. 2000; Gilmour et al. 2005). Low social status suppresses feeding, growth and condition, and may increase immunosuppression and mortality (McCarthy et al. 1992; Gilmour et al. 2005). Competitive interactions result in winners and losers. The ability to compete successfully may have basis in innate factors such as aggressiveness (Adams and Huntingford 1996), motivation to feed, and size (Huntingford and Turner 1987; Johnsson et al. 1996). In addition, physiological status such as energy reserves, condition, growth hormone level, and metabolic capacity at the onset of competitive interaction may affect an individual's probability of early success and ultimately determine its position in the hierarchy (reviewed by Gilmour et al. 2005). Winners of initial competitive interactions have been shown to have increased brain dopaminergic activity while losers exhibit increased serotonergic activity and subsequent decreases in aggression, feeding response, and locomotor activity (reviewed by Winberg and Nilsson 1993). Finally, a correlation has been established between high circulating cortisol levels, which may be the result of innate predisposal (Sloman et al. 2001) or induced stress (Barton and Iwama 1991), and the above-described monoaminergic activity (DiBattista et al. 2005). In the non-teleost paddlefish, plasma cortisol has been identified as the principle steroid released as the result of stress (Barton et al. 1998; Mims et al. 2006). Although the levels are of lower magnitude than is found in teleosts (Barton et al. 1998), it is probable that paddlefish respond similarly, and may also be subject to the same innate, physiological, and brain activity factors, which contribute to hierarchic size structures in teleosts. Therefore, in fed ponds, paddlefish juveniles that are winners in some form or because of some factor, utilize the feed well and grow at a faster rate than less successful fish. Thus, the result of competitive interaction affecting interindividual growth may actually be more than a matter of which individual arrives at the food first, or learns to accept supplemental feed and retains this behavior.

In a practical sense, there is little a culturist can do to influence interindividual size variation in paddlefish when techniques such as size-grading and feeding frequency have little effect, as illustrated in this study. An understanding of the underlying social/physiological factors casts doubt on the effectiveness of any pond management technique when high-density production is desired. Selective breeding for faster growth is possible; however, the long periods required for maturation (8–10 yr for females) bring into question the practicality of this process as well. Multiple harvests to remove fish that have reached the desired size and allow for compensatory growth of remaining paddlefish is one method that should reduce feed cost and the overall grow-out period, as the resultant reduction in density should allow remaining paddlefish to grow at an increased rate.

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