SURVIVAL AND SHIFTS IN FOOD OF YOUNG-OF-YEAR *MICROPTERUS* PENNED AT HIGH DENSITIES IN AN OKLAHOMA POND

Michael D. Clady
Oklahoma Cooperative Fishery Research Unit, Oklahoma State University, Stillwater, Oklahoma 74074

Young-of-year northern and Florida largemouth bass (*Micropterus salmoides salmoides* and *M. s. floridanus*) and spotted bass (*M. punctulatus*) were stocked at relatively high densities in pens in an Oklahoma pond. Survival was estimated when the pond was drained. Although survival of Florida largemouth bass was significantly lower than that of the other basses, this difference was apparently due to handling mortality of Florida largemouth bass that occurred independently of the experimental design. Fish were seined periodically, and weight and composition of stomach contents were determined. Relative weight of food usually did not differ significantly within and among species and subspecies, but there often were greater differences in variety and relative importance of various invertebrate taxa in the diet. Shifts in stomach contents suggested that significant competition for food occurred among *Micropterus* basses during March-June.

INTRODUCTION

Reproduction and recruitment of northern largemouth bass (*Micropterus salmoides salmoides*) in reservoirs in the southern Great Plains may be limited by low water levels and meteorological conditions (1, 2, 3). Variation in habitat preference and environmental tolerance among species of *Micropterus* (4) suggests that full use of aquatic resources, as occurs in polyculture, could increase production by polytypic bass populations beyond that attained by northern largemouth bass alone. The purpose of this study was to investigate the potential for polytypic stocking through a comparison of survival and food of young-of-year northern and Florida largemouth bass (*Micropterus salmoides floridanus*) and spotted bass (*Micropterus punctulatus*) in Oklahoma. In order to intensify potential competition, the bass were stocked in pens in an Oklahoma pond at such high densities that the fish did not grow significantly.

METHODS

Ten pens, 4 × 2.5 × 1 m deep, were constructed adjacent to each other on the bottom of a 0.1-hectare pond by placing vinylcoated 12.7-mm mesh wire fencing over wooden frames. The pond was not fertilized and was supplied with water by gravity flow through a pipe from Lake Carl Blackwell, a 1400-hectare reservoir in Payne and Noble counties, Oklahoma.

On 7 September 1976 each pen was stocked with 20 largemouth bass (= 2 fish/m^2). Three pens were stocked with only young-of-year Florida largemouth bass (average weight = 14.0 g; range, 7-19 g) that were the offspring of fish originally obtained in 1974-75 from the federal fish hatchery at Tyler, Texas and placed in ponds adjacent to the one in which the pens were located. Three pens were stocked with only young-of-year northern largemouth bass (average weight = 10.6 g; range, 7-13 g) that were the offspring of fish originally taken in 1974-75 from local waters not previously stocked with Florida largemouth bass and placed in other adjacent ponds. Four pens were stocked with 10 fish of each subspecies. A right or left pelvic fin was removed from all fish for subspecific identification. On 14 October and 19 November 1976 and 18 April 1977, the pond was partly drained and bass were removed by seine. (Random selection of the stocking combinations for the pens and varying the sequence in which pens were seined assured that differences in results due to temporal sampling bias were minimized.) Not all bass were captured because water in the pens remained 0.3 m deep and some escaped by moving to the catch basin present in each pen, or behind the supporting framework. Fish were individually weighed, stomach contents were removed by suction with a glass tube (5), and the fish were returned to the pens immediately. Enough natural light passed into the glass tube so that I could see into the stomach to verify that all food had been removed. Food items were preserved in 70% alcohol. On 2 June 1977, the pond was completely drained and all surviving bass were removed and processed as above. Survival was based on one interval the duration of the experiment. Mean survival rates of the subspecies were tested for significant differences by using the Mann-Whitney U test (6).

Food items in each stomach were identified to the lowest taxon practical (usually family). Individual stomach samples for each subspecies in each pen were then combined and the total weighed to the nearest 0.01 g (blotted wet weight). Monthly mean relative weights of food and number of taxa present in fish from various stocking combinations were tested for significant differences by using the Wilcoxin matched-pairs signed-ranks test (6) and a paired *t*-test, respectively. Because of apparent shifts in the variety of food eaten in polytypic pens, I calculated a measure of food overlap,

$$\hat{C}_\lambda = 2\sum^{s} P_{ij} P_{ik} / \left(\sum_{i=1}^{s} P_{ij}^2 + \sum_{i=1}^{s} P_{ik}^2\right)$$

(7), where *s* equals the total number of categories of food organisms, and P_{ij} and P_{ik} equal the proportions of the total weight of food for fishes *j* and *k*, respectively, made up of category *i*. Because of the similarity of the study areas, no attempt was made to quantify availability of invertebrates during the experiment. No forage fish were present in the pens.

In 1977-78 spotted bass were added to the study. On 28 September 1977 two pens were stocked with 20 spotted bass (average weight = 9.8 g; range, 7-14 g) that were the offspring of adult fish taken in spring 1977 from Blue River, Oklahoma and placed in adjacent ponds. One pen was stocked with 20 northern largemouth bass (average weight = 11.9 g; range, 9-23 g), three with 10 northern largemouth bass and 10 spotted bass, two with 10 Florida largemouth bass (average weight = 10.5 g; range, 6-15 g) and 10 spotted bass, and two pens with seven of the three types of bass. Northern and Florida largemouth bass were offspring of the same stocks used the previous year. The fish were marked and sampled and the data processed as during the 1976-77 experiment with three exceptions: (a) only one-half of a right pelvic fin was removed from the spotted bass, (b) all stomach contents from fish of a given species or subspecies in each pen were consolidated before processing, and (c) Kruskal-Wallis one-way analysis of variance (6) was used to test for differences in mean survival rates of the three basses. Fish were seined on 19 November 1977, and the pond was drained and fish removed on 9 March 1978.

RESULTS

Survival

A total of 100 northern and 100 Florida largemouth bass were stocked in the pens on 7 September 1976. On 2 June 1977, 58 northern and 15 Florida largemouth bass survived (Table 1). Range of survival of northern and Florida largemouth bass in individual pens was 40-85% and 0-40%, respectively. These differences were highly significant (Mann-Whitney $\mu = 1$; $P = .001$). There were no significant differences, however, in the survival of a given subspecies stocked alone or with individuals of the other subspecies. Survival of northern largemouth bass ranged from 40 to 85% when stocked alone and from 40 to 80% when Florida largemouth bass were present. Survival of Florida largemouth bass varied from 0 to 30% when stocked alone and from 10 to 40% when northern laregmouth bass were present.

A total of 64 northern largemouth bass, 34 Florida largemouth bass, and 104 spotted bass were stocked 28 September 1977. On 9 March 1978, 54 northern largemouth bass (84.4%), 21 Florida largemouth bass (61.8%), and 86 spotted bass (82.7%) survived (Table 1). Respective ranges of survival were 71.4-100% for northern largemouth bass, 50-71.4% for Florida largemouth bass, and 70-95% for spotted bass. As in 1976-77, these differences in survival were significant (Kruskal-Wallis, $H = 6.30$, $P<.05$), but survival of a given species or subspecies was not significantly related to stocking combination. Survival of northern largemouth bass was 75% when stocked alone, 70-100% when stocked with spotted bass, and 71.4-100% when stocked with both spotted bass and Florida largemouth bass. Survival of Florida largemouth bass was 71.5% in the two pens with northern largemouth bass and spotted bass and 50-60% when stocked with spotted bass only. Survival of spotted bass was 95% in

TABLE 1. *The number of fish stocked and sampled and food in stomachs of northern and Florida largemouth bass and spotted bass in pens, 7 September 1976 — 9 March 1978.*

	Species and subspecies present					
	Northern			Florida		
	Only	With Florida	Total	Only	With Northern	Total
1976						
7 September						
No. fish stocked	60	40	100	60	40	100
14 October						
No. fish seined	51	27	78	9	10	19
No. taxa	13	10	13	7	12	12
Biomass mg/g fish	2.2	1.9	2.1	2.2	2.2	2.2
19 November						
No. fish seined	50	25	75	9	10	19
No. taxa	12	12	16	7	9	10
Biomass mg/g fish	1.4	2.0	1.6	0.8	2.3	1.6
1977						
18 April						
No. fish seined	48	26	74	7	9	16
No. taxa	11	5	12	6	8	9
Biomass mg/g fish	15.1	8.9	13.0	18.9	4.1	9.0
2 June						
No. fish at draining	37	21	58	7	8	15
No. taxa	11	6	11	6	6	8
Biomass mg/g fish	71.3	18.6	53.7	21.7	15.5	17.6

	Northern				Florida		
	Only	With spotted	With spotted & Florida	Total	With spotted	With spotted & northern	Total
19 August							
No. fish stocked	20	30	14	64	20	14	34
19 November							
No. fish seined	13	21	12	46	16	15	31
No. taxa	4	3	4	5	3	4	5
Biomass mg/g fish	2.8	2.0	1.9	2.2	0.9	1.4	2.4
1978							
9 March							
No. fish at draining	15	26	14	55	11	10	21
No. taxa	4	6	6	7	5	6	7
Biomass mg/g fish	6.1	4.0	4.8	4.8	5.0	4.8	4.9

	Spotted				
	Only	With northern	With Florida	With Florida & northern	Total
1977					
19 August					
No. fish stocked	40	30	20	14	104
19 November					
No. fish seined	32	26	20	14	92
No. taxa	5	5	4	3	7
Biomass mg/g fish	2.8	4.2	1.9	2.2	2.9
1978					
9 March					
No. fish at draining	37	21	16	12	86
No. taxa	3	4	3	3	5
Biomass mg/g fish	1.0	2.8	1.3	0.7	1.4

both pens where stocked alone, 70-80% were stocked with northern largemouth bass, 80% in both pens with Florida largemouth bass, and 70-85% with both northern and Florida largemouth bass.

Food

During 1976-77, mean quantities of food in stomachs of bass varied considerably by month (Table 1), although stomachs of all northern largemouth bass contained relative weights of food that were statistically similar to weights in Florida largemouth bass (Wilcoxin T = 11). Total values (mg/g fish) for northern and Florida largemouth bass in October, November, and April were 2.1 and 2.2, 2.0 and 1.6, 13.0 and 9.0, respectively. In both subspecies in April the weight of food present was about five times greater than in previous months. In June, weight of food increased again, but the increase was much greater for northern (to 53.7 mg/g fish) than for Florida largemouth bass (to 17.6 mg/g fish).

There were no significant differences or general trends in the relative weight of food present within treatments (monotypic vs. polytypic) of a given subspecies. For example, in November the weight of food in stomachs of bass in polytypic pens was two to three times greater than in monotypic pens (Table 1). Conversely, in April and June, consumption of food by weight in monotypic populations far exceeded that in polytypic populations.

During 1976-77, differences in the variety of food eaten were statistically significant, however. All northern largemouth bass contained significantly more taxa than all Florida largemouth bass ($t = 1.90$, $df = 15$, $p<.05$). This difference was most pronounced when the subspecies were stocked alone ($t = 21.0$, $df = 7$, $p<.05$). In monotypic ponds, northern largemouth bass contained 11 to 13 taxa, but Florida largemouth bass only 6 or 7 (Table 1). Northern largemouth bass stocked alone contained significantly more (up to six more) taxa of invertebrates during each sampling period than did northern largemouth bass stocked with Florida largemouth bass ($t = 2.65$, $df = 7$, $p<.05$). The opposite was true of Florida largemouth bass; they significantly expanded the breadth of their diet when in company of northern largemouth bass ($t = 2.18$, $df = 7$, $p<.05$). Florida largemouth bass stocked with northern largemouth bass contained as many, or up to five more taxa than Florida largemouth bass stocked alone (Table 1).

When one subspecies was compared to the other, degree of overlap ($\hat{C}_\lambda$) of food fell within the range of 0.87 to 0.99 during all sampling periods when stocked monotypically and during October and November 1976 when stocked polytypically (Table 2). Food habits apparently shifted in April and June 1977, however, since overlap coefficients in the polytypic pens were only 0.32 and 0.68, respectively. Even though the total number of taxa eaten suggested that Florida largemouth bass diversified their diet but northern largemouth bass concentrated more on a few organisms when stocked polytypically (Table 1), the degree of change appeared to be similar (Table 2). Coefficients of overlap in diet were 0.65 to 0.98 for all northern largemouth bass and 0.69 to 0.99 for all Florida largemouth bass. As with the comparisons

TABLE 2. *Niche overlap coefficients ($\hat{C}_\lambda$) for northern and Florida largemouth bass and spotted bass stocked in monotypic (M) and polytypic (P) combinations in pens, October 1976 through March 1978.*

Subspecies and species compared	Date and coefficient			
	11 Oct. 76	18 Nov. 76	18 Apr. 77	2 June 77
Northern — M and Florida — M	0.87	0.88	0.93	0.99
Northern — P and Florida — P	0.95	0.93	0.32	0.68
Northern — M and Northern — P	0.94	0.80	0.65	0.98
Florida — M and Florida — P	0.99	0.77	0.72	0.69
	19 Nov. 77		9 Mar. 78	
Northern — M and Spotted — M	0.93		0.93	
Northern — P and Spotted — P	0.88		0.67	
Northern — M and Northern — P	0.97		0.55	
Spotted — M and Spotted — P	0.99		0.35	

between subspecies, the least overlap in diet of fish within a given subspecies occurred in April and June (Table 2), also suggesting shifts in food habits during these months.

Shifts occurred primarily in the consumption of odonate naiads (Table 3). In April northern largemouth bass in the polytypic pens contained almost three times the relative weight of anisopterans and

TABLE 3. *Percentage of total weight made up of the most important invertebrate feed categories in stomachs of northern and Florida largemouth bass and spotted bass stocked in monotypic (M) and polytypic (P) combinations in pens, October 1976 through March 1978.* (T = less than 1%).

Date and fish examined	Percentage of the total weight of food made up of each organism						
	Baetinae	Anisoptera	Zygoptera	Corixidae	Chironomidae	Daphnidae	*Hyalella azteca*
11 Oct. 76							
Northern — M	52	—	T	11	17	11	2
Northern — P	64	—	2	6	T	12	T
Florida — M	82	—	1	15	T	T	—
Florida — P	85	—	1	3	T	2	—
18 Nov. 76							
Northern — M	38	17	14	9	1	19	T
Northern — P	28	11	42	7	—	9	—
Florida — M	41	—	32	12	—	14	—
Florida — P	19	22	36	7	—	5	—
18 Apr. 77							
Northern — M	1	24	56	—	—	—	—
Northern — P	—	68	23	—	—	—	—
Florida — M	—	43	44	—	—	—	—
Florida — P	—	—	63	—	—	—	—
2 June 77							
Northern — M	15	61	11	—	T	T	T
Northern — P	11	66	15	—	—	—	—
Florida — M	11	68	9	—	—	—	—
Florida — P	57	40	—	—	—	—	—
19 Nov. 77							
Northern — M	3	5	22	—	—	70	—
Northern — P	—	11	30	—	—	59	—
Spotted — M	2	2	8	—	—	93	—
Spotted — P	3	1	7	—	—	89	—
9 Mar. 78							
Northern — M	—	22	2	—	—	—	76
Northern — P	—	22	35	—	14	—	24
Spotted — M	—	—	22	—	—	—	78
Spotted — P	—	64	14	—	—	—	21

one-half the zygopterans as in the monotypic pens. Florida largemouth bass did not eat anisopterans when stocked with northern largemouth bass, but when stocked alone, anisopterans made up 43% of the weight of the diet. In June Florida largemouth bass in polytypic pens contained roughly one-half the relative weight of anisopterans and five times the ephemeropteran nymphs as they did when stocked alone.

In November 1977, weights of food found in all northern largemouth bass (2.2 mg/g fish), all Florida largemouth bass (2.4 mg/g fish), and all spotted bass (2.9 mg/g fish) were similar (Table 1). In March 1978, however, amount of food in northern largemouth bass (4.8 mg/g fish) and Florida largemouth bass (4.9 mg/g fish) far exceeded that in spotted bass (1.6 mg/g fish).

As during the first experiment relative weights of food within species and subspecies did not suggest consistent differences between fish stocked in monotypic and polytypic combinations (Table 1). The number of taxa of food present in a given species or subspecies varied between 3 and 6 (in contrast to the 1976-77 study when 6 to 13 taxa were present) and did not appear to be related to the stocking combination (Table 1).

Even though feeding was confined largely to the same taxa, changes in the relative weight of food made up of various taxa suggested shifts similar to those in 1976-77 (Table 2). Food overlap of northern largemouth bass and spotted bass in monotypic pens was almost complete 0.93 in both November and March. The food overlap coefficient in polytypic pens was similar in November (0.88) but declined to 0.67 in March. Markedly lower overlap in March between individuals of a species stocked in mono- and polytypic pens 0.55 vs. 0.97 for northern largemouth bass and 0.35 vs. 0.99 for spotted bass suggested increased competition for food in March as compared to November (Table 2). Although the data are not presented in Table 2 (because no monotypic population of Florida largemouth bass was available), overlap coefficients for six groups of spotted bass and northern largemouth bass stocked in pens with Florida largemouth bass and compared to the respective monotypic situations ranged from 0.94 to 0.99 in November and from 0.58 to 0.78 in March.

Shifts in March 1978 occurred mainly in the consumption of odonate naiads and the amphipod *Hyalella azteca* (Table 3). When stocked together northern largemouth bass and spotted bass consumed only one-third and one-fourth, respectively, of the relative weight of *Hyalella* eaten when stocked alone. In polytypic pens, northern largemouth bass and spotted bass ate markedly greater relative proportions of zygopterans and anisopterans, respectively.

DISCUSSION

The results of the present study related to survival were consistent. Survival of northern largemouth bass was significantly greater than that of Florida largemouth bass in both experiments and the 1977-78 data suggest that survival of spotted bass was similar to that of northern largemouth bass. Survival rates were subspecies- or species-specific and independent of the combination of *Micropterus* basses stocked in the pen.

The differences in survival may not occur naturally, however. The numbers of Florida largemouth bass seined from the pens on the intervening sampling days of the first experiment (Table 1), although not absolute estimates of the number of fish surviving, indicated that mortality of Florida largemouth bass was much higher during the month following stocking than during the winter months. One hundred Florida largemouth bass were stocked in September, but only 19, 19, 16, and 15 were taken in October, November, April, and June, respectively. Florida largemouth bass held at 4 C may be more sensitive to rapid declines in temperature than are northern largemouth bass (8). However, even though the pond used in the present study was frozen over and water temperatures were near 4 C for extended periods during both years, few Florida largemouth bass died during the winter.

Florida largemouth bass may be more affected by handling than northern largemouth bass and suffer a higher incidence of handling-related diseases (8). The adverse effect of the relatively great amount of handling during stocking in August and September (when water temperatures were in the range of 17-27 C) could account for the much greater initial mortality of Florida largemouth bass stocked in pens as well as the significantly higher overall survival rates of northern largemouth bass in adjacent ponds (9). Subsequent seining and handling during October through April (when water temperatures were below 17 C) apparently did not cause any significant mortality, however.

Significantly fewer survivors of Florida largemouth bass than of northern largemouth bass and spotted bass in the pens probably did not contribute to the observed shifts in food. Mortality appeared to be related to handling during fin-clipping and most deaths occurred within one month after stocking. Therefore, the relative proportions of various species and subspecies surviving in the pens were similar when food habits overlapped in fall and winter and when they shifted in spring (Table 1). However, the much smaller numbers of Florida largemouth bass present in 1976-77 could have contributed to the generally lower number of taxa eaten by this subspecies, since the probability of ingesting incidental prey was probably lower. Fish grew little or not at all during the two experiments, probably because (a) they were stocked late in the growing season, (b) stocking densities were high relative to natural systems (20,000/ha vs. 0.05-94/ha in nearby Lake Carl Blackwell (1), (c) forage fish were absent from the pens, and (d) confinement in pens, per se, may reduce growth of bass (8). Conditions (b) and (c) (albeit somewhat unnatural ones) were set up specifically to maximize competitive interactions.

Greater consumption of food (both in terms of weight and diversity) by monotypic populations of northern largemouth bass in April and June of the first experiment supports other findings that segregation by cohabiting fish species results in consumption of a narrower range of food items by each species than when only one species is present (10, 11, 12). Greater diversity of the diet does not necessarily suggest better feeding conditions, however, since fish populations often consume a greater variety of food items under adverse food conditions than when food supplies are unlimited (13). The similarity in the types of organisms present in stomachs of the three species and subspecies of *Micropterus* during the second experiment was probably at least partly due to the limited variety of organisms in the pens. In polytypic situations in Oklahoma streams, largemouth bass ate mainly fish, but spotted bass consumed mainly invertebrates (14).

An overlap coefficient of 0.6 or greater has been assumed to be significant (15). I considered overlap in diet between and within subspecies and species of *Micropterus* to be very high for all except the monotypic-polytypic comparisons of northern and Florida largemouth bass in April 1977 and of spotted bass in March 1978 (Table 2). However, the existence of overlap is not evidence of competitive interaction (although it may indicate the potential for competition) and actually may suggest the opposite avoidance of competition (16). Shifts in response to the presence of a potential competitor, however, such as occurred in the pens in April and June 1977 and March 1978, constitute direct evidence of competition (15, 16) and may represent the realized, or postcompetitive food niches (17) of the three basses.

Interpretation of ecological shifts is often difficult because of differences between the environments supporting allopatry and sympatry (16). In the present study, however, it was likely that differences in food resources between the pens were insignificant since all pens were adjacent in one pond and the sites were similar in size, temperature, depth of water, current, and water chemistry. Provided that this assumption is true, the shifts in food observed in polytypic pens in March to June likely reflect a response to competition. Competition for food in some months, as well as poorer survival of Florida largemouth bass, suggest that stocking Florida largemouth bass and spotted bass to augment populations of northern largemouth bass may not greatly increase overall standing crops of *Micropterus* basses (9), although it may temporarily increase the use of different resources and the diversity of fishes and their prey (16). Hybrid populations produced by interbreeding between the subspecies of largemouth bass, as may have occurred in California (18), could also potentially limit benefits of polytypic stocking. However, the existence of young-of-year hybrids or Florida largemouth bass has not been documented in nearby Boomer Lake (19) or other Oklahoma reservoirs stocked with the Florida subspecies.

Shifts in the food of three other species of centrarchids in temperate lakes showed that food habits diverged as resources declined during the warmer months (20). However, the weights of food eaten per gram of largemouth bass in my pens were generally greater in March to June than in October and November (Table 1), and also were well above those (2.4-11.1 mg/g) in bass stocked at lower densities in adjacent ponds with forage fish (9). Thus, absolute availability of food was probably not lower when diets diverged in the present study, but pronounced food shifts and heightened competition during spring and summer were probably due to reduced availability of food relative to needs as a result of increased metabolism, activity, and feeding rates of the fishes at this time of year. The shifts in food did not appear to be directly related to environmental conditions such as temperature. Similar shifts in diet of different species Florida largemouth bass and spotted bass stocked with northern largemouth bass during the spring months of two years were more likely due to the presence of a common competitor (the northern largemouth bass) than to changing environmental conditions that affected both Florida largemouth bass and spotted bass in the same manner.

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