POPULATION DYNAMICS AND INTERACTIONS OF THREE BLACK BASS SPECIES IN AN OKLAHOMA RESERVOIR AS INFLUENCED BY ENVIRONMENTAL VARIABILITY AND A DIFFERENTIAL HARVEST REGULATION

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TABLE OF CONTENTS

Chapter Page

LIST OF TABLES

Table Page

Chapter II

Table Page

Chapter III

Chapter IV

LIST OF FIGURES

Figure Page

Chapter II

Chapter III

Chapter IV

CHAPTER I.

This thesis is comprised of three manuscripts written for submission to North American Journal of Fisheries Management. Chapter I is an introduction to the rest of the thesis. The manuscripts are complete as written and do not require supporting material. The manuscript contained in Chapter II is titled 'Population characteristics of three black bass species as affected by a differential-harvest regulation in an Oklahoma reservoir.' The manuscript contained in Chapter III is titled 'Resource use among three black bass species in a trophically heterogenous Oklahoma reservoir.' The manuscript contained in Chapter IV is titled 'Environmental influences on recruitment of three black bass species in a southern Great Plains flood control reservoir.'

CHAPTER II.

POPULATION CHARACTERISTICS OF THREE BLACK BASS SPECIES AS AFFECTED BY A DIFFERENTIAL-HARVEST REGULATION IN AN OKLAHOMA RESERVOIR

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Abstract.–In 1997, a differential-harvest regulation implemented at Skiatook Lake in Oklahoma allowed harvest of 15 spotted bass Micropterus punctulatus per day with no minimum length limit and six largemouth bass M. salmoides and smallmouth bass M. dolomieu in aggregate per day with a 356 mm minimum length limit. Data from the Oklahoma Department of Wildlife Conservation showed no differences in electrofishing catch rates of spotted bass between two years pre-regulation and two years post-regulation. I sampled largemouth bass, smallmouth bass, and spotted bass in the spring and fall of 1997, 1998, and 1999 to evaluate the response of these black bass populations to this regulation. Largemouth bass were evenly distributed throughout the reservoir in fall and less abundant in Hominy Creek in spring during the entire study period . Largemouth bass abundance increased in fall, but not in spring, over the three years, while recruitment, relative weights, and survival remained unchanged. Largemouth bass growth was greatest in 1998 but proportional stock density (PSD) decreased in spring 1999. Smallmouth bass were distributed primarily in the lower-lake regardless of season. Smallmouth bass abundance increased over the study period in spring, but not in fall and recruitment remained constant. Relative weights of smallmouth bass were depressed in spring 1998 but constant in fall during the three years. Smallmouth bass survival remained constant while PSDs were constant in fall and greatest in spring 1999. Growth rates of smallmouth bass were also greatest in spring 1999. Spotted bass were distributed more in the upper lake in spring and in the mid- and lower-lake areas

in fall. Spotted bass abundance remained constant over the study period, as did recruitment. Mean relative weights of spotted bass were greatest in both spring and fall of 1997. Spotted bass PSDs and survival remained unchanged over the study period and growth rates were depressed in 1999. The stable survival rates for all species, coupled with the constant trend in spotted bass abundance, indicate that the 15 fish creel limit with no minimum length limit regulation for spotted bass failed to reduce spotted bass abundance in Skiatook Lake.

Reservoir fisheries in Oklahoma have historically been managed for largemouth bass *Micropterus salmoides* and, where they have been introduced, smallmouth bass *M. dolomieu*. Spotted bass *M. punctulatus* are native to Oklahoma waters and are often found in sympatry with the other two black bass species. However, spotted bass do not regularly attain the statewide minimum harvest length of 356 mm and, therefore, have not received much attention from anglers and fisheries managers.

In 1994, Oklahoma Department of Wildlife Conservation (ODWC) biologists observed an approximate five-fold increase in the relative abundance of spotted bass in Skiatook Lake, Oklahoma compared with prior years (Hicks 1994; Figure 1). Concerned that the increased abundance of spotted bass might negatively affect largemouth bass and smallmouth bass fisheries, the ODWC enacted a differential harvest regulation on January 1, 1997 aimed at reducing the abundance of spotted bass. Previously, all three species were managed with a minimum size limit of 356 mm and a daily harvest of 6 fish in aggregate. The new regulation removed the length-limit on spotted bass and allowed a harvest of 15 per day, while maintaining the previous regulation for largemouth bass and smallmouth bass. The expected outcome of this regulation change was a decrease in abundance and survival of spotted bass and an improvement of the population structure (i.e., increases in relative abundance, survival, and/or growth) of the largemouth bass and smallmouth bass populations.

Fisheries regulations have often been used to modify or enhance population characteristics of target species (Noble and Jones 1993). Redmond (1986) reported alterations such as altered size structure, proportional stock density (PSD), growth, and reproduction of largemouth bass populations in response to a variety of management regulations. Zagar and Orth (1986) demonstrated with computer simulations the relationship between various fisheries management regulations and population characteristics of largemouth bass. Their modeling indicated that a trophy fishery was best achieved with a high minimum-length limit, whereas maximum harvest was best obtained with a low minimum-length limit. Novinger (1987) reported increased catch rates of black bass (largemouth bass and spotted bass combined) after implementation of a 381-mm minimum-length limit on Table Rock Lake, Missouri; however, growth rates for both species declined during the study, possibly due to decreased forage or density-dependent growth depression. Wilde (1997) analyzed data from 91 fisheries regulation evaluations around the U.S. and found that the size structure of largemouth bass populations was improved with minimum-length limits except when 305 mm minimum-length limits were excluded from the analysis. Additionally, he found that minimum-length limits failed to increase PSD and the number and weight of fish harvested by anglers. These studies demonstrate the varying ability of fisheries regulations to alter the population characteristics of their target species, however, they say nothing about how they might impact non-target, ecologically similar species.

Buynak et al. (1991a) provide the only published study of a fisheries regulation that was implemented to alter the population characteristics of both a target and non-target species. A differential harvest regulation was enacted on Cave Run Lake, Kentucky in 1985 that removed the size limit for spotted bass in an attempt to reduce the potential for overharvest of largemouth bass (Buynak et al. 1991). Additionally, the largemouth bass minimum-length limit was changed from 305 mm to 381 mm. As a result of these changes, largemouth bass exploitation declined whereas spotted bass exploitation increased. Electrofishing catch rates increased for all sizes of largemouth bass, but declined for 229-mm and longer spotted bass. Total weight of harvested largemouth bass remained unchanged but angler catch of quality-size fish increased.

The objective of this study was to monitor abundance, condition, growth, survival, and size structure of largemouth bass, smallmouth bass, and spotted bass in Skiatook Lake for three years following implementation of the differential-harvest regulation.

STUDY AREA

Skiatook Lake is a 4,266-ha flood-control impoundment of Hominy Creek in north-central Oklahoma. The lake has a mean depth of 9.7 m and a shoreline development index of 11.3. The upper end of the reservoir is more turbid than the lower end, with average spring Secchi depths of 0.1 m and 1.2 m, respectively, and was classified as mesotrophic in 1997 with a mean chlorophyll-a concentration of 5.10 mg/m^3 (Long et al. 1999). The top of the conservation pool is 217.6 meters above mean sea level. Sportfish species in the lake consist mainly of largemouth bass, smallmouth bass, spotted bass, sunfish Lepomis spp., hybrid striped bass Morone saxatilis X M. chrysops, walleye Stizostideon vitreum, channel catfish Ictalurus punctatus, and flathead catfish Pylodictis olivaris.

METHODS

I obtained standardized electrofishing data from the ODWC collected at Skiatook Lake from 1987 through 1998. Since the objective of the regulation was to reduce spotted bass abundance because of their marked increase in 1994, I classified the years 1994 and 1996 as the pre-regulation period (1995 was not sampled) and 1997 and 1998 as the post-regulation period. I did not include the years prior to 1994 because spotted bass abundance was consistently low until that year (Figure 1). I then used a t-test (SAS Institute 1992) to test for pre- and post-regulation differences in mean catch rates (number of fish per electrofishing hour) of each species.

I sampled black bass with night-time, boat-mounted electrofishing during spring and fall 1997-1999 using a stratified-random design (Wilde and Fisher 1996). I stratified Skiatook Lake into four areas (lower-lake, mid-lake, Hominy

Creek, and Bull Creek) based on morphometry and Secchi depth measurements (Figure 2). Sampling sites were identified by delineating shoreline habitat types in a Geographic Information Systems (GIS) database and randomly selected within strata for each season and year. At least 10% of the shoreline was sampled. Habitat types consisted of substrate (i.e., silt, sand, gravel, cobble, rip-rap, boulder, and bedrock) and cover-type (i.e., non-woody vegetation, shrub, standing timber, and fallen timber) combinations that were classified by surveying the entire perimeter of Skiatook Lake by boat in winter 1996. Sites selected for sampling were electrofished with varying amounts of effort, depending on site length and habitat complexity. All black bass captured were identified, measured to the nearest 1 mm, and weighed to the nearest 0.01 kg. Scale samples were taken from the left side posterior to the opercle from all fish in spring 1997 and 1999; sagittal otoliths were removed from a representative sub-sample in spring 1997, and from all fish in spring 1998 and 1999.

I tracked trends in abundance (mean catch rates), distribution, and mean relative weight (Wr) of each species over the three years for spring and fall using ANOVA and trend analysis with orthogonal polynomials (Kuehl 1994). Distribution was assessed by comparing the abundance of each species among the four strata of the lake (lower-lake, mid-lake, Hominy Creek, and Bull Creek) and among the three sample years with a 4x3 factorial ANOVA. Relative weight (Wr) is a measure of condition (Anderson and Neumann 1996) and was assessed using the standard weight (Ws) equations developed by Henson

(1991; cited in Anderson and Neumann 1996) for largemouth bass, Kolander et al. (1993) for smallmouth bass, and Wiens et al. (1996) for spotted bass and was calculated with the equation

$$Wr=100(W/Ws),$$

where W is the measured weight of the fish and Ws is the standard weight of the fish.

I tracked recruitment by analyzing the abundance of yearling fish in the spring, which were produced from the previous year's spawn, for each species by using ANOVA and trend analysis with orthogonal polynomials (Kuehl 1994). I classified juveniles according to the respective upper value of the central 50% length range of age-one fish in Oklahoma waters, as reported by Carlander (1977). Thus, largemouth bass less than 226 mm, smallmouth bass less than 185 mm, and spotted bass less than 178 mm were considered juveniles. Multiple comparisons for all ANOVA tests were made using the LSMEANS procedure in SAS (SAS Institute 1992).

I estimated ages of all fish collected during spring electrofishing for all three sample years. Ages were estimated with scales in 1997 and 1999 and with whole otoliths in 1998 and 1999. I also estimated age using whole otoliths for a subsample of fish in 1997. Ages were determined with scales by making impressions in acetate slides and counting annuli with a microfiche reader and with otoliths by immersing the otolith in clarifying oil and counting annuli with a dissecting microscope (DeVries and Frie 1996). Each structure was read twice (once each by two separate readers) and then the modal age was calculated for each fish. When a modal age could not be calculated from two readings, then a third reading was taken and the modal age recalculated. Fish whose modal age could not be calculated after three readings were considered unageable and were removed from the analyses. Annuli from scales were delineated and measured using a digitizer.

I compared growth over the three year study period by fitting the length-at-age data to a power model and comparing the slopes of log-log transformed data with ANCOVA (SAS Institute 1992) using whole otoliths to estimate age. Additionally, I compared growth using the Weisberg (1993) method of back-calculated length-at-age data from annuli measurements using scales. The Weisberg (1993) method allowed me to separate differences in growth due to age and year via 2-way ANOVA.

I calculated survival for each species for each year by using catch curve analysis (Van Den Avyle 1993) based on ages estimated from whole otoliths and compared the slopes of the catch curve regression lines with ANCOVA (SAS Institute 1992) to determine if survival changed annually over the study period. Only those age classes represented by five or more individuals were used in the catch curve analysis (Van Den Avyle 1993). Since the ages of only a subsample of fish were estimated by whole otoliths in 1997, I constructed an age-length key with 25-mm length groups to enumerate numbers of each species for each age class in 1997 (DeVries and Frie 1996).

Finally, I calculated proportional stock density (PSD; Anderson 1976) for each species, season, and year to document changes in population size structure. Stock and quality sizes were taken from Anderson and Neumann (1996). I compared PSD estimates by using the approximation to the normal distribution for comparing two proportions (Zar 1999) between all possible pairs of years for each species and season. I used a Bonferroni correction for alpha = 0.05 with three groups to test for significance (Kuehl 1994).

RESULTS

Abundance, Distribution, Condition, and Recruitment

Largemouth bass.--There was no difference in the ODWC mean catch rates of largemouth bass between pre- and post-regulation periods ($P = 0.97$; Table 1). I captured 144, 151, and 100 largemouth bass in the spring of 1997, 1998, and 1999, respectively. In the corresponding fall seasons, I captured 65, 55, and 118 largemouth bass. In spring, there was no difference in largemouth bass catch rates among years ($P = 0.20$). Fall largemouth bass catch rates differed among years ($P < 0.01$) and there was an increasing linear trend ($P = 0.03$; Table 2). Largemouth bass were equally abundant among the four strata among the three years in spring ($P = 0.60$ for year*stratum interaction and $P = 0.30$ for stratum) and less abundant in Hominy Creek in fall ($P = 0.76$ for year*stratum interaction and P = 0.02 for stratum; Table 3). Mean relative weights remained unchanged over the three years (P = 0.23 for spring and P = 0.85 for fall; Table 4). Abundance of juvenile largemouth bass nearly doubled from 1997 to 1999, but was not statistically different among years (P = 0.08; Table 5).

Smallmouth bass.--The ODWC data showed a significant increase in mean catch rates of smallmouth bass between pre- and post-regulation periods (P = 0.02; Table 1). In the spring of 1997, 1998, and 1999, I captured 74, 137, and 116 smallmouth bass, respectively. In the corresponding fall seasons, I captured 81, 105, and 51 smallmouth bass. Catch rates of smallmouth bass increased linearly over the three year sampling period during spring (P = 0.02), but remained constant during fall (P = 0.70; Table 2). During all three years, smallmouth bass were always more abundant in the lower-lake stratum in spring (P = 0.30 for stratum*year interaction and P < 0.01 for stratum) and fall (P = 0.98 for stratum*year interaction and P < 0.01 for stratum; Table 3). In spring, mean relative weights fluctuated with the lowest in 1998 and the highest in 1997 (P < 0.01; Table 4). Mean relative weights in the fall remained unchanged over the three years (P = 0.11; Table 4). Recruitment, as indexed by catch rates of juvenile fish, was variable and not significantly different among years (P = 0.16; Table 5).

Spotted bass.--I found no significant decrease in ODWC's mean catch rates of spotted bass between pre- and post-regulation periods (P = 0.84; Table

1). I captured 305, 144, and 138 spotted bass in the spring and 125, 128, and 128 in the fall of 1997, 1998, and 1999, respectively. Mean catch rates were constant over the three years in spring ($P = 0.12$) and fall ($P = 0.46$; Table 2). Spotted bass were more abundant in Bull Creek in the spring regardless of year ($P < 0.01$ for stratum and $P = 0.30$ for the year*stratum interaction), but were more abundant in the lower-lake and mid-lake strata in the fall ($P < 0.01$ for stratum and $P = 0.99$ for the year*stratum interaction; Table 3). Mean relative weight of spotted bass fluctuated over the three years with the highest relative weights in spring ($P < 0.01$) and fall ($P < 0.01$) 1997 (Table 4). Mean catch rates of juvenile spotted bass in spring were not significantly different among years ($P = 0.12$; Table 5).

Age and Growth, Survival, and Size Structure

Largemouth bass.--I was able to determine ages from 39, 143, and 92 largemouth bass from 1997, 1998, and 1999, respectively, using whole otoliths. Analysis of covariance of the log-log transformed length-at-age data showed an increased growth rate for largemouth bass in 1998 compared to 1999 ($P = 0.01$; Figure 3A), but the Weisberg (1993) method found no differences in growth among years ($P = 0.18$ for 1997 scale age data and $P = 0.36$ for 1999 scale age data; Table 6). Survival was constant among years and averaged 66.82% (Table 7). Proportional stock density (PSD) in spring was lowest in 1999 compared to 1998 (corrected $P < 0.05$) and 1997 (corrected $P = 0.02$), but in fall was constant among years (Table 8).

Smallmouth bass.--Using whole otoliths, I aged 22, 133, and 113, smallmouth bass from 1997, 1998, and 1999, respectively. Growth rates were greater in 1999 compared to 1998 ($P < 0.01$; Figure 3B) with the ANCOVA method, but no differences in growth were found with the Weisberg (1993) method ($P = 0.84$ for 1997 scale age data and $P = 0.80$ for 1999 scale age data; Table 6). Survival was constant among years and averaged 57.41% (Table 7). Proportional stock density (PSD) in fall was greatest in 1999 compared to 1997 (corrected $P < 0.01$) and 1998 (corrected $P < 0.01$), but in spring was constant among years (Table 8).

Spotted bass.--I aged 56, 139, and 136 spotted bass using whole otoliths from 1997, 1998, and 1999, respectively. Growth rates were lowest in 1999 compared to 1997 and 1998 ($P < 0.01$, respectively; Figure 3C) with the ANCOVA method, but not with the Weisberg (1993) method ($P = 0.99$ for 1997 scale age data and $P = 0.37$ for 1999 scale age data; Table 6). Survival was constant over the three years and averaged 60.54% (Table 7). Proportional stock density (PSD) was also constant among years, averaging 31.68% in spring and 49.69% in fall (Table 8).

DISCUSSION

The differential harvest regulation for black bass in Skiatook Lake was aimed primarily at improving the largemouth bass and smallmouth bass fisheries by reducing the abundance of spotted bass. There was, however, no significant reduction in spotted bass abundance following the regulation change, whereas there was an indication of increased abundances of largemouth bass and smallmouth bass, although probably not attributable directly to the differential-harvest regulation.

If black bass abundances in Skiatook Lake were controlled by the effects of the regulation on angler harvest, there should have been changes in survival of all three species, as shown in similar situations by Novinger (1987) and Buynak et al. (1991a). A working hypothesis is that increased abundance of largemouth bass and smallmouth bass would have resulted from decreased harvest and thus increased survival over time. I saw no changes in survival for any of the three species over the three year study period. Assuming constant natural mortality, then only fishing morality can lead to changes in survival (Van Den Avyle 1993). I did not directly measure fishing mortality; however, creel surveys of anglers on Skiatook Lake show decreasing trends in harvest and in the harvest-to-catch ratio for all three species from 1997 through 1999 (Long et al. 2000). These results indicate no increase in fishing mortality and thus verify that the post-regulation trends in spotted bass abundance were not related to the regulation.

Reasons for the increased abundance of largemouth bass and smallmouth bass are unclear, but probably result from natural processes.

Smallmouth bass were initially stocked in 1990 in Skiatook Lake and their relative abundance has increased every year since (Hicks 1994). This population has probably not yet reached carrying capacity and will continue to expand. The largemouth bass population has fluctuated over the lifetime of the reservoir (Hicks 1994) and the trends I observed may represent another population cycle. The constant relative abundance of spotted bass since 1997 suggests an equilibrium level of abundance that will probably continue unless resources fluctuate (Pianka 1994). It is possible that the spotted bass population might have increased along with largemouth bass and smallmouth bass populations and that harvest was insufficient to reduce spotted bass abundance, but sufficient to prevent population increases. However, that is unlikely given the declining harvest of all three black bass species during this study (Long et al. 2000).

In general, minimum-length limits have performed well at restructuring largemouth bass populations (Fox 1975; Novinger 1986; Redmond 1986; Wilde 1997). However, the literature on effects of fisheries management regulations on smallmouth bass and spotted bass populations in reservoirs is sparse at best, making generalizations difficult. Buynak et al. (1991a) provide the only published results of the effects of a differential harvest regulation. Although they found that the regulation was effective at restructuring relative abundances and size structures of largemouth bass and spotted bass populations, these changes were attributed to a reduced minimum-length limit on spotted bass and increased minimum-length limit on largemouth bass. Therefore, it is difficult to determine which of the changes caused the responses in the two species.

Although certain population characteristics other than abundance of each of three black bass species changed during my study, it is not certain that they were directly influenced by the differential harvest regulation. For example, environmental conditions can influence population characteristics and confound interpretations of regulation changes. Novinger (1987) was unable to conclusively demonstrate changes in largemouth bass and spotted bass survival in Table Rock Lake, Missouri because of variations in electrofishing sampling efficiency in several years. These variations were presumably due to differences in the water chemistry. Buynak et al. (1991b) found that they could not evaluate the effects of a regulation change on the largemouth bass populations in Kentucky and Barkley lakes, Kentucky because of a drought that occurred during their study. Most differences in the black bass population characteristics at Skiatook Lake were associated with 1998, which was one of the warmest years on record for the area (National Oceanographic and Atmospheric Administration, unpublished data). For example, mean relative weight of smallmouth bass in spring was lowest in 1998 and growth rates of smallmouth bass were lower in 1998 than in 1999, but the opposite was true for largemouth bass.

Further research is needed to examine the influences of the environment on the black bass populations in Skiatook Lake. Long-term monitoring of the black bass populations is needed to assess the effects of minimum-length regulations on smallmouth bass and spotted bass in reservoirs and the effects of regulations on non-target species.

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Table 1.–Differences between pre- and post-regulation mean electrofishing catch-per-effort (CPE; number of fish per hour) estimates of largemouth bass, smallmouth bass, and spotted bass populations in Skiatook Lake, Oklahoma. N = number of sites and SE = standard error. Data courtesy of the ODWC.

		Largemouth Bass		Smallmouth Bass		Spotted Bass	
Period	N	Mean	SE	Mean	SE	Mean	SE
Pre-regulation	19	80.85	16.88	17.48	6.13	58.01	11.95
Post-regulation	24	81.53	10.57	53.58	13.54	61.48	8.73
t-test		$\underline{P} = 0.97$		$\underline{P} = 0.02$		$\underline{P} = 0.84$	

Table 2.–Electrofishing catch-per-effort (CPE; number of fish per hour) statistics for largemouth bass, smallmouth bass, and spotted bass in Skiatook Lake, Oklahoma in spring and fall 1997, 1998, and 1999. N = number of sites and SE = standard error.

		Largemouth Bass		Smallmouth Bass		Spotted Bass	
Year	N	Mean	SE	Mean	SE	Mean	SE
				Spring			
1997	45	4.38	1.37	3.64	1.79	17.64	2.51
1998	34	7.67	1.58	7.85	2.06	9.71	2.89
1999	40	7.37	1.46	10.96	1.90	15.03	2.67
ANOVA		$P = 0.20$		$P = 0.02$		$P = 0.12$	
Linear		$P = 0.14$		$P < 0.01$		$P = 0.48$	
				Fall			
1997	21	8.49	3.05	10.77	4.67	11.63	4.37
1998	40	7.53	2.15	13.73	3.38	15.93	3.17
1999	37	16.90	2.24	9.63	3.62	18.43	3.30
ANOVA		$P < 0.01$		$P = 0.70$		$P = 0.46$	
Linear		$P = 0.03$		$P = 0.86$		$P = 0.22$	

Table 3.–Electrofishing catch-per-effort (CPE; number of fish per hour) statistics among strata for largemouth bass, smallmouth bass, and spotted bass in Skiatook Lake, Oklahoma in spring and fall. Since the year*stratum interaction was never significant, I grouped data for 1997, 1998, and 1999. N = number of sites and SE = standard error. P-values for ANOVA indicate probability that strata are different. Similar letters indicate no significant difference between means among strata for each species and season at ∝ = 0.05.

		Largemouth Bass		Smallmouth Bass		Spotted Bass	
Stratum	N	Mean	SE	Mean	SE	Mean	SE
				Spring			
Bull Creek	19	4.13zy	2.08	0.24z	2.33	25.27zw	3.55
Hominy Creek	22	2.14y	1.99	0.03z	2.22	2.44y	3.39
lower-lake	59	8.81z	1.19	14.12y	1.33	14.39xw	2.03
mid-lake	19	6.06zy	2.08	1.82z	2.33	15.34w	3.55
ANOVA		$P = 0.02$		$P < 0.01$		$P < 0.01$	
				Fall			
Bull Creek	18	8.78z	3.31	0.15z	4.72	9.73zy	4.73
Hominy Creek	16	5.83z	3.49	0.70z	4.97	1.55zx	4.98
lower-lake	50	12.30z	2.08	21.88y	2.93	19.44y	2.89
mid-lake	14	14.29z	3.86	2.68z	5.50	23.34y	5.51
ANOVA		$P = 0.30$		$P < 0.01$		$P < 0.01$	

Table 4.–Relative weight (*Wr*) statistics for largemouth bass, smallmouth bass, and spotted bass at Skiatook Lake, Oklahoma in spring and fall 1997, 1998, and 1999. SE = standard error, LIN indicates linear trend, and LOF ('lack of fit') indicates quadratic or higher order trend in means among years for each species and season.

	Largemouth Bass		Smallmouth Bass		Spotted Bass	
Year	Mean	SE	Mean	SE	Mean	SE
			Spring			
1997	92.88	1.51	94.99	1.85	104.57	1.36
1998	91.62	1.58	81.20	1.66	92.81	1.87
1999	95.17	1.81	86.72	1.37	96.55	1.89
ANOVA	$P = 0.33$		$P < 0.01$		$P < 0.01$	
LOF	$P = 0.33$		$P < 0.01$		$P < 0.01$	
			Fall			
1997	89.45	2.05	91.16	1.92	93.57	1.48
1998	86.93	1.82	77.96	1.20	84.19	1.46
1999	86.02	1.34	75.67	1.83	83.55	1.52
ANOVA	$P = 0.38$		$P < 0.01$		$P < 0.01$	
LOF	$P = 0.72$		$P < 0.01$		$P < 0.01$	

Table 5.–Electrofishing catch-per-effort (CPE; number of fish per hour) statistics for juvenile largemouth bass, smallmouth bass, and spotted bass in Skiatook Lake, Oklahoma in spring 1997, 1998, and 1999. SE = standard error and linear indicates linear trend in means among years for each species.

	Largemouth Bass		Smallmouth Bass		Spotted Bass	
Year	Mean	SE	Mean	SE	Mean	SE
1997	1.71	0.66	1.41	0.84	6.14	1.06
1998	3.91	0.75	3.76	0.89	3.42	1.16
1999	3.21	0.67	2.50	0.97	3.25	1.14
ANOVA	$\underline{P} = 0.08$		$\underline{P} = 0.16$		$\underline{P} = 0.12$	
Linear	$\underline{P} = 0.11$		$\underline{P} = 0.40$		$\underline{P} = 0.07$	

Table 6.–Sources of variation, F statistics, and P-values for comparing growth among age, growth-year, and age*growth-year interaction using annuli measurements from scales taken in 1997 and 1999 from largemouth bass, smallmouth bass, and spotted bass in Skiatook Lake, Oklahoma.

	Largemouth Bass		Smallmouth Bass		Spotted Bass	
Source	F	P	F	P	F	P
			1997			
Age	10.53	< 0.01	2.48	0.04	0.72	0.72
Growth-year	1.45	0.18	0.41	0.84	0.11	0.99
Age*Growth-year	0.37	0.98	1.47	0.20	0.25	0.99
			1999			
Age	10.70	< 0.01	16.85	< 0.01	18.06	< 0.01
Growth-year	1.13	0.36	0.47	0.80	1.08	0.37
Age*Growth-year	1.53	0.12	0.80	0.63	1.54	0.17

Table 7.–Survival estimates (S) and catch-curve statistics for largemouth bass, smallmouth bass, and spotted bass in Skiatook Lake, Oklahoma as aged by whole otoliths in spring 1997, 1998, and 1999. Similar letters indicate no significant differences in the slopes or y-intercepts (y-int) of the catch-curves at ∝ = 0.05.

	Largemouth Bass			Smallmouth Bass			Spotted Bass		
Year	S	Slope	Y-int	S	Slope	Y-int	S	Slope	Y-int
1997	59.63	-0.51z	2.82z	56.89	-0.56z	2.65z	59.04	-0.53z	3.19z
1998	76.41	-0.27z	2.15z	52.78	-0.64z	2.96z	50.76	-0.68z	3.23z
1999	64.40	-0.44z	2.49z	62.56	-0.47z	2.67z	71.82	-0.33z	2.41z

Table 8.–Proportional stock density (PSD) estimates for largemouth bass, smallmouth bass, and spotted bass in spring and fall 1997, 1998, and 1999 in Skiatook Lake, Oklahoma. Similar letters indicate no significant differences between PSD estimates among years for each species and season at $\propto = 0.017$ ($\propto = 0.05$ corrected for 3 groups with Bonferroni correction).

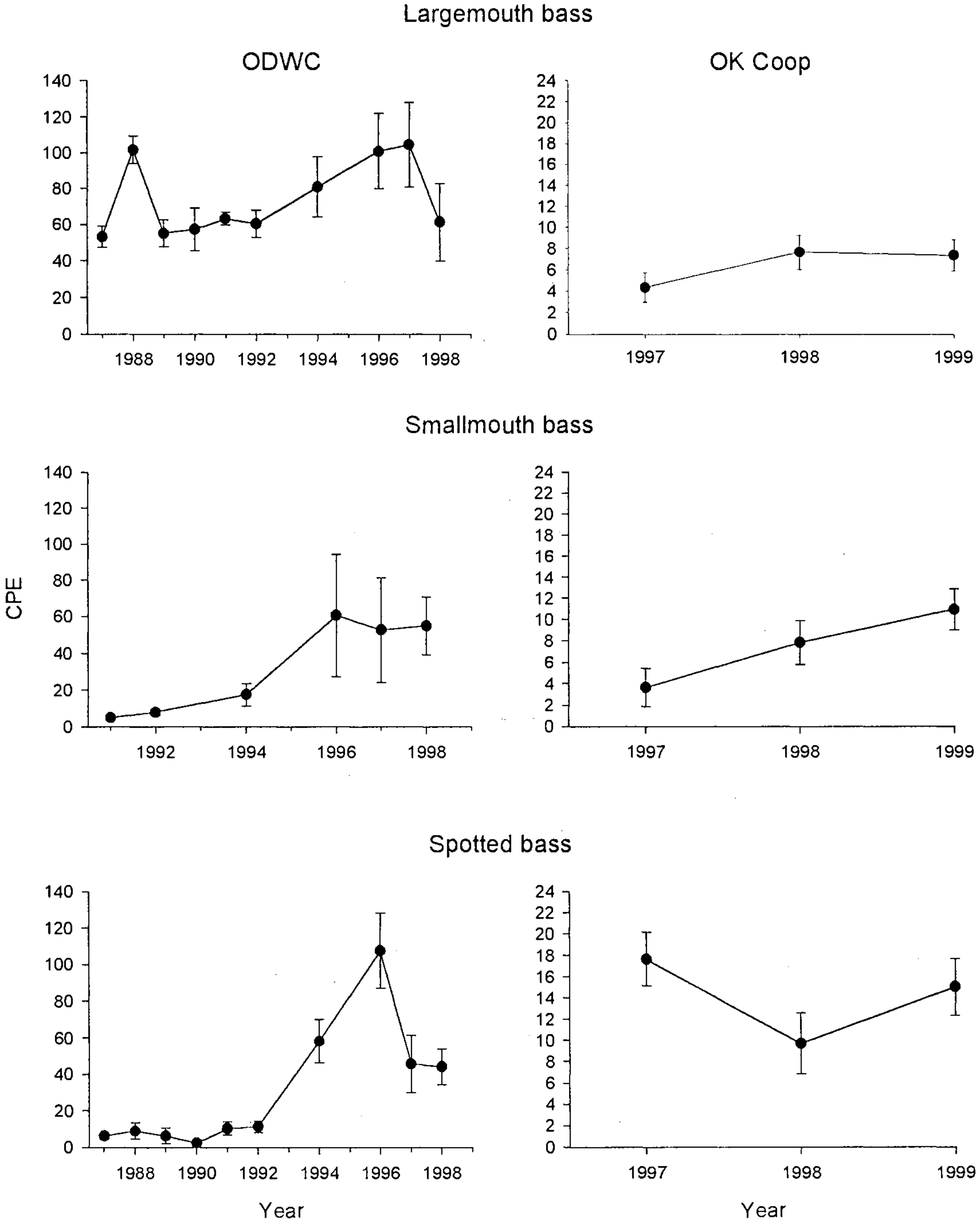
	Largemouth Bass	Smallmouth Bass	Spotted Bass
Year	PSD	PSD	PSD
	Spring		
1997	52.14z	45.45z	28.03z
1998	55.10z	42.67z	26.67z
1999	35.21y	37.86z	40.34z
	Fall		
1997	61.29z	23.68z	34.31z
1998	61.90z	33.00z	48.11z
1999	53.42z	84.85y	66.67z

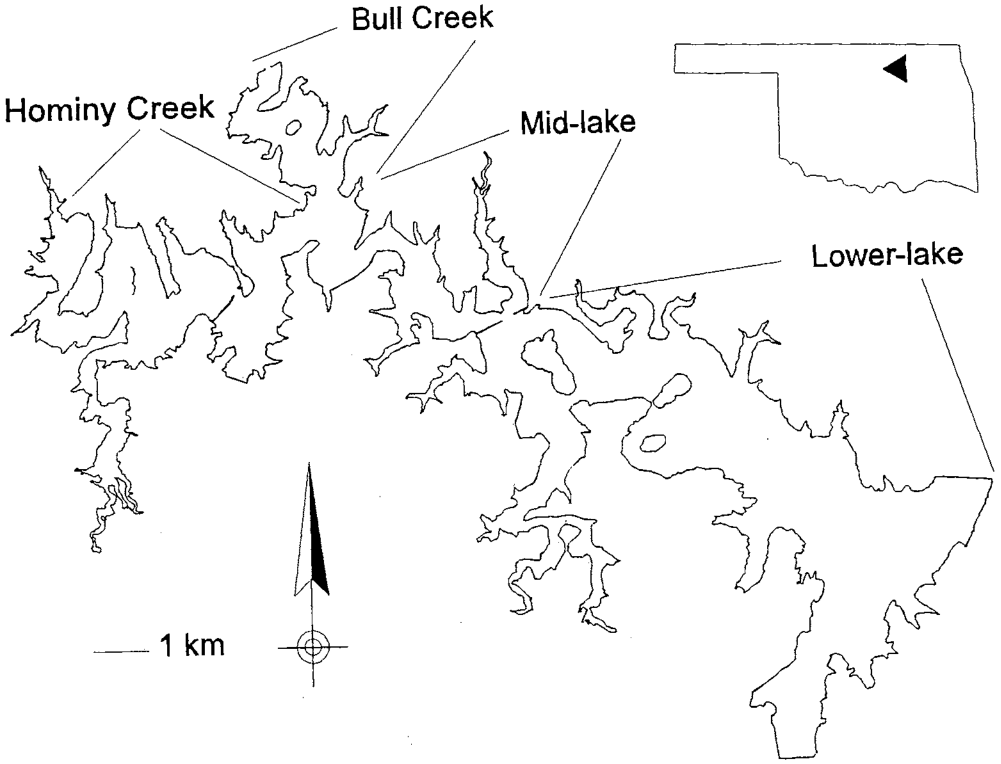
FIGURE LEGENDS

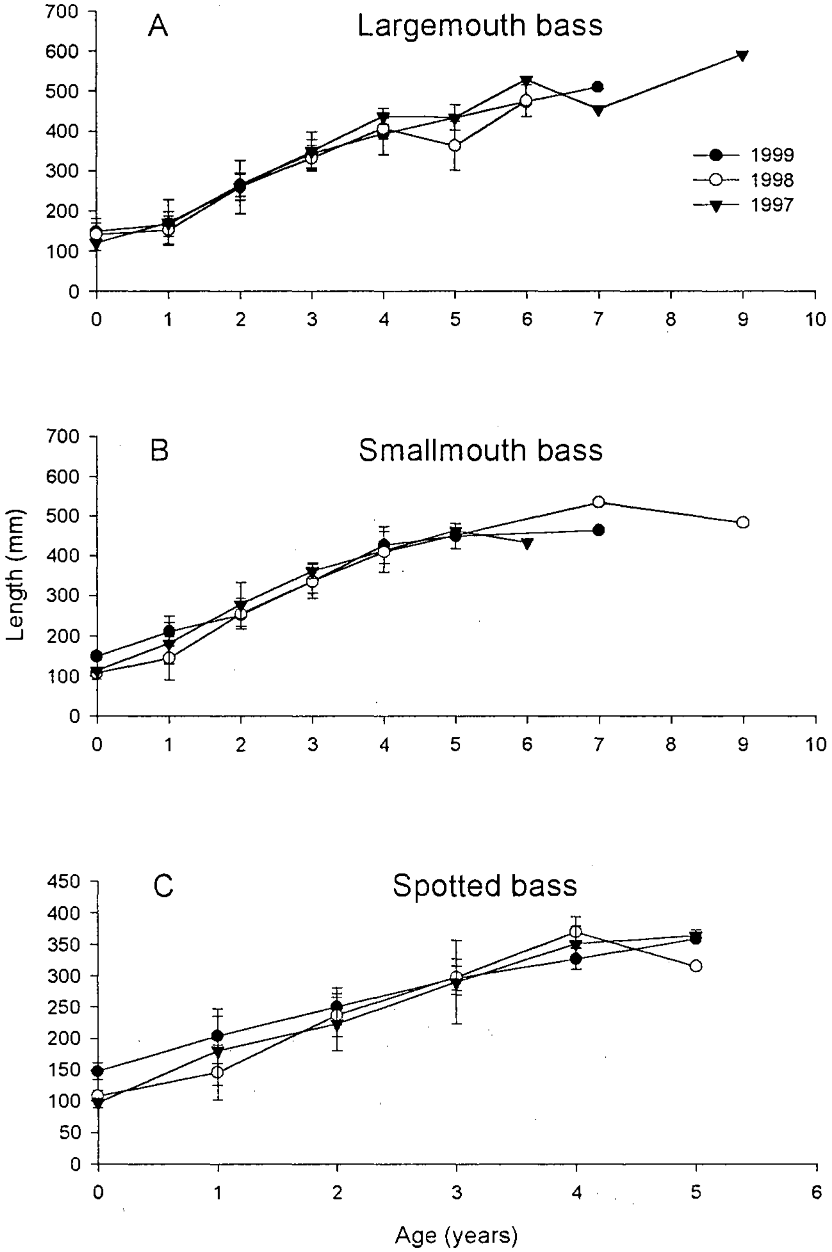
Figure 1.–Trends in mean catch-per-effort (CPE; number of fish per electrofishing hour) of largemouth bass, smallmouth bass, and spotted bass in Skiatook Lake, Oklahoma 1987 - 1999. The left half of the page are data collected by the Oklahoma Department of Wildlife Conservation (ODWC) before (1987 - 1996) and after (1997 - 1998) the differential harvest regulation and the right half of the page are data collected by the Oklahoma Cooperative Fish and Wildlife Research Unit (OK Coop) after (1997 - 1999) the differential harvest regulation. Error bars are 1 standard error on either side of the mean CPE (note differences of scale on y-axes).

Figure 2.–Map of Skiatook Lake, Oklahoma indicating Bull Creek, Hominy Creek, mid-lake, and lower-lake strata.

Figure 3.–Mean length-at-age graphs for largemouth bass, smallmouth bass, and spotted bass from Skiatook Lake, Oklahoma in spring 1997, 1998, and 1999. Error bars are 1 standard deviation on either side of the mean length.


Largemouth bass
ODWC
OK Coop
Smallmouth bass
Spotted bass
CPE
Year
Year
0
20
40
60
80
100
120
140
0
2
4
6
8
10
12
14
16
18
20
22
24
1988
1990
1992
1994
1996
1998
1997
1998
1999


Bull Creek
Hominy Creek
Mid-lake
Lower-lake
1 km



A
Largemouth bass
B
Smallmouth bass
C
Spotted bass
1999
1998
1997
Length (mm)
Age (years)
0
100
200
300
400
500
600
700
0
1
2
3
4
5
6
7
8
9
10
0
50
150
250
350
450

CHAPTER III.

RESOURCE USE AMONG THREE BLACK BASS SPECIES IN A TROPHICALLY HETEROGENOUS OKLAHOMA RESERVOIR

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Abstract.–I examined prey and habitat use by juvenile and adult largemouth bass Micropterus salmoides, smallmouth bass M. dolomieu, and spotted bass M. punctulatus in Skiatook Lake, Oklahoma during spring and fall 1997-1999. The greatest amount of niche segregation for prey was in spring 1997 when juvenile and adult largemouth bass and adult smallmouth bass consumed various fish species, juvenile smallmouth bass and spotted bass consumed insects, and adult spotted bass consumed crayfish. Prey overlap increased, although not significantly, from 1997 to 1999 and all sizes and species consumed fish while adults of all three species also consumed crayfish. Prey overlap was greater than expected from random expectations in all years and seasons after 1997. I measured 22 habitat variables in spring 2000 and fall 1999, summarized those variables with principal components analysis, interpreted the first four axes (PC 1-4), and analyzed habitat use patterns over the three years in spring and fall with stepwise regression of density against the four PC axes. I used geographic information systems (GIS) technology to produce estimates of water quality at sampling sites, to provide visual aid to interpretation of results, and to estimate the effect of spatial autocorrelation. The largest source of variation in habitat (PC 1) was associated with water quality variables (Secchi depth, surface water temperature, and dissolved oxygen) along a longitudinal gradient in the reservoir in spring and fall. Principal component 4 in spring and PC 3 in fall were shoreline axes while the remaining axes were combinations of substrate and cover variables. Density of both size classes of largemouth bass was related to

PC 2 in spring and PC 3 and 4 in fall. Model fit was least in 1997 and increased in 1999, indicating an increase in habitat selectivity possibly due to increased density of competitor species (i.e., smallmouth bass) as proposed by the niche compression hypothesis. Density of both size classes of smallmouth bass was associated with PC 1 in both seasons in all years, and smallmouth bass were restricted to the lower-end of the reservoir. Smallmouth bass densities exhibited significant spatial autocorrelation in spring but not in fall, except in 1997, demonstrating a clumped distribution in spring but uniform in fall. Only one relationship, in spring 1999, was found between density of juvenile spotted bass and habitat in any season or year. Adult spotted bass density was related to similar variables as smallmouth bass in fall, except that PC 3 (i.e., shoreline slope) was often also included in the models of this species. Adult spotted bass densities was associated with either PC 2 or 3 in spring. These results indicate that largemouth bass is a habitat generalist, smallmouth bass is a habitat specialist, and that spotted bass use habitat most similar to smallmouth bass, but exhibit seasonal differences in Skiatook Lake. Habitat was most likely stronger than prey in segregating the niches of these three species in Skiatook Lake, although finer scale measurements are needed to verify this hypothesis.

The genus Micropterus is composed of at least six black bass species, the most widespread of which are largemouth bass M. salmoides, smallmouth bass M. dolomieu, and spotted bass M. punctulatus (Robbins and MacCrimmon 1974; Coble 1975; Heidinger 1975; Vogele 1975). These three species are economically important sportfishes, ecologically similar, occur sympatrically in reservoirs in the southeastern United States, and have been extensively studied (Aggus 1972; Lewis 1976; Farquhar and Whiteside 1995; Scott and Angermeier 1998; Ward and Newmann 1998). An interest among ecologists studying sympatric, ecologically-similar species is interspecific resource partitioning (Schoener 1970; Ross 1986; Stauffer et al. 1996), because resource partitioning is one mechanism that allows for coexistence of competing species (Schoener 1974).

Schoener (1974) concluded that important resources, in descending order, were habitat, food, and time. However, his synthesis poorly represented studies on fish. Ross (1986) reviewed resource partitioning studies for fish assemblages and reported that among 37 studies that incorporated all three major groups of resources, most (57%) exhibited segregation by food, followed by habitat (32%) and time (11%).

Resource partitioning among black bass species seems primarily related to habitat. Miller (1975) reported differences in habitat preferences among largemouth bass, smallmouth bass, and spotted bass, with largemouth bass preferring lacustrine environments with abundant vegetation, smallmouth bass preferring clear, cooler areas of rivers and lakes, and spotted bass utilizing areas intermediate to those preferred by the other two species. Buynak et al. (1989) found longitudinal segregation of three black bass species in Cave Run Lake, Kentucky with largemouth bass more abundant in the eutrophic upper end, spotted bass more abundant in the lower and middle lake, and smallmouth bass more abundant in the oligotrophic lower end. Janssen (1992) concluded that largemouth bass, smallmouth bass, and spotted bass segregated by habitat but not by food resources in the upper portion of Pickwick Reservoir, Alabama, and that prey consumption was habitat specific for prey other than fish and insects. Farquhar and Whiteside (1995) examined habitat and food differences among native Guadalupe bass (M. treculi), largemouth bass, and non-native smallmouth bass in the Blanco River, Texas. They found largemouth bass inhabited areas with wood and mud/silt substrate, whereas smallmouth bass inhabited areas with rocks, and Guadalupe bass inhabited areas with rocks and wood. Additionally, largemouth bass consumed more fish than either smallmouth bass or Guadalupe bass, both of which consumed more aquatic insects. Their study primarily focused on the potential negative impacts of smallmouth bass introduction in the Blanco River, and they concluded that smallmouth bass and Guadalupe bass segregated by habitat more than by prey, but that largemouth bass were segregated from both species by habitat and prey. Scott and Angermeier (1998) studied habitat and prey use between smallmouth bass and spotted bass in impounded and riverine sections of the New River, Virginia. They found segregation for habitat on two scales: between impounded and riverine sections and within each section. Spotted bass were predominately found in the reservoir and smallmouth bass in the river portion. Within the reservoir, spotted bass were widely distributed whereas smallmouth bass were concentrated in steep-sloping dropoffs with rock substrate. Within the river, spotted bass were restricted to habitats near banks away from high flow but smallmouth bass were not. Both species ate predominately the same forage items and differed only in proportion consumed. Long and Fisher (in press) found segregation for prey among two sizes of sympatric largemouth bass, smallmouth bass, and spotted bass in Skiatook Lake, Oklahoma in one year but little segregation two years later. They did not assess habitat but hypothesized that it may be more important than prey in segregating the three species in that reservoir.

Intraspecific resource partitioning among black bass species can also be important in niche segregation. Wanjala et al. (1986) found that three size groups of largemouth bass in Alamo Lake, Arizona segregated by habitat and prey resources. They found small fish restricted to the littoral zone, intermediate-sized fish in the limnetic zone, whereas large fish occurred as solitary individuals near submerged structure. Lynch and Johnson (1989) experimentally showed size-related use of structure by largemouth bass, with small (<300 mm) individuals using a wider range in size of interstitial spaces than larger fish, which were confined to the largest interstice size structure. Janssen (1992) showed body length to be important in determining habitat use within and among largemouth bass, smallmouth bass, and spotted bass. Long (1995) found that larger largemouth bass in experimental pools preferentially used different artificial structures than smaller individuals when structure was abundant and could displace smaller ones from areas preferred by both size groups.

In this paper, I assessed resource (habitat and food) use by two size classes of sympatric populations of the three black bass species in Skiatook Lake, Oklahoma.

STUDY SITE

Skiatook Lake is a 4,266-ha flood-control impoundment of Hominy Creek in north-central Oklahoma that was formed in 1984 by the U.S. Army Corps of Engineers. The lake has a mean depth of 9.7 m and a shoreline development index of 11.3. The lake perimeter consists largely of steep, bedrock substrata with little aquatic vegetation. The upper end of the reservoir is more turbid than the lower end, with average Secchi depths in the spring of 0.1 m and 1.2 m, respectively. Additionally, there is a longitudinal gradient in primary productivity with higher chlorophyll-a concentrations in the upper end than in the lower end (Fisher et al. 2000). The top of the conservation pool is 217.6 m above mean sea level. Largemouth bass were supplementally stocked in 1985 and 1986 and non-native smallmouth bass were stocked in 1990 and 1991. Other sportfish species in the lake consist mainly of spotted bass, sunfish Lepomis spp., hybrid striped bass Morone saxatilis X M. chrysops, walleye, channel catfish Ictalurus punctatus, and flathead catfish Pylodictis olivaris.

METHODS

Black Bass Sampling

I sampled black bass with night-time, boat-mounted electrofishing during spring and fall 1997-1999 using a stratified-random design (Wilde and Fisher 1996). I stratified Skiatook Lake into four areas (lower-lake, mid-lake, Hominy Creek, and Bull Creek) based on morphometry and Secchi depth measurements (Figure 1). Sampling sites were identified by delineating shoreline habitat types in a Geographic Information Systems (GIS) database and randomly selected within strata for each season and year. At least 10% of the shoreline was sampled. Habitat types consisted of substrate and cover-type combinations classified by surveying the entire perimeter of Skiatook Lake by boat in winter 1996. Sites selected for sampling were electrofished with varying amounts of effort, depending on site length and habitat complexity. All black bass captured were identified and measured to the nearest 1 mm total length. I classified each species into two size classes, juveniles and adults, according to the upper end of the central 50% length range for age-one fish in Oklahoma waters, as reported by Carlander (1977). Thus, largemouth bass less than 226 mm, smallmouth bass less than 185 mm, and spotted bass less than 178 mm were considered juveniles.

Electrofishing sampling sites in the GIS were converted from lines to polygons by creating 10-m buffers inside the reservoir boundary using ArcView. Ten meters was chosen because it represented the approximate maximum area that the electrofishing boat sampled. Numbers of each size class of the three species of black bass were added as attributes to these sampling sites in the GIS database and the density of each size class/species combination was estimated for each sampling site. I tested for differences among years for each size/species/season combination with ANOVA (SAS Institute 1992). I tested for the existence of spatial autocorrelation for each species in each year and season by calculating Moran's I and performing randomization tests using ROOKCASE (Sawada 1999). Spatial autocorrelation is a measure of association of a single variable in relation to the proximity and similarity of values for that variable in space. For example, if sites close to each other tend to have high values for a common variable, then that variable would exhibit positive spatial autocorrelation. Values of Moran's I tend to range between -1 and +1; values near -1 indicate that sampling sites close together have dissimilar densities of each black bass species, values near +1 indicate that sampling sites near each other have similar black bass densities, and values near 0 indicate a more random distribution of black bass densities among sampling sites.

Prey Use

During spring electrofishing in 1997-1999, black bass were sacrificed by placing them on ice immediately after capture and prey items were removed from the stomach via dissection. Dissection was used because a concurrent study of black bass in this reservoir required removing otoliths for age analysis that also requires sacrificing the fish (DeVries and Frie 1996). During fall electrofishing in 1998-1999, I used acrylic tubes (Van Den Avyle and Roussel 1980; Caliteux et al. 1990) to remove prey items from the stomachs of all captured black bass and returned the fish to the water. Prey use was not assessed in fall 1997. Preliminary analysis of the spring 1997 data showed that prey segregation among these three species in Skiatook Lake could be accurately shown with only four categories; thus, I identified prey accordingly as fish, crayfish, insects, and miscellaneous.

Habitat Use

I scanned the five 7.5' topographic maps (USGS 1966, photo-revised 1983) that contained the boundaries of Skiatook Lake and exported them into ArcView (Environmental Systems Research Institute, Redlands, California) GIS software. This GIS coverage was then used to produce a digital elevation model (DEM) using ARC/INFO (Environmental Systems Research Institute, Redlands, California; Figure 2). A DEM interprets the discrete values assigned to contour lines and interpolates values between them to create a smooth surface that represents the topography of the coverage. The DEM was used to compute shoreline slope in ArcView.

Substrate types (based on particle size using the modified Wentworth scale) and cover types (dominant features seen above the water surface) were classified, delineated using shoreline landmarks, and added as binary codes. The main river channel and the location of the dam was delineated from the topographic map and distances from these features to the sampling sites were calculated using GIS. In fall 1999 and spring 2000, I conducted longitudinal sampling of four physicochemical variables (Secchi depth, surface water temperature, surface dissolved oxygen, and surface conductivity) from 30 fixed stations throughout the reservoir to quantify the spatial limnological characteristics of the reservoir (Figure 3). Four longitudinal samples each were collected during fall 1999 and spring 2000.

I used the ArcView GIS to interpolate values between sampling sites to create a smooth surface of the entire reservoir for each physicochemical variable in each season. These surfaces were then used to calculate and visually display the mean and variance of each of the four physicochemical variables in spring and fall. I used inverse direct weighting (IDW) and nearest neighbor distance with three neighbors as the interpolation method in ArcView (Environmental Systems Research Institute, Inc. 1998). All surfaces created with the GIS were based on a 10x10-m cell size to correspond with the 10-m polygons created for the electrofishing sampling sites.

Statistical Methods

Prey use.–I calculated frequency of occurrence (number of stomachs containing one or more of a particular prey type) and compared prey use among juvenile and adult size largemouth bass, smallmouth bass, and spotted bass with Chi-square (SAS Institute 1992). I compared prey overlap by calculating Pianka's (1973) index of niche overlap for each season and year and then compared the overlap values among seasons and years with ANOVA and least square means (LSMEANS) for pairwise comparisons (SAS Institute 1992) to look for temporal patterns in prey overlap. I tested the degree of niche overlap with randomization tests using EcoSim 4.0 software (Gotelli and Entsminger 1999) to ascertain whether or not mean niche overlap was greater than expected by chance for each season and year.

Habitat use.–I used principal components analysis (PCA; ter Braak 1995) on the physicochemical characteristics of the reservoir measured in fall 1999 and spring 2000 to determine the most important environmental gradients in the reservoir in each season. Habitat data were standardized to account for differences in measurement scales, binary variables were entered as dummy variables, and the eigenvalues and corresponding eigenvectors of the first four principal components (axes) were calculated. I regressed density of each size/bass species combination against the first four principal components (PC 1-4) using a stepwise approach and $\propto = 0.05$ for including variables in the models (SAS Institute 1992) to examine the relationship between habitat and density in fall and spring 1997-1999. The site scores for the first four principal components in fall 1999 and spring 2000 were then interpolated among sampling sites in the ArcView GIS to produce surface maps as visual aids to interpretation. Interpolation methods followed the methods previously mentioned in the habitat use section.

I only used the habitat variables in fall 1999 and spring 2000 because I assumed they represented the spatial variability that occurred in the reservoir over the sampling period better than concurrent measurements taken during electrofishing. To verify this assumption, I used a two-way ANOVA to test for differences in water quality variables measured concurrently with fish sampling (e.g., surface water temperature, conductivity, and dissolved oxygen) among years and strata for each season. A non-significant interaction would show that the spatial arrangement of that variable was constant over the three year study period.

RESULTS

Black Bass Density

Adult largemouth bass and juvenile spotted bass densities were not significantly different among years in spring ($\underline{P} = 0.79$ and > 0.05, respectively; Table 1) or fall ($\underline{P} = 0.57$ and 0.31, respectively; Table 2). Juvenile largemouth bass densities were not significantly different among years in spring ($\underline{P} = 0.13$)

but were depressed in fall 1998 ($\underline{P} < 0.01$). Adult smallmouth bass densities were greatest in spring 1999 ($\underline{P} = 0.02$) but constant in fall ($\underline{P} = 0.07$). Juvenile smallmouth bass densities were similar among years in spring ($\underline{P} = 0.15$) and greatest in fall 1997 ($\underline{P} < 0.01$). Adult spotted bass exhibited their lowest densities in spring 1999 ($\underline{P} = 0.02$) but remained constant among years in fall ($\underline{P} = 0.31$).

Largemouth bass showed no evidence of spatial autocorrelation ($\underline{P} > 0.05$), except for juveniles in fall 1999 (Moran's $I = 0.22$, $\underline{P} = 0.02$). Smallmouth bass always exhibited spatial autocorrelation in spring ($\underline{P} < 0.03$) with Moran's I ranging from 0.20 to 0.43. However, in fall smallmouth bass only exhibited significant spatial autocorrelation in 1997 ($I = 0.31$, $\underline{P} < 0.02$ for juveniles and $I = 0.58$, $\underline{P} < 0.01$ for adults). There was no evidence of spatial autocorrelation for spotted bass except for adults in fall 1997 ($I = 0.42$, $\underline{P} = 0.02$) and 1998 ($I = 0.13$, $\underline{P} = 0.04$).

Prey Use

Prey use among the two size classes of black bass differed by season and year (Chi-square $\underline{P} < 0.01$ for each season and year; Figure 4). Juvenile and adult largemouth bass were mainly piscivorous, whereas adult spotted bass mainly consumed crayfish. In fall, juvenile smallmouth bass and juvenile spotted bass consumed insects, but fish contributed more to their diet in spring. The diet of adult smallmouth bass showed marked temporal variation, with the dominant items being insects in spring 1997, fish and crayfish in spring 1999, crayfish in fall 1999, and fish in fall 1998.

Mean niche overlap ranged from 0.70 in spring 1997 to 0.84 in fall 1999 (Table 3). Overlap was not significantly different among seasons and years ($\underline{P}$ = 0.09). Niche overlap was greater than expected by chance ($\underline{P} < 0.01$) in fall 1998 and 1999 and in spring 1999, but not in spring 1997 or 1998 ($\underline{P} > 0.05$; Table 3).

Habitat Use

Spring.–Summary statistics and explanation of variable names for habitat variables in spring are found in Table 4. There was not a significant interaction between year and stratum for water temperature ($\underline{P}$ = 0.91) or dissolved oxygen ($\underline{P} > 0.05$), but there was a significant interaction for conductivity ($\underline{P} < 0.01$). Thus, the assumption of similar spatial arrangement of water quality variables among years was verified for water temperature and dissolved oxygen, but not for conductivity; therefore conductivity was excluded from the PCA.

The first four principal components of the habitat variables explained 59.8% of the variation. The first axis explained 28.1% of the variation and represented longitudinal variation in water quality (Table 5; Figure 5, 6, and 7). High factor loadings ($\geq|0.30|$) for the first principal component (Table 5; Figure 7) corresponded with high mean Secchi depth and mean dissolved oxygen and low mean surface water temperature in the lower end of the reservoir (Figure 5).

Prinicipal component 2 was a physical structure axis representing distance to river channel, presence of standing timber, and also longitudinal variation in Secchi depth which was greatest in the mid-reach and the southwestern end of the reservoir (Figure 6 and 7). Principal component 3 was a cover and substrate axis and principal component 4 was a shoreline slope axis.

The relationships between habitat variables and density of each size class and black bass species in each year were variable. I found no significant models for juvenile largemouth bass in 1997 or 1998 (Table 6). In 1999, juvenile largemouth bass density was associated with PC 2. No significant model was found for adult largemouth bass in 1998, but density was positively associated with PC 2 in 1997 and 1999. Juvenile smallmouth bass were positively associated with PC 1 and PC 3 in 1997 and with PC 1 in 1998 and 1999. Adult smallmouth bass were positively associated with PC 1 in 1997 and 1998. In 1999, adult smallmouth bass were positively associated with PC 1 and negatively associated with PC 4. No significant model was found for juvenile spotted bass in 1997 or 1998, but in 1999 there was a positive association with PC 3. Adult spotted bass were positively associated with PC 3 in 1997 and with PC 2 in 1998.

Fall.–Summary statistics and explanation of variable names for habitat variables in fall are found in Table 7. There was not a significant interaction between year and stratum for dissolved oxygen ($\underline{P} = 0.08$). However, there was a significant interaction for conductivity ($\underline{P} < 0.01$) and water temperature ($\underline{P} <$

0.01). Therefore, the assumption of similar spatial arrangement of water quality variables among years was verified for dissolved oxygen, but not for conductivity or water temperature. Conductivity and water temperature were, therefore, excluded from the PCA in fall.

The first four principal components of the habitat variables explained 64.1% of the variation with the first axis, again, representing longitudinal variation in water quality parameters (Table 8; Figure 5,6, and 7). High PC 1 factor loadings (Table 8; Figure 7) corresponded with high mean Secchi depths in the lower end of the reservoir, while low PC 1 factor loadings corresponded with high dissolved oxygen in the upper-end (Figure 5). The spatial distribution of mean dissolved oxygen and variance of dissolved oxygen in fall 1999 was the opposite of the trend in spring 2000 (Figure 5 and 6). Principal component 2 represented substrate and cover types, principal component 3 was a shoreline slope, substrate, and cover axis, and principal component 4 was a fallen timber, substrate, and distance to main river channel axis.

Relationships between habitat and density generally were different in fall compared to spring, except for smallmouth bass. In 1997 and 1998, I found no significant relationships between juvenile largemouth bass density and any of the environmental variables (Table 9). In 1999, juvenile largemouth bass were positively associated with PC 3. Adult largemouth bass were not associated with any PC axis in 1997, positively with PC 4 in 1998, and positively with PC 4 and negatively with PC 2 in 1999. Juvenile smallmouth bass were positively associated with PC 1 in 1997 and with PC 1 and PC 4 in 1998. No model was significant for juvenile smallmouth bass in 1999. Adult smallmouth bass were positively associated with PC 1 in 1997, 1998, and 1999. No significant models were produced for juvenile spotted bass in fall. Adult spotted bass were positively associated with PC 1 and 3 in 1997, with PC 1,3, and 4 in 1998, and with PC 4 in 1999.

DISCUSSION

Prey Use

I found evidence of niche segregation among the three black bass species in Skiatook Lake by prey type. However, there was also evidence of an increase in prey overlap by the end of the study. Although significant increases in prey overlap were lacking, overlap increased each year and randomization tests showed that overlap was greater than expected by chance for every year after 1998. There are at least two alternative explanations for the observed changes in prey overlap. The first is that a competitive "crunch" for prey may have occurred, allowing for a concomitant increase in prey overlap (Matthews 1998). Both smallmouth bass densities and prey overlap increased over the study period. Prey abundance apparently decreased over the study period, which may have led to increased prey overlap. Long and Fisher (in press), using unpublished data from the Oklahoma Department of Wildlife Conservation, reported a declining trend in abundance of the major forage fish, bluegill Lepomis macrochirus and gizzard shad Dorosoma cepedianum. Additionally, relative weights for smallmouth bass and spotted bass declined over the study period (Chapter II of this dissertation). This evidence suggests there was a competitive "crunch" for prey resources, increasing the similarity of diets among these three species over the sampling period.

Another trend in diet composition for most species was an increased use of crayfish from 1997 to 1999. Since I did not collect available prey data, I can only speculate on what effects crayfish abundance might have had on interpretation of these results. If crayfish had increased, then these bass may have simply been taking advantage of another abundant prey source which would have caused the increased prey overlap. Black bass are known to be prey generalists (Coble 1975; Heidinger 1975; Vogele 1975), taking advantage of whatever prey is available. Therefore, the changes in diet overlap might still be due to changes in the composition of the prey base rather than increased competition.

The use of only four prey categories in the analysis could have affected my interpretation of the results (Schoener 1968). However, the effect would be only in the magnitude of the prey overlap values and would have increased them. The use of the randomization tests put the overlap values in context of the level of resolution of the data, rather than relying on an arbitrary rule of thumb (i.e., using 0.60 as "high" and therefore indicating competition).

Additionally, Long and Fisher (in press) using data from the same species and lake during the study period but with finer grained prey groupings (13 groups in 1997 and 15 groups in 1999), found similar results.

Habitat Use

Of the 12 possible models that were generated for largemouth bass, juveniles and adults in spring and fall 1997 through 1999, only six were statistically significant. Of those models that were significant, all had low explanatory power, with the exception of spring 1999. This leads me to conclude that largemouth bass, as juveniles and adults, have low preference for any particular habitat type and are habitat generalists in Skiatook Lake. The significant models that were derived mostly showed relationships with environmental variables (PC axes) that differed from the other bass species, indicating some habitat segregation. For example, in spring, largemouth were positively associated with PC 2 in 1997 and 1999 and no other species showed an association with that variable in the same year.

The increased explanatory power of the models in spring 1999 suggests increasing habitat specialization over time. In spring 1997, the coefficient of determination for adult largemouth bass was 0.12, but increased to 0.37 in 1999. One explanation for this increase is that smallmouth bass density increased during the same time, and they may have driven largemouth bass out of some habitats, resulting in increased habitat specialization by largemouth bass. One hypothesis, the expanding population hypothesis (Pianka 1994) states that the range of resources used by an organism will increase under an expanding population. This hypothesis might explain the increase in habitat "preference" by largemouth bass, if largemouth bass and smallmouth bass are considered as one population. But, my results contradict the predictions of the hypothesis (i.e., range of habitat use shrank, not vice-versa). Alternatively, largemouth bass may have responded with increased habitat use due to decreased densities of the other potential competitor, spotted bass. This hypothesis, termed ecological release (Pianka 1994), states that niches tend to expand under conditions of reduced competition. If the change in habitat specialization by largemouth bass was due to decreased spotted bass density, then my results would have been the opposite of what I observed. Another hypothesis, the niche compression hypothesis (Pianka 1994), might better explain my results. This hypothesis states that as competition among species increases over ecological time, habitat use will narrow and prey use will broaden. This is precisely what I found for largemouth bass in Skiatook Lake.

Werner and Hall (1979) demonstrated similar results with other centrarchids. They used three Lepomis spp. and demonstrated that each species preferred one common habitat type when alone, but each preferred another different type when together. These species were simply choosing a habitat type that they were best able to exploit in the presence of competitors resulting in decreases habitat niche breadth for two of the three species. The remaining species was better able to use the one habitat preferred by all species and therefore its' habitat niche breadth was not altered. In a paper summarizing his research involving niche shifts and habitat use in centrarchids, Werner (1984) stated that his overall data conformed to the niche compression model. In Skiatook Lake, largemouth bass apparently were narrowing their habitat niche breadth in response to an increase in smallmouth bass densities.

Smallmouth bass was the most specialized species in terms of habitat. Juveniles and adults were consistently and positively associated with variation in water quality (PC 1). The strengths of those relationships were generally greater for this species than for other species and were related to season. In spring, coefficients of determination were higher than in the corresponding fall indicating expanded habitat use in fall, although it was still related to PC 1 variables (i.e., water quality). Personal observations during sampling corroborated these results. In fall, the upper end of the reservoir tended to be less turbid than in spring, and I often caught more smallmouth bass in the upper end compared to spring sampling. Buynak et al. (1989) noted that smallmouth bass in Cave Run Lake, Kentucky were also more abundant in the lower, oligotrophic end and less abundant in the eutrophic, upper end. However, they did not look at seasonal trends in smallmouth bass distribution. Other studies that have examined seasonal habitat use by smallmouth bass in reservoirs include Hubert and Lackey (1980) in Pickwick Reservoir, Tennessee and Kraai et al. (1991) in Meredith Reservoir, Texas. However, both of these studies examined habitat use by individual fish at microhabitat scales and neither noted distributional patterns over the entire reservoir. Hubert and Lackey (1980) found no relationship between habitat use by smallmouth bass and turbidity, no relationship between habitat use and specific cover types, that smallmouth bass were always in the range of tolerable water temperatures, and noted that movement was dependent on season, but not between spring and fall. They concluded by stating that smallmouth bass distribution was influenced by bottom contour and presence of cover. Kraai et al. (1991) evaluated habitat use by smallmouth bass in Meredith Reservoir by examining seasonal relationships between number of locations found by ultrasonic telemetry and distance from shore, depth, and physical habitat (i.e., substrate and cover). They found that smallmouth bass were located farther from shore in winter and summer than in spring and fall.

Although other researchers have found relationships between smallmouth bass and habitat (Rankin 1986; Todd and Rabeni 1989; Kraai et al. 1991), Bevelhimer (1996) found through experimental manipulation that smallmouth bass habitat use was associated with water quality (i.e., temperature) and food availability. In a thermally graduated environment, smallmouth bass used cover in areas with higher-than-optimal water temperature over areas with no cover and optimal water temperature. Therefore, on a large scale (i.e., entire reservoir) with uniform cover and forage availability, water quality is probably the primary cue that smallmouth bass use to determine macrohabitat use in reservoirs. Additionally, as conditions change, smallmouth bass adapt by expanding or contracting their range within the reservoir. Within these areas of suitable water quality, smallmouth bass may then use habitat on a smaller scale. I have no data on forage availability and distribution in Skiatook Lake, but the PCA of habitat shows that cover is largely uniform throughout the reservoir suggesting that smallmouth bass distribution in Skiatook Lake is determined largely by water quality.

I found with the measures of spatial autocorrelation further evidence for within-lake expansion by smallmouth bass in fall. In spring, spatial autocorrelation was higher from random expectations indicating a clumped distribution. Conversely, in fall, spatial autocorrelation was high only in 1997 but not in 1998 or 1999. This lack of autocorrelation indicated a more random distribution during fall which agrees with my personal observations of more smallmouth bass in the upper end of the lake in fall compared to spring.

Associations between spotted bass density and habitat were variable among years and seasons. No significant relationships were found for juvenile spotted bass in fall and only in spring 1999. Adult spotted bass were associated with PC 3 in spring 1997 and PC 2 in spring 1998, but with no PC axes in spring 1999, indicating a lack of consistent habitat preference. In fall, however, habitat preferences by adult spotted bass were markedly different from spring with different habitat variables being utilized. In fall, spotted bass were associated with PC 1 and PC 3 in two of three years and with PC 4 in two of three years.

The differences in habitat associations between seasons may be due, in part, to differences in abundance within the reservoir between seasons. In Chapter II of this dissertation, I found that spotted bass were more abundant in the upper end in spring but more abundant in the lower end in fall. Additionally, smallmouth bass occurred primarily in the lower end of the reservoir. Therefore, spotted bass and smallmouth bass had more potential to interact in fall than in spring due to overlap in distributions. In fall, spotted bass were associated with similar variables as smallmouth bass (PC 1, water quality variables) but spotted bass were also associated with other variables (PC 3, shoreline slope; and PC 4, proximity to river channel and bedrock substrate). This suggests that in fall, spotted bass preferred suitable water quality and additional physical features (i.e., high shoreline slope near bedrock close to the main river channel), possibly as a means to segregate habitat when their distribution overlapped with smallmouth bass. In spring, spotted bass distribution did not overlap that of smallmouth bass to a great extent, and spotted bass then used habitats other than those used in fall.

Jenkins (1975) found that standing crop of spotted bass was inversely related to that of smallmouth bass, indicating either very different or very similar habitat requirements. He suggested the former explanation inferring that the reservoirs with high smallmouth bass numbers exist because they have optimal conditions for smallmouth bass (e.g. cool water). However, the latter explanation would suggest that because smallmouth bass and spotted bass have such similar habitat preferences that only one can exist in high densities. Buynak et al. (1989) showed that spotted bass were more abundant in areas that contained smallmouth bass than in areas with largemouth bass suggesting similar habitat preferences between smallmouth bass and spotted bass. My data show that smallmouth bass densities have increased and that spotted bass densities have decreased. Since there has not been an increase in harvest or mortality of either of these two species (Fisher et al. 2000), it seems more than coincidental that this trend should have occurred. Since smallmouth bass were not introduced to the Skiatook Lake drainage until 1990, but have been increasing in abundance, suggests that this species has impacted the abundance of spotted bass in Skiatook Lake. The seasonal shift in habitat use on a reservoir scale may serve as a mechanism that allows spotted bass to coexist with smallmouth bass in Skiatook Lake at reasonably high densities.

Conclusions

Others have found that black bass segregate by habitat more markedly than by prey (Janssen 1992; Scott and Angermeier 1998) and my results generally agree. In Skiatook Lake, prey overlap among juveniles and adults of these three black bass species increased from 1997 to 1999 while habitat preferences remained consistent or increased, although there were some seasonal differences in habitat use. Increased overlap in prey use, coupled with an increase in habitat preference, is predicted by the niche compression hypothesis (Pianka 1994) and corresponds with the data for largemouth bass in Skiatook Lake during this study period. However, the niche compression hypothesis does not fit for smallmouth bass and spotted bass in Skiatook Lake. But, largemouth bass has more generalized preferences for habitat and prey than the other bass species (Heidinger 1975) in Skiatook Lake and, therefore, is more likely than smallmouth bass or spotted bass to change preferences.

I know of no other literature on seasonal differences in habitat use by spotted bass. Additional research that would be useful would not only incorporate seasonal effects within reservoirs but measures of habitat use on several levels, from macro- to micro-.

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Table 1.–Summary statistics of density (number of fish per hectare) of juvenile and adult largemouth bass, smallmouth bass, and spotted bass in spring samples in Skiatook Lake, Oklahoma. N = number of sampling sites.

		Largemouth Bass		Smallmouth Bass		Spotted Bass	
Year	N	Mean	SD	Mean	SD	Mean	SD
				Juvenile			
1997	45	1.23	2.51	1.12	2.82	3.96	7.55
1998	35	2.60	3.62	2.42	3.90	2.19	3.71
1999	40	1.90	2.96	1.15	3.11	1.21	2.11
_P_-value		0.13		0.15		>0.05	
				Adult			
1997	45	2.67	5.38	2.29	4.89	14.92	21.92
1998	35	3.52	5.24	3.00	4.44	5.80	6.99
1999	40	3.09	6.05	6.59	10.47	8.15	8.87
_P_-value		0.79		0.02		0.02	

Table 2.–Summary statistics of density (number of fish per hectare) of juvenile and adult largemouth bass, smallmouth bass, and spotted bass in fall samples in Skiatook Lake, Oklahoma. N = number of sampling sites.

		Largemouth Bass		Smallmouth Bass		Spotted Bass	
Year	N	Mean	SD	Mean	SD	Mean	SD
				Juvenile			
1997	22	3.89	3.78	6.79	12.68	3.09	6.85
1998	40	0.68	1.61	1.13	2.58	1.42	3.40
1999	37	2.79	3.65	0.85	3.15	3.41	7.36
_P_-value		<0.01		<0.01		0.31	
				Adult			
1997	22	3.43	6.27	5.37	10.67	7.58	7.65
1998	40	2.19	3.36	5.40	11.56	6.27	8.70
1999	37	2.91	4.60	1.03	2.28	3.87	6.26
_P_-value		0.57		0.07		0.31	

Table 3.–Pianka's (1973) niche overlap values of prey use among juvenile (J) and adult (A) largemouth bass (LMB), smallmouth bass (SMB), and spotted bass (SPB) in spring 1997 - 1999 and fall 1998 - 1999 in Skiatook Lake, Oklahoma. P-values are the probability that the mean niche overlap values could have occurred by chance.

	Spring			Fall	
Species Pairs	1997	1998	1999	1998	1999
ALMB-ASMB	0.75	0.86	0.90	0.93	0.88
ALMB-ASPB	0.43	0.66	0.78	0.51	0.91
ALMB-JLMB	0.84	0.94	0.98	0.99	0.90
ALMB-JSMB	0.81	0.45	0.63	0.94	0.90
ALMB-JSPB	0.38	0.68	0.93	0.99	0.94
ASMB-ASPB	0.60	0.77	0.95	0.78	0.99
ASMB-JLMB	0.96	0.86	0.90	0.92	0.66
ASMB-JSMB	0.91	0.73	0.73	0.91	0.63
ASMB-JSPB	0.89	0.88	0.93	0.91	0.74
ASPB-JLMB	0.43	0.50	0.74	0.48	0.69
ASPB-JSMB	0.75	0.43	0.55	0.48	0.67
ASPB-JSPB	0.47	0.72	0.78	0.47	0.77
JLMB-JSMB	0.83	0.67	0.76	0.98	0.99
JLMB-JSPB	0.79	0.78	0.97	0.98	0.99
JSMB-JSPB	0.68	0.93	0.86	0.93	0.98
Mean	0.70	0.72	0.83	0.81	0.84
P-value	>0.05	0.07	< 0.01	< 0.01	< 0.01

Table 4.–Summary statistics of habitat variables in spring 2000 used in principal components analysis in Skiatook Lake, Oklahoma.

Variable Name	Variable	Mean	SD	Min	Max
SECCHM	Mean Secchi depth (m)	0.61	0.25	0.18	0.92
SECCHV	Variance of Secchi depth (m)	0.03	0.03	0.01	0.10
TEMPM	Mean water temperature (°C)	18.27	0.67	17.27	19.45
TEMPV	Variance of water temperature (°C)	12.66	1.45	10.52	16.06
CONDM[1]	Mean conductivity (mS/cm)	230.60	19.28	202.90	259.70
CONDV[1]	Variance of conductivity (mS/cm)	3839.60	4172.50	316.30	12550.6
DOM	Mean dissolved oxygen (mg/L)	8.82	0.96	7.11	10.40
DOV	Variance of dissolved oxygen (mg/L)	3.84	1.93	0.89	7.24
SLOPE	Shoreline slope	21.19	11.30	2.42	43.69
RIVER	Distance to main river channel (m)	297.30	283.60	33.72	1123.30
DAM	Distance to dam	8045.90	4428.00	0.00	14928.10

[1] Not used in final analysis.

Table 5.–Eigenvectors of the first four prinicpal components (PC 1-4) of habitat variables [1] in Spring 2000 in Skiatook Lake, Oklahoma. Explanation of continuous variable names are given in Table 4 . Eigenvectors ≥|0.30| are in bold.

Variable Name[2]	PC 1	PC 2	PC 3	PC 4
Eigenvalue	5.06	2.27	1.77	1.67
(percent of variation explained)	(28.1)	(12.6)	(9.9)	(9.3)
Water Quality				
SECCHM	**0.41**	-0.01	0.02	0.09
SECCHV	0.05	**0.38**	0.06	0.07
TEMPM	**-0.39**	0.03	0.07	-0.03
TEMPV	0.20	-0.28	0.17	0.01
DOM	**0.42**	-0.04	0.01	0.12
DOV	**-0.37**	0.21	-0.08	-0.19
Physical				
SLOPE	0.11	-0.02	0.07	**-0.54**
RIVER	0.12	**0.40**	0.05	**0.36**
DAM	**-0.42**	0.01	0.06	-0.03
Substrate				
RIP-RAP	-0.07	-0.15	**0.65**	-0.05
BOULDER	0.20	0.22	**-0.38**	**-0.30**
COBBLE	-0.11	-0.18	-0.14	**0.39**
BEDROCK	-0.09	0.01	0.02	0.09
SILT	0.01	-0.08	-0.08	0.18

Table 5.–continued.

Variable Name[2]	PC 1	PC 2	PC 3	PC 4
Cover				
SHRUB	-0.09	**-0.33**	**-0.48**	0.19
STANDTIM	0.06	**0.56**	0.01	0.01
VEG	0.07	0.03	**0.35**	0.21
FALLTIM	0.17	-0.17	0.01	**-0.38**

[1] NOCOVER = no cover present and GRAVEL were left out of the analysis to allow for inclusion of the other cover and substrate variables as dummy variables.

[2] STANDTIM = standing timber, VEG = vegetation, and FALLTIM = fallen timber.

Table 6.–Regression models for relations between habitat (principal component axes, PC 1-4) and density of juvenile (J) and adult (A) largemouth bass (LMB), smallmouth bass (SMB), and spotted bass (SPB) in spring 1997-1999 in Skiatook Lake, Oklahoma. N = number of sampling sites.

Dependent variable	Regression model and associated statistics
	1997 (N = 45)
ALMB	2.99 + 1.92(PC 2); $r^2 = 0.12$; $P = 0.02$
JSMB	1.21 + 1.22(PC 1) + 1.21(PC 3); $R^2 = 0.51$; $P < 0.01$
ASMB	2.45 + 2.32(PC 1); $r^2 = 0.24$; $P < 0.01$
ASPB	14.99 + 10.39(PC 3); $r^2 = 0.31$; $P < 0.01$
	1998 (N = 35)
JSMB	2.26 + 2.11(PC 1); $r^2 = 0.34$; $P < 0.01$
ASMB	2.81 + 2.55(PC 1); $r^2 = 0.39$; $P < 0.01$
ASPB	5.68 + 2.35(PC 2); $r^2 = 0.14$; $P = 0.03$
	1999 (N = 40)
JLMB	1.63 + 1.91(PC 2); $r^2 = 0.37$; $P < 0.01$
ALMB	2.60 + 3.42(PC 2); $r^2 = 0.28$; $P < 0.01$
JSMB	1.13 1.58(PC 1); $r^2 = 0.21$; $P < 0.01$
ASMB	6.30 + 7.41(PC 1) - 2.96(PC 4); $R^2 = 0.47$; P 0.01
JSPB	1.19 + 0.93(PC 3); $r^2 = 0.18$; $P < 0.01$

Table 7.–Summary statistics of habitat variables in fall 1999 used in principal components analysis in Skiatook Lake, Oklahoma.

Variable Name	Variable	Mean	SD	Min	Max
SECCHM	Mean Secchi depth (m)	0.99	0.22	0.45	1.27
SECCHV	Variance of Secchi depth (m)	0.30	0.16	0.06	0.68
TEMPM [1]	Mean water temperature (°C)	18.65	0.40	17.97	19.24
TEMPV [1]	Variance of water temperature (°C)	11.78	1.72	9.46	14.60
CONDM [1]	Mean conductivity (mS/cm)	212.00	9.10	200.60	236.80
CONDV [1]	Variance of conductivity (mS/cm)	16.42	12.07	2.72	56.94
DOM	Mean dissolved oxygen (mg/L)	8.66	0.69	7.88	9.77
DOV	Variance of dissolved oxygen (mg/L)	0.85	0.33	0.32	1.58
SLOPE	Shoreline slope	20.40	10.12	2.36	41.23
RIVER	Distance to main river channel (m)	337.80	274.00	30.25	1179.20
DAM	Distance to dam	8447.80	4171.70	944.90	14531.90

[1] Not used in final analysis.

Table 8.–Eigenvectors of the first four prinicpal components (PC 1-4) of habitat variables[1] in Fall 1999 in Skiatook Lake, Oklahoma. Explanation of continuous variable names are given in Table 7. Eigenvectors ≥|0.30| are in bold.

Variable Name[2]	PC 1	PC2	PC 3	PC 4
Eigenvalue	5.21	1.83	1.75	1.47
(percent of variation explained)	(32.6)	(11.4)	(10.9)	(9.2)
Water Quality				
SECCHM	**0.38**	0.18	0.05	0.01
SECCHV	**0.40**	0.08	0.07	-0.06
DOM	**-0.42**	-0.12	-0.01	-0.06
DOV	**0.32**	0.22	0.01	0.18
Physical				
SLOPE	0.18	0.03	**0.49**	-0.21
RIVER	0.22	-0.25	**-0.31**	**0.30**
DAM	**-0.41**	-0.10	-0.01	0.02
Substrate				
RIP-RAP	-0.15	-0.29	**0.43**	-0.05
BOULDER	0.19	-0.22	**-0.42**	**-0.42**
COBBLE	-0.13	0.16	-0.17	0.14
BEDROCK	-0.05	**0.33**	**0.34**	**0.44**
SILT	0.02	0.22	-0.07	0.10

Table 8.–continued.

Variable Name[2]	PC 1	PC 2	PC 3	PC 4
	Cover			
SHRUB	-0.16	**0.55**	**-0.30**	-0.14
STANDTIM	0.23	**-0.45**	0.01	**0.30**
VEG	-0.02	0.01	0.01	0.24
FALLTIM	0.10	0.09	0.22	**-0.51**

[1] NOCOVER = no cover present and GRAVEL were left out of the analysis to allow for inclusion of the other cover and substrate variables as dummy variables.

[2] STANDTIM = standing timber, VEG = vegetation, and FALLTIM = fallen timber.

Table 9.–Regression models for relations between habitat (principal component axes, PC 1-4) and density of juvenile (J) and adult (A) largemouth bass (LMB), smallmouth bass (SMB), and spotted bass (SPB) in fall 1997-1999 in Skiatook Lake, Oklahoma. N = number of sampling sites.

Dependent variable	Regression model and associated statistics
	1997 (N = 22)
JSMB	6.84 + 4.65(PC 1); $r^2 = 0.19$; $P < 0.05$
ASMB	5.42 + 4.14(PC 1); $r^2 = 0.21$; $P = 0.03$
ASPB	8.31 + 3.53(PC 1) + 3.75 (PC 3); $R^2 = 0.45$; $P < 0.01$
	1998 (N = 40)
ALMB	2.32 + 1.05(PC 4); $r^2 = 0.11$; $P = 0.04$
JSMB	1.11 + 0.93(PC 1) - 0.82(PC 4); $R^2 = 0.26$; $P < 0.01$
ASMB	5.73 + 3.89(PC 1); $r^2 = 0.11$; $P = 0.03$
ASPB	6.47 + 2.58(PC 1) + 3.61(PC 3) + 3.26(PC 4); $R^2 = 0.41$; $P < 0.01$
	1999 (N = 37)
JLMB	2.81 + 1.29(PC 3); $r^2 = 0.11$; $P < 0.05$
ALMB	3.00 - 1.37(PC 2) + 1.92(PC 4); $R^2 = 0.20$; $P = 0.02$
ASMB	0.94 + 0.93(PC 1); $r^2 = 0.14$; $P = 0.02$
ASPB	3.71 + 2.67(PC 4); $r^2 = 0.14$; $P = 0.02$

FIGURE LEGENDS

Figure 1.–Map of Skiatook Lake, Oklahoma indicating Bull Creek, Hominy Creek, mid-lake, lower-lake strata, and the location of the dam.

Figure 2.–Digital elevation model (DEM) of Skiatook Lake used to estimate shoreline slope.

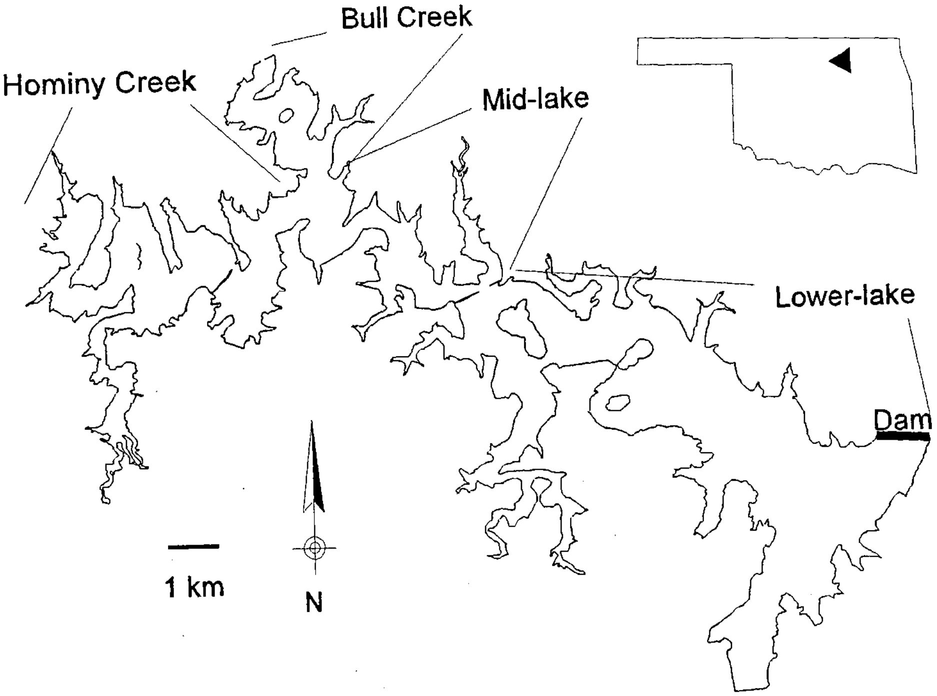
Figure 3.–Map of the 30 sites where Secchi depth, surface water temperature, conductivity, and dissolved oxygen were measured in Skiatook Lake in Fall 1999 and Spring 2000.

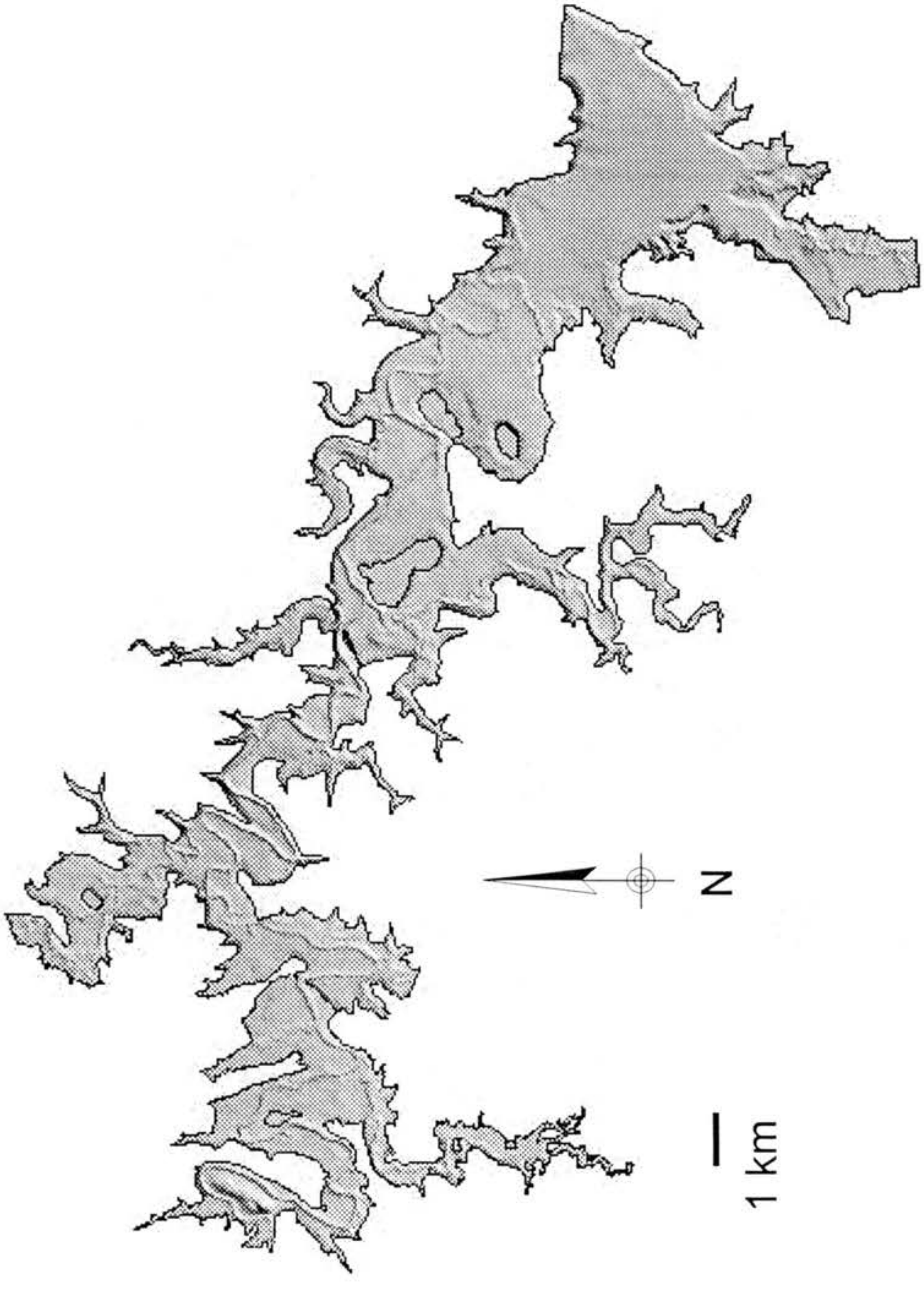
Figure 4.–Percent number of prey items found in the guts of juvenile (J) and adult (A) largemouth bass (LMB), smallmouth bass (SMB), and spotted bass (SPB) in Fall 1998 and 1999 and Spring 1997 - 1999 in Skiatook Lake.

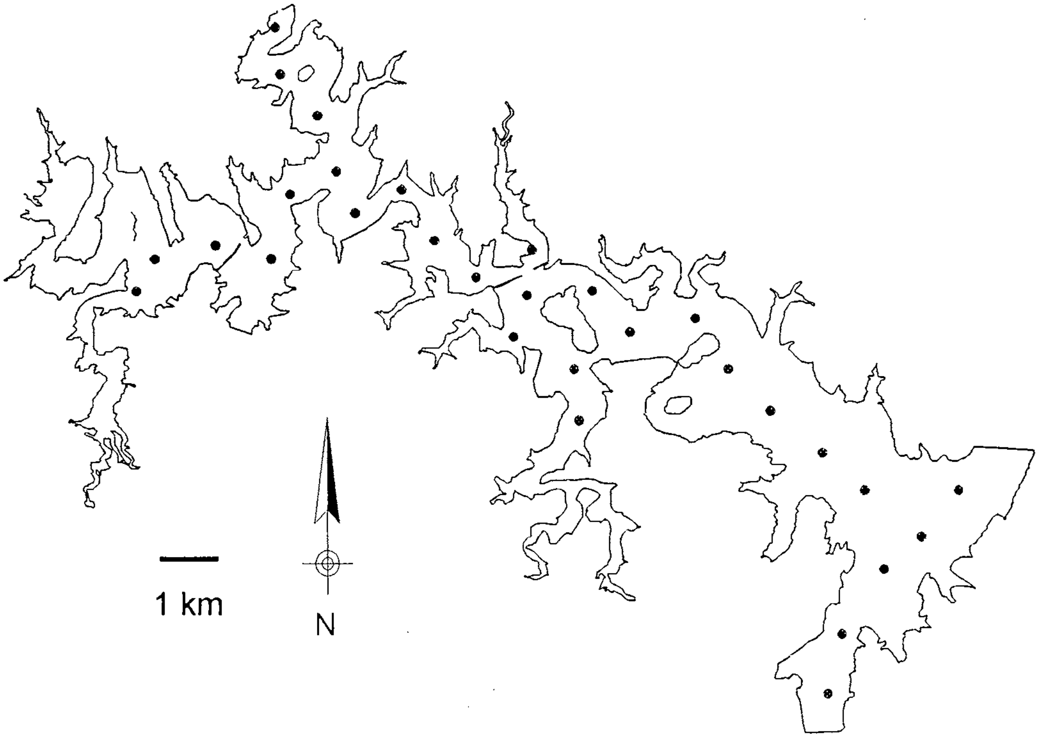
Figure 5.–Maps of the surfaces produced for the means of Secchi depth, surface water temperature, conductivity, and dissolved oxygen in Skiatook Lake in Fall 1999 and Spring 2000. All maps are presented at the same scale. Darker areas represent higher values for the respective variables (See Table 4 and 7 for summary statistics).

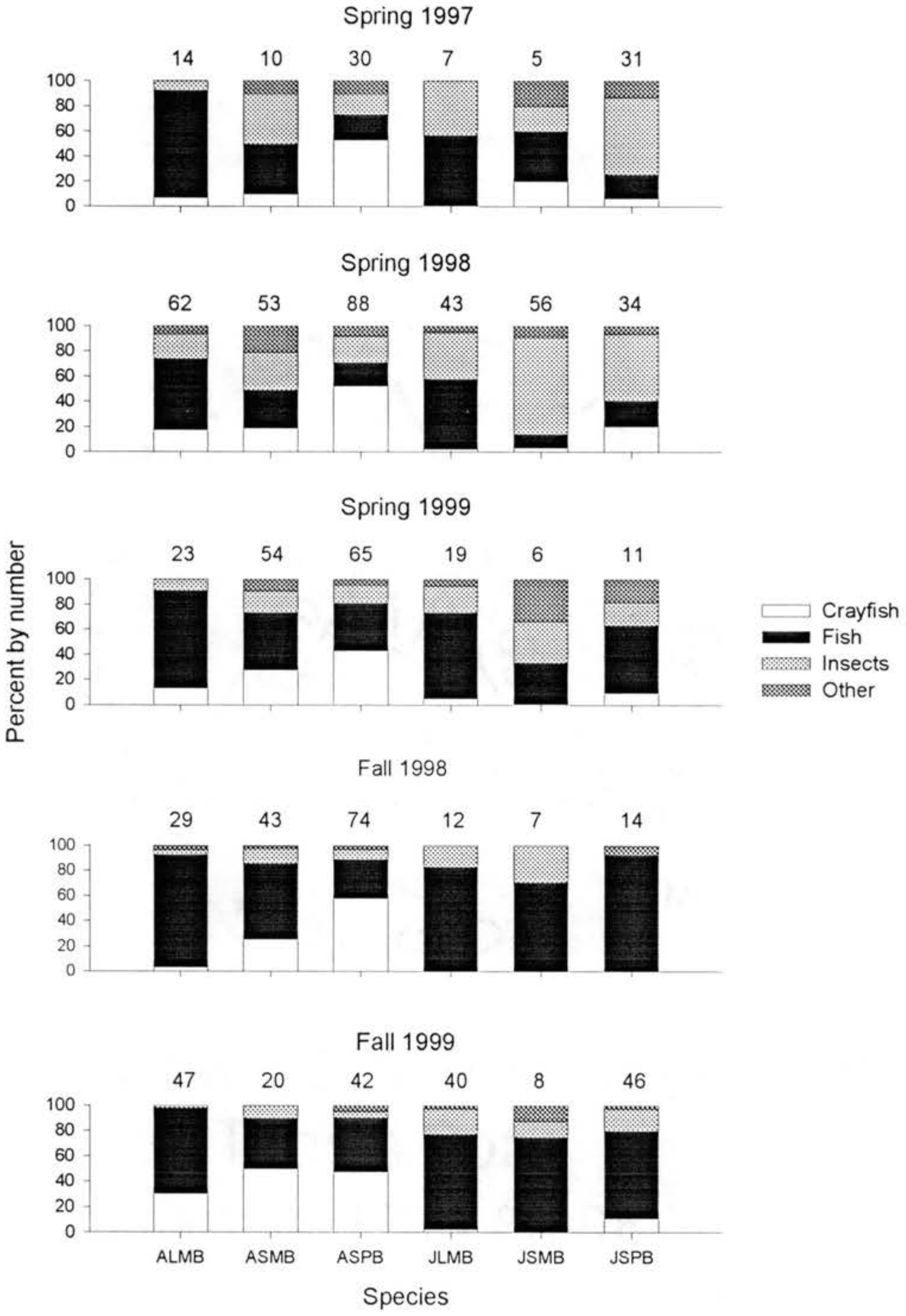
Figure 6.–Maps of the surfaces produced for the variances of Secchi depth, surface water temperature, conductivity, and dissolved oxygen in Skiatook Lake in Fall 1999 and Spring 2000. All maps are presented at the same scale. Darker areas represent higher values for the respective variables (See Table 4 and 7 for summary statistics).

Figure 7.–Maps of the surfaces produced for the first four principal components in Skiatook Lake in Fall 1999 and Spring 2000. All maps are presented at the same scale. Darker areas represent higher values (See Table 5 and 8 for eigenvectors of principal component axes).

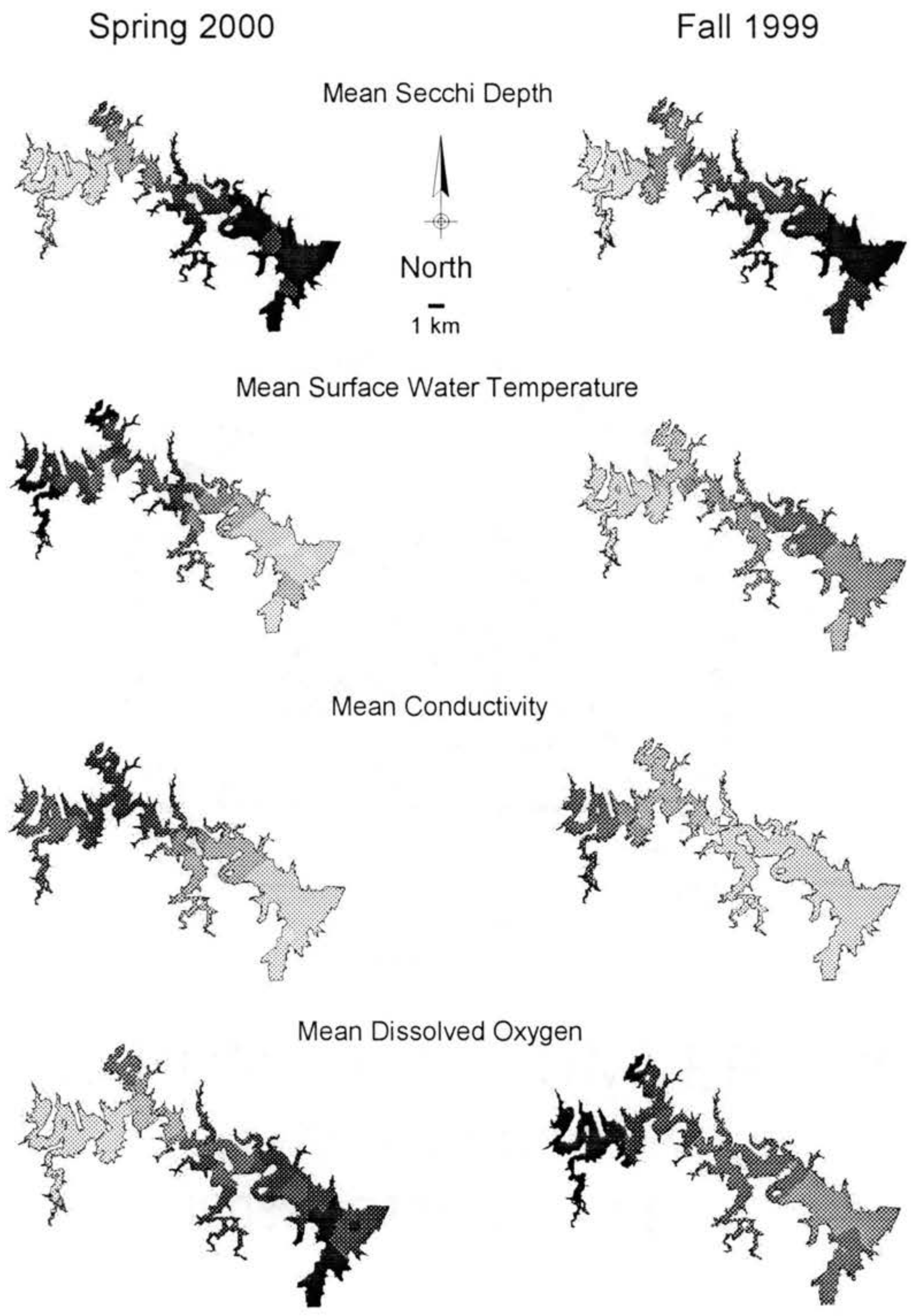

Bull Creek
Hominy Creek
Mid-lake
Lower-lake
Dam
1 km
N


N
1 km


1 km
N



Spring 1997
14
10
30
7
5
31
Spring 1998
62
53
88
43
56
34
Spring 1999
23
54
65
19
6
11
Fall 1998
29
43
74
12
7
14
Fall 1999
47
20
42
40
8
46
100
80
60
40
20
0
Percent by number
□ Crayfish
■ Fish
▨ Insects
▩ Other
ALMB
ASMB
ASPB
JLMB
JSMB
JSPB
Species



Spring 2000

Fall 1999

Mean Secchi Depth

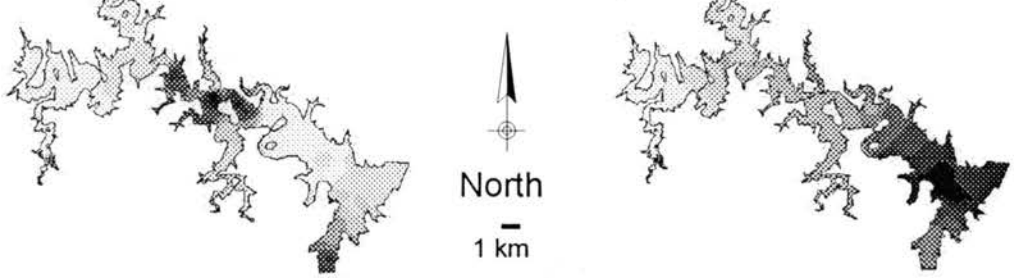
Mean Surface Water Temperature

Mean Conductivity

Mean Dissolved Oxygen

Spring 2000 Fall 1999

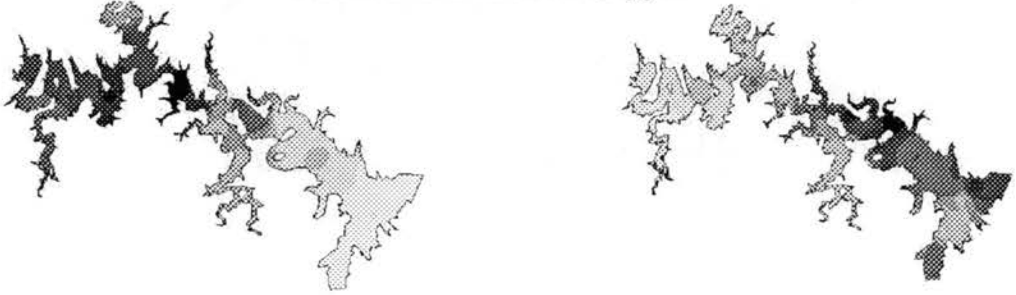
Variance of Secchi Depth

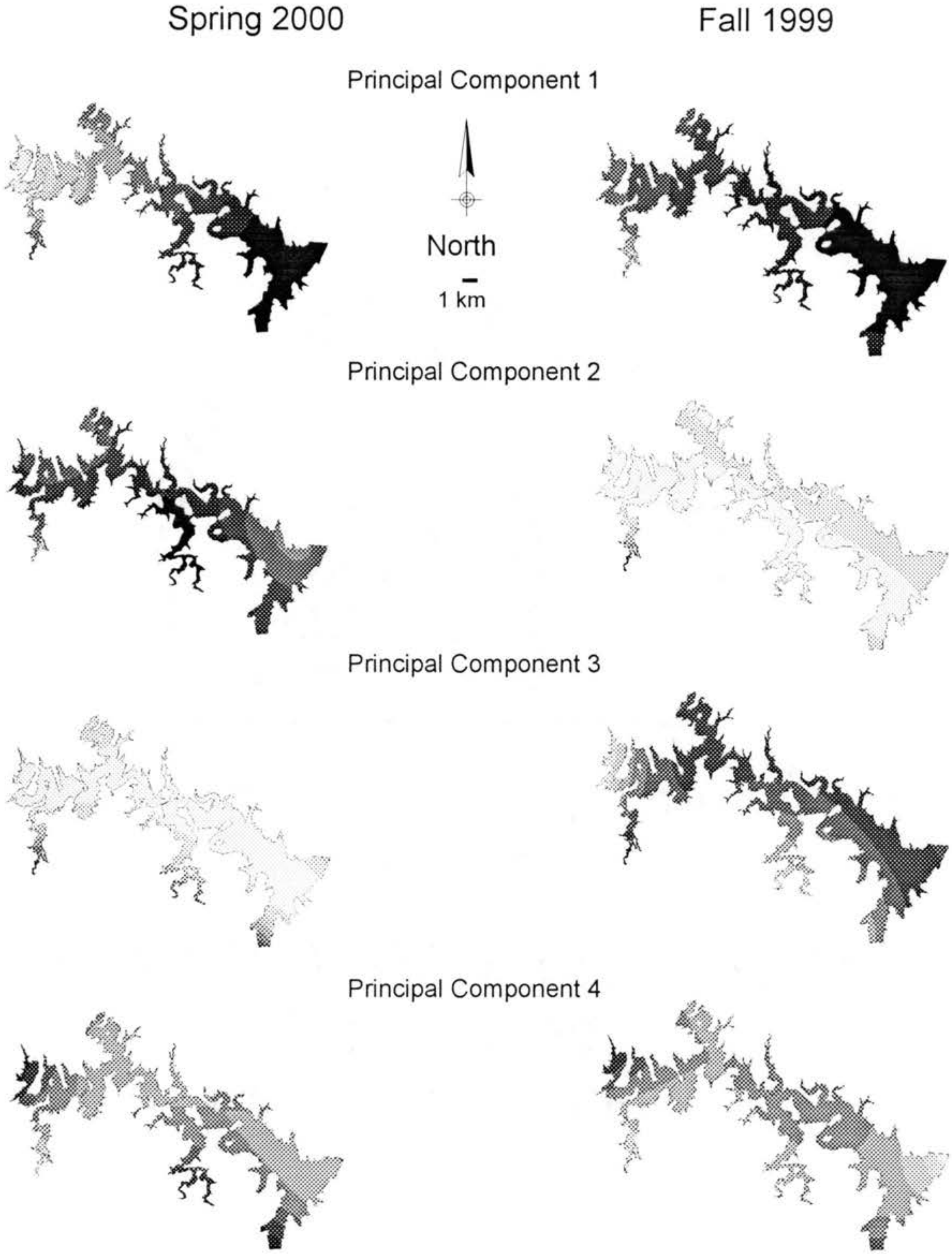


Variance of Surface Water Temperature

Variance of Conductivity

Variance of Dissolved Oxygen





Spring 2000

Fall 1999

Principal Component 1

Principal Component 2

Principal Component 3

Principal Component 4

CHAPTER IV.

ENVIRONMENTAL INFLUENCES ON RECRUITMENT OF THREE BLACK BASS SPECIES IN A SOUTHERN GREAT PLAINS FLOOD CONTROL RESERVOIR

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Abstract.–I analyzed relationships between recruitment and environmental variables for largemouth bass Micropterus salmoides, smallmouth bass M. dolomieu, and spotted bass M. punctulatus in Skiatook Lake, Oklahoma from 1997 through 1999. I assessed correlations between catch rates of young-of-year (YOY) and juvenile largemouth bass, juvenile smallmouth bass, and juvenile spotted bass and three weather variables and five reservoir hydrology variables Correlations between catch rates of black bass species and environmental variables were not statistically significant after correcting for table-wide error rates, but certain trends were evident. Catch rates of young-of-year largemouth bass were positively associated with inflows into the reservoir during the spawning season (April - June) while those of juveniles were positively related to reservoir releases during the post-spawning period (June - November). Catch rates of juvenile smallmouth bass were positively related to days of flooding during the spawning season and catch rates of juvenile spotted bass were positively related to accumulated rainfall during the spawning season. Abundance of juvenile largemouth bass increased from 1997 through 1999 based on fall electrofishing samples while juvenile smallmouth bass and spotted bass abundance remained constant. No evidence of over-winter mortality was detected. Juvenile largemouth bass and spotted bass were distributed equally throughout the reservoir in fall but largemouth bass were found in higher abundance in the mid- and lower-end of the reservoir in spring while spotted bass were more abundant in the upper-end in spring. Juvenile smallmouth bass

were more abundant in the lower-end of the reservoir regardless of season. Swim-up dates for young-of-year largemouth bass, based on daily otolith ring counts, were later every year from 1997 to 1999. Swim-up dates for young-of-year smallmouth bass were variable with the earliest dates in 1998. No young-of-year spotted bass were collected in 1997 and swim-up dates were similar between 1998 and 1999. Growth of YOY largemouth bass was greatest in 1999 and greatest in 1998 for YOY smallmouth bass. There was no statistical test of YOY spotted bass growth among years due to low sample sizes. Growth of YOY largemouth bass was not correlated with any of the environmental variables and growth of YOY smallmouth bass and spotted bass were not included in the correlation analysis due to low sample size. The general low degree of association between black bass recruitment and environmental variables at Skiatook Lake may reflect little relationships, increased influence of density-dependent factors, or complex interactions among environmental variables.

Environmental variability has long been known to affect population dynamics of bass. Recruitment, or year-class strength, is particularly susceptible to environmental variability and has been quantified directly by measuring production of offspring after spawning (Miranda et al. 1984; Fisher and Zale 1991; Ploskey et al. 1996) and indirectly by measuring juvenile growth and timing of spawn (Serns 1982; Goodgame and Miranda 1993; Miranda and Hubbard 1994a and 1994b). Since bass only reproduce once per year, recruitment varies as conditions change from year to year.

Environmental factors that have been shown to affect recruitment of reservoir bass can be lumped into two distinct categories: reservoir hydrology and weather. Variation in water levels or water temperature during spawning often correlate with reproductive success of reservoir fishes (Matthews 1998). In a review of the effects of water-level manipulations on reservoir ecosystems, Ploskey (1986) found that rapidly rising water-levels inundate terrestrial vegetation and enhance food sources for fish.

Most of the research on the effects of reservoir hydrology on black bass recruitment have focused on largemouth bass. Summerfelt and Shirley (1978) found that year-class strength of largemouth bass Micropterus salmoides in Lake Carl Blackwell, Oklahoma was most strongly affected by water level fluctuations than by factors such as turbidity, water chemistry, and weather, with stronger year-classes associated with higher water levels. Miranda et al. (1984) reported positive relationships between young-of-year (YOY) largemouth bass survival and water level during the spawning and post-spawning seasons in West Point Reservoir, Alabama-Georgia. However, YOY growth responded negatively to water level during the post-spawning period. Willis (1986) found that a four-stage water-level management plan in Kansas reservoirs resulted in decreased production of largemouth bass, although there was increased production of walleye Stizostedion vitreum, white crappie Pomoxis annularis, and white bass Morone chrysops. Fisher and Zale (1991) found positive correlations between largemouth bass abundance and days of littoral flooding during the spawning and post-spawning periods in Grand Lake, Oklahoma. Kohler et al. (1993) showed peak spawning success during periods of stable water levels but found no relationship between timing of peak hatch and abundance in the first year of life in two Illinois reservoirs.

Fewer studies exist that have examined the effects of reservoir hydrology on reproduction of smallmouth bass Micropterus dolomieu and spotted bass M. punctulatus. Rainwater and Houser (1975) found positive correlations between water level and inflow with total black bass (largemouth bass, smallmouth bass, and spotted bass) numbers and standing crop in Bull Shoals Reservoir, Missouri-Arkansas. Reinert et al. (1995) developed predictive models that related largemouth bass and spotted bass reproductive success to reservoir hydrology in four southeastern U.S. reservoirs. In West Point Reservoir, Georgia-Alabama, YOY spotted bass abundance increased with greater reservoir volume in spring whereas largemouth bass YOY increased with greater ratios of inflow to release in summer. Ploskey et al. (1996) found positive relationships between several measures of reservoir hydrology and abundance of small and intermediate largemouth bass, spotted bass, and smallmouth bass in Bull Shoals Reservoir, Missouri-Arkansas.

The effects of weather on black bass recruitment has largely focused on over-winter survival. Winter starvation, due to decreased feeding activity because of lower water temperatures, has been shown to be a major factor affecting over-winter survival of smallmouth bass in the northern limits of their range (Shuter et al. 1989). Serns (1982) found that recruitment of smallmouth bass in Nebish Lake, Wisconsin responded positively to higher water temperatures in June-August resulting increased over-winter survival because of accumulated energy reserves. Over-winter survival of largemouth bass has been shown in many cases to be length-dependent (Miranda and Hubbard 1994a and 1994b). However, Kohler et al. (1993) found that over-winter survival of largemouth bass in an Illinois reservoir was length-dependent in only one out of three years. Goodgame and Miranda (1993) showed that earlier swim-up dates of larval largemouth bass, which could be influenced by weather and/or reservoir hydrology, resulted in lower over-winter mortality.

My objective for this study was to examine the effects of environmental conditions (i.e., weather and reservoir hydrology) on recruitment and growth of largemouth bass, smallmouth bass, and spotted bass in Skiatook Lake, a southern Great Plains reservoir in Oklahoma .

STUDY SITE

Skiatook Lake is a 4,266-ha flood control impoundment of Hominy Creek in north-central Oklahoma that was formed in 1984 by the U.S. Army Corps of Engineers. The lake has a mean depth of 9.7 m and a shoreline development index of 11.3. The lake perimeter consists largely of steep, bedrock substrate with little aquatic vegetation. The upper end of the reservoir is more turbid than the lower end, with average spring Secchi depths of 0.1 m and 1.2 m, respectively. Skiatook Lake was classified as mesotrophic in 1997 with a mean chlorophyll-a concentration of 5.10 mg/m^3 (Long et al. 1999). The top of the conservation pool is 217.6 meters above mean sea level. Largemouth bass were supplementally stocked in 1985 and 1986 and non-native smallmouth bass were stocked in 1990 and 1991. Other sportfish species in the lake consist mainly of spotted bass, sunfish Lepomis spp., hybrid striped bass Morone saxatilis X M. chrysops, walleye, channel catfish Ictalurus punctatus, and flathead catfish Pylodictis olivaris. Figure 1 shows the location and strata of Skiatook Lake and Figure 2 shows the daily average water level and daily average air temperature at Skiatook Lake over the three-year study period 1997 through 1999.

METHODS

Fisheries Data

I electrofished at night for black bass in spring and fall of 1997 through 1999 using a randomized sampling design with a boat mounted electrofishing unit. For each fish collected, I measured total length to the nearest 1-mm and classified juveniles based on data from Carlander (1977) for age-1 fish in fall and spring samples. Therefore, largemouth bass less than 226 mm, smallmouth bass less than 185 mm, and spotted bass less than 178 mm were considered age-1 or less and classified as juveniles in spring and fall samples.

In summers (June - July) of 1997, 1998, and 1999, I collected YOY black bass by backpack electrofishing. Sites for collection of YOY fish were arbitrarily selected from probable spawning sites of each species. I identified and measured fish to the nearest 1-mm, and removed their sagittae otoliths to estimate age in days. Ages were estimated by mounting, sanding, and polishing the otolith in the sagittal plane and then counting rings with a compound microscope. I counted the rings in each otolith until the counts differed by no more than 2 and then assigned the highest count as the age in days since larval swim-up. Daily ring formation has been validated for largemouth bass (Miller and Storck 1982), smallmouth bass (Graham and Orth 1987) and spotted bass (DiCenzo and Bettoli 1995).

Environmental Data

I obtained daily weather data (average air temperature, average wind speed, and accumulated rainfall) from the Oklahoma Mesonet station at Skiatook for the period 1997 through 1999. I obtained daily reservoir hydrology data (elevation, storage, inflows, and releases) for Skiatook Lake from the U.S. Army Corps of Engineers for the period 1997 through 1999.

I grouped the daily environmental data into two seasons: spawning (April - May) and post-spawning (June - November). For the Mesonet data, I calculated average air temperature, average wind speed, and accumulated rainfall for each year and season from 1997 through 1999. For the reservoir hydrology data, I calculated average water elevation, average storage, total releases, total inflows for each year and season from 1997 through 1999, and number of days above conservation pool elevation (217.6 m above mean sea level).

Statistical Analyses

I used correlation analysis (SAS Institute 1992) to examine the relationship between environmental variables during the spawning season and mean catch rates of YOY black bass species captured in summer electrofishing, and between environmental variables during the spawning and post-spawning seasons and the mean catch rates of juvenile bass captured in fall electrofishing. I used ANOVA and orthogonal polynomial contrasts (Kuehl 1994) to compare catch rates of juvenile bass among years to determine recruitment trends for spring and fall 1997 through 1999. Additionally, I used ANOVA (SAS Institute 1992) to compare catch rates of juvenile fish in fall 1997 and 1998 with those in the following spring (1998 and 1999, respectively) as a measure of over-winter mortality. I compared the catch rates of each of the bass species among years and strata with a 2-way ANOVA (SAS Institute 1992) in spring and fall to examine differences in distribution within the reservoir.

Using the summer electrofishing data, I used ANOVA (SAS Institute 1992) and two-sample Kolmogorov-Smirnov (K-S) tests (Conover 1980) to compare swim-up dates (Julian days) among years (1997-1999) for each black bass species and ANOVA to compare average daily growth rates (mm/day) among years. Finally, I searched for correlations between mean growth rates of YOY bass species and the environmental variables during the spawning season. Since the correlation analyses were based on small sample sizes and I was interested in finding relationships, I used ∝ = 0.10 to detect differences with these analyses, but used ∝ = 0.05 for all other analyses. Table-wide error rates for alpha for the correlation analyses were controlled with a sequential-Bonferroni correction (Rice 1989).

RESULTS

Summary statistics for environmental variables from 1997 - 1999 are in Table 1. I collected 41, 87, and 61 YOY largemouth bass, 18, 9, and 2 YOY smallmouth bass, and 0, 1, and 6 YOY spotted bass in summer 1997, 1998, and 1999 respectively (Table 2). Low catch rates precluded analysis between environmental variables and YOY smallmouth bass and spotted bass. Young-of-year largemouth bass catch rates were not significantly correlated with any environmental variable after applying the sequential-Bonferroni correction to alpha ($\propto$ = 0.10, k = 8, corrected $\propto$ = 0.0125), but the correlation with the lowest P-value was with accumulated inflow during the spawning season (P = 0.02, r = 0.99; Figure 3a).

Juvenile catch rates for all three black bass species were not significantly correlated with any environmental variables after applying the sequential-Bonferroni correction to alpha ($\propto$ = 0.10, k = 16, corrected $\propto$ = 0.006). However, the correlation with the lowest P-value for largemouth bass was with accumulated releases during the post-spawning season (P = 0.02, r = 0.99; Figure 3b), for smallmouth bass with accumulated days of flooding during the spawning season (P = 0.09, r = 0.99; Figure 3c), and for spotted bass with accumulated rainfall during the spawning season (P = 0.02, r = 0.99; Figure 3d).

Catch rates of juvenile largemouth bass increased from 1997 through 1999 in fall (P < 0.01; Table 3) but not in spring (P = 0.08; Table 3). There was no temporal difference in catch rates of juvenile smallmouth bass and spotted bass (Table 3). I detected no evidence of over-winter mortality among the three black bass species (Table 3).

Distribution of juvenile largemouth bass and spotted bass among strata within the reservoir was dependent on season, but not on year (P > 0.25 for the year*stratum interaction for all species in both seasons; Table 4). Largemouth bass were less abundant in Hominy Creek in spring (P = 0.03) but equally abundant throughout the reservoir in fall (P = 0.40). Spotted bass were more abundant in Bull Creek in spring ($\underline{P} < 0.01$) and equally abundant throughout the reservoir in fall ($\underline{P} = 0.28$). Smallmouth bass were always more abundant in the lower-lake regardless of season ($\underline{P} < 0.01$ in spring and $\underline{P} = 0.01$ in fall).

I collected and aged 31, 79, and 69 YOY largemouth bass in summer 1997, 1998, and 1999, respectively. Mean Julian dates for largemouth bass swim-up were 133.4 in 1997, 132.1 in 1998, and 140.5 in 1999 and differed among years ($\underline{P} < 0.01$; Figure 4). Pairwise comparisons between years of the distribution of swim-up dates with the K-S tests were significantly different in all cases. Growth of YOY largemouth bass increased significantly from 1997 through 1999 ($\underline{P} < 0.01$; Table 5) and was not correlated with any of the measured environmental variables. From 17, 6, and 2 YOY smallmouth bass captured and aged in 1997, 1998, and 1999, respectively, I calculated mean Julian swim-up dates of 140.4, 125.7, and 144. I omitted 1999 from the swim-up date and growth comparison for smallmouth bass due to low sample size and found a significant different in swim-up dates between 1997 and 1998 ($\underline{P} < 0.01$; Figure 5), but no difference in growth ($\underline{P} = 0.50$; Table 5). The distribution of swim-up dates were different between 1997 and 1998 according to the K-S test. No correlations between environmental variables and smallmouth bass growth were computed due to low sample sizes. No YOY spotted bass were collected in 1997 and only 1 and 6 were collected in 1998 and 1999, respectively. The Julian day of swim-up for spotted bass in 1998 was 138 and the mean Julian day of swim-up in 1999 was 143 (Figure 6) and growth appeared constant (Table 5), however, no statistical tests were performed due to low sample size in every year.

DISCUSSION

Observations from black bass recruitment in Skiatook Lake are consistent with the hypothesis that increased spring water levels and inflows result in enhanced nutrient loading and thus enhanced fish production (Ploskey et al. 1996). First, although statistically nonsignificant, catch rates of YOY largemouth bass tended to be greater in years with increased inflow during the spawning period (April - May). Second, catch rates of juvenile smallmouth bass tended to be greater with increasing number of days of flooding (water level above 217 msl) during the spawning season. Third, catch rates of juvenile spotted bass tended to be higher in years with more rainfall during the spawning season. Additionally, reservoir operations during the post-spawning season may also be an important factor influencing recruitment of largemouth bass since catch rates of juveniles of this species tended to be greater in years with increased releases from the reservoir during this period (June - November).

In general, inflow to a reservoir brings nutrients from upstream and water releases from the dam act to distribute those nutrients from the eutrophic upper-end to the rest of the reservoir (Kennedy and Walker 1990) and increase mixing (Ford 1990). Flooding provides additional cover and foraging opportunities for juvenile bass by making terrestrial vegetation available (Ploskey et al. 1996). All of these variables (inflow, releases, and days of flooding) are driven by rainfall; increased rainfall increases inflow, increasing days of flooding, and thus increased releases to regulate storage in the reservoir. Although reservoirs can be operated to modify days of flooding and releases, they cannot influence inflows or rainfall and it is the increased rainfalls which presumably drive the nutrient input cycle. Without a wet spring to enhance nutrient levels, increased days of flooding or increased releases may not have the desired impact of increasing fish production (Miranda et al. 1984; Ploskey et al. 1996). It would seem intuitive, then, that rainfall or inflow would be a good predictor of year-class strength for all three black bass species in Skiatook Lake, but, in fact, was the case only for spotted bass and largemouth bass. Distribution of smallmouth bass in fall provides some insight as to why one of these two variables did not influence this species in Skiatook Lake.

In the lower, lacustrine end of Skiatook Lake where juvenile smallmouth bass are constrained to live, the input of nutrients may be less dependent on rainfall or inflow (Ford 1990; Kennedy and Walker 1990). I have found through personal observation that high water turbidity in Skiatook Lake never extended much past the mid-lake area (about half-way down the reservoir), even after large amounts of recent rainfall and inflow. Reservoir releases provide one mechanism for distribution of nutrients from up-reservoir to down-reservoir (Ford 1990), but may not be enough to benefit the fishes residing in the lower-end of

Skiatook Lake. Lateral transport of nutrients, like the mechanisms proposed for large rivers (Junk et al. 1989), may be more important for these lower-end areas of reservoirs than longitudinal transport. However, fish populations in the lower end of reservoirs may also be more dependent on density-dependent processes rather than density-independent ones. Since the greatest environmental changes in a reservoir environment occur in the upper-end, where the largest input of water and nutrients occur (Kennedy and Walker 1990), they can be classified as more variable than the lower-end areas. Since smallmouth bass do not occupy these highly variable areas in Skiatook Lake (Long et al. 1999), or in other reservoirs such as Bull Shoals and Beaver reservoirs (Rainwater and Houser 1975), they exist in a more stable environment, where density-dependent processes (e.g., predation and competition) become more important than density-independent processes (Winemiller 1992; Matthews 1998) . Days of flooding during the spawning season, along with concomitant increases in cover from flooded terrestrial vegetation, would therefore influence density-dependent survival by protecting juvenile smallmouth bass from predation and enhancing foraging.

The ability to derive models of recruitment for largemouth bass, smallmouth bass, and spotted bass against environmental variables have met with varying degrees of success, depending on the species. Reinert et al. (1995) were able to produce more significant models for largemouth bass than for spotted bass based on reservoir hydrology in southeastern reservoirs, and they could not produce any models for smallmouth bass. Ploskey et al. (1996) could produce only one significant model for smallmouth bass recruitment based on reservoir hydrology but produced nine models for largemouth bass and six models for spotted bass in Bull Shoals Reservoir, Arkansas-Missouri. Summerfelt and Shirley (1978) were unable to find any correlation between year-class strength of largemouth bass and weather variables in Lake Carl Blackwell, Oklahoma, but were able to find significant correlations with reservoir hydrology.

Given that I was not able to derive statistically significant relationships between YOY and juvenile bass abundance and environmental variables suggests a lack of detectability between recruitment and environmental variables (Rose 2000) in Skiatook Lake. Additionally, this study was also negatively influenced by low sample size (3 years) which would also have decreased the ability to detect differences. Other studies have also suffered from low detectability between recruitment and environmental variables, and this issue seems to vary depending on bass species. Reinert et al. (1995) and Ploskey et al. (1996) collected data on these three black bass species and failed to produce models for smallmouth bass and spotted bass as good as those for largemouth bass. Rainwater and Houser (1975) found that annual fluctuations in standing crop in Bull Shoals and Beaver reservoirs were greatest for largemouth bass than for smallmouth bass or spotted bass. Ploskey et al. (1996) found that both largemouth bass and spotted bass responded positively to increased water levels, but that spotted bass contribution to overall black bass biomass declined because the largemouth bass contribution was overwhelming. Apparently, largemouth bass respond much more to changes in the reservoir environment than do spotted bass or smallmouth bass. Additionally, Ploskey et al. (1996) found that smallmouth bass responses to water level fluctuations in Bull Shoal Reservoir were different from the other two black bass species. Moreover, the coefficient of variation in biomass estimates from their 22 years of standardized sampling were much higher for smallmouth bass than for spotted bass or largemouth bass indicating that catches of smallmouth bass were much more difficult and sporadic, that might result in decreased ability to detect environmental influences. Alternatively, smallmouth bass populations may be less susceptible to environmental change than largemouth bass, especially in Skiatook Lake.

The dynamics of the environment at Skiatook Lake may also be such that environmental effects on recruitment are minimal when they do occur. The hydrology of Skiatook Lake is much less variable than many other reservoir systems in the southeastern U.S. (e.g., Bull Shoals Reservoir) that have been studied more extensively and tend to have better correspondence between environmental variability and black bass recruitment. For example, Aggus and Elliot (1975) found that the average water level fluctuation in Bull Shoal Reservoir from 1968 - 1973 was 6.9 m. The mean water level fluctuation from 10 years of record at Skiatook Lake was 2.9 m and the greatest was 4.2 m. Therefore, conditions at Skiatook Lake may not act in such a way to be the most important variable that impacts these black bass populations, or at least not in a way to be very detectable.

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Table 1.–Summary statistics for the environmental variables used in correlations with catch rates of young-of-year largemouth bass and juvenile largemouth bass, smallmouth bass, and spotted bass at Skiatook Lake, Oklahoma from 1997 - 1999.

Year	XELE	XSTO	SREL	SINF	TFLOOD	XTEM	XWND	SRAIN
Spawning Season								
1997	217.80	405,458,551	641.97	714.86	56	18.15	11.84	32.41
1998	217.90	410,046,057	1,131.74	1,203.61	47	20.58	13.15	28.45
1999	218.90	455,502,915	1,444.02	2,425.48	61	19.35	12.37	61.01
Post-spawning Season								
1997	217.67	400,037,108	507.75	660.35	29	25.27	9.35	36.88
1998	217.46	391,290,725	201.96	151.21	19	27.69	9.12	15.34
1999	217.66	399,201,850	785.91	312.62	23	27.85	10.45	6.30

XELE = mean water elevation (msl), XSTO = mean water storage in reservoir (m^3), SREL = sum of reservoir releases (m^3/sec/day), SINF = sum of inflow to reservoir (m^3/sec/day), TFLOOD = total number of days above conservation pool elevation, XTEM = mean air temperature (°C), XWND = mean wind speed (km/hour), SRAIN = sum of rainfall (cm).

Table 2.–Summary statistics of young-of-year (YOY) largemouth bass catch rates (number of fish per electrofishing hour) during summer 1997 - 1999 in Skiatook Lake. N = number of sampling sites and SE = standard error.

Year	N	Mean	SE
1997	6	15.74	2.87
1998	11	22.14	8.80
1999	10	39.27	10.35

Table 3.–Mean electrofishing catch rate (number of fish per hour) statistics for juvenile black bass in Skiatook Lake, Oklahoma in fall and spring 1997, 1998, and 1999. SE = standard error. P-values for recruitment indicate significant differences among years for spring electrofishing only for each species. P-values for LOF indicates quadratic or higher trend in means among years for each species.

	Largemouth Bass		Smallmouth Bass		Spotted Bass	
Year	Mean	SE	Mean	SE	Mean	SE
			Fall			
1997	5.60	1.47	6.23	3.30	5.17	3.39
1998	2.23	1.13	3.14	2.79	4.56	2.30
1999	8.98	1.02	7.14	2.79	10.97	2.09
Recruitment	$P < 0.01$		$P = 0.58$		$P = 0.10$	
LOF	$P < 0.01$		$P = 0.32$		$P = 0.25$	
			Spring			
1997	1.71	0.66	1.41	0.84	6.14	1.06
1998	3.91	0.75	3.76	0.89	3.42	1.16
1999	3.21	0.67	2.50	0.97	3.25	1.14
Recruitment	$P = 0.08$		$P = 0.16$		$P = 0.12$	
LOF	$P = 0.10$		$P = 0.10$		$P = 0.37$	

Table 4.–Electrofishing catch-per-effort (CPE; number of fish per hour) statistics among strata for juvenile largemouth bass, smallmouth bass, and spotted bass in Skiatook Lake, Oklahoma in spring and fall. Since the year*stratum interaction was never significant, I grouped data for 1997, 1998, and 1999. N = number of sites and SE = standard error. P-values for ANOVA indicate probability that strata are different. Similar letters indicate no significant difference between means among strata for each species and season at $P \leq 0.05$.

		Largemouth Bass		Smallmouth Bass		Spotted Bass	
Stratum	N	Mean	SE	Mean	SE	Mean	SE
				Spring			
Bull Creek	19	3.48z	1.01	0.00z	1.00	8.78y	1.58
Hominy Creek	22	0.71y	0.92	0.00z	0.94	0.32z	1.36
lower-lake	59	3.90z	0.56	5.65y	0.68	4.69x	0.84
mid-lake	19	2.30zy	0.97	0.54z	1.21	3.50zx	1.58
ANOVA		$P = 0.03$		$P < 0.01$		$P < 0.01$	
				Fall			
Bull Creek	18	6.47z	1.66	0.00z	3.57	5.56z	4.57
Hominy Creek	16	3.39z	1.70	0.48z	3.75	0.85z	3.33
lower-lake	50	5.37z	0.95	12.23y	2.59	8.61z	2.57
mid-lake	14	7.55z	2.00	1.46z	4.14	8.55z	3.58
ANOVA		$P = 0.40$		$P = 0.01$		$P = 0.28$	

Table 5.–Mean growth rates (mm/day) of young-of-year black bass in Skiatook Lake in 1997, 1998, and 1999. N = number of fish used to calculate mean growth, SE = standard error, NA = not applicable, and LOF indicates quadratic or higher trend in means among years.

	Largemouth bass			Smallmouth bass			Spotted bass		
Year	N	Mean	SE	N	Mean	SE	N	Mean	SE
1997	31	0.80	0.03	17	0.99	0.03	0	NA	NA
1998	79	1.07	0.02	6	0.95	0.05	1	1.07	NA
1999	69	1.14	0.02	2	1.32	0.09	6	1.14	0.07
ANOVA		$\underline{P} < 0.01$			$\underline{P} = 0.50$			NA	
LOF		$\underline{P} < 0.01$			NA			NA	

FIGURE LEGEND

Figure 1.–Map of Skiatook Lake, Oklahoma indicating Bull Creek, Hominy Creek, mid-lake, and lower-lake strata.

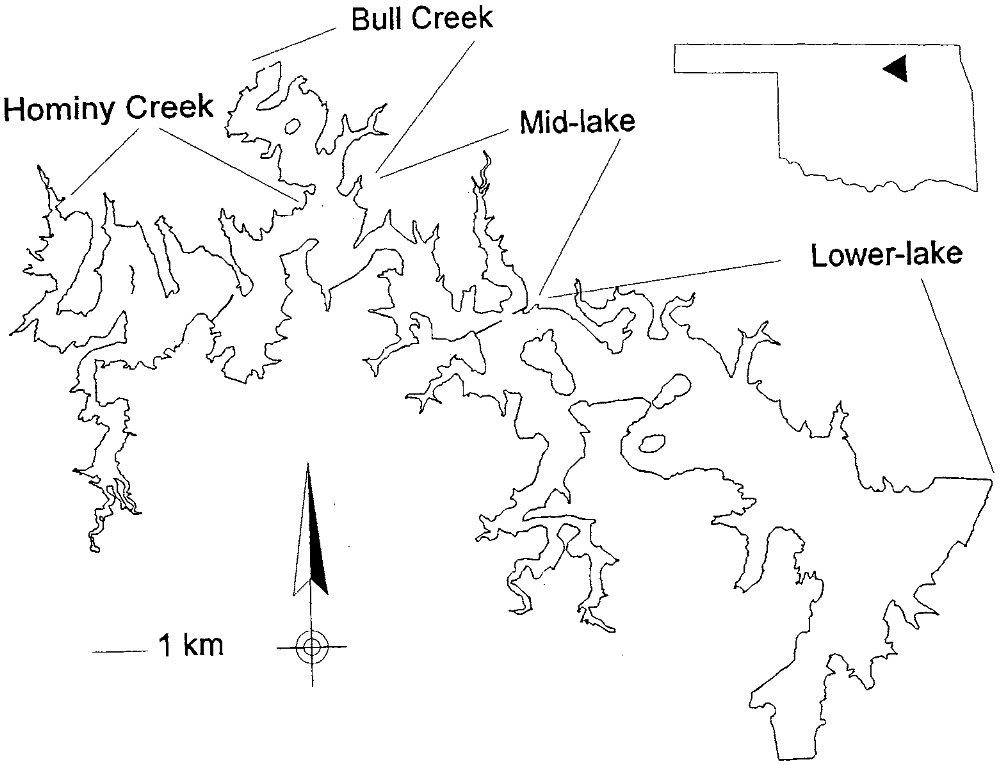
Figure 2.–Graph of water level elevation (meters above sea level; msl) and air temperature from the period 1997 through 1999 at Skiatook Lake, Oklahoma.

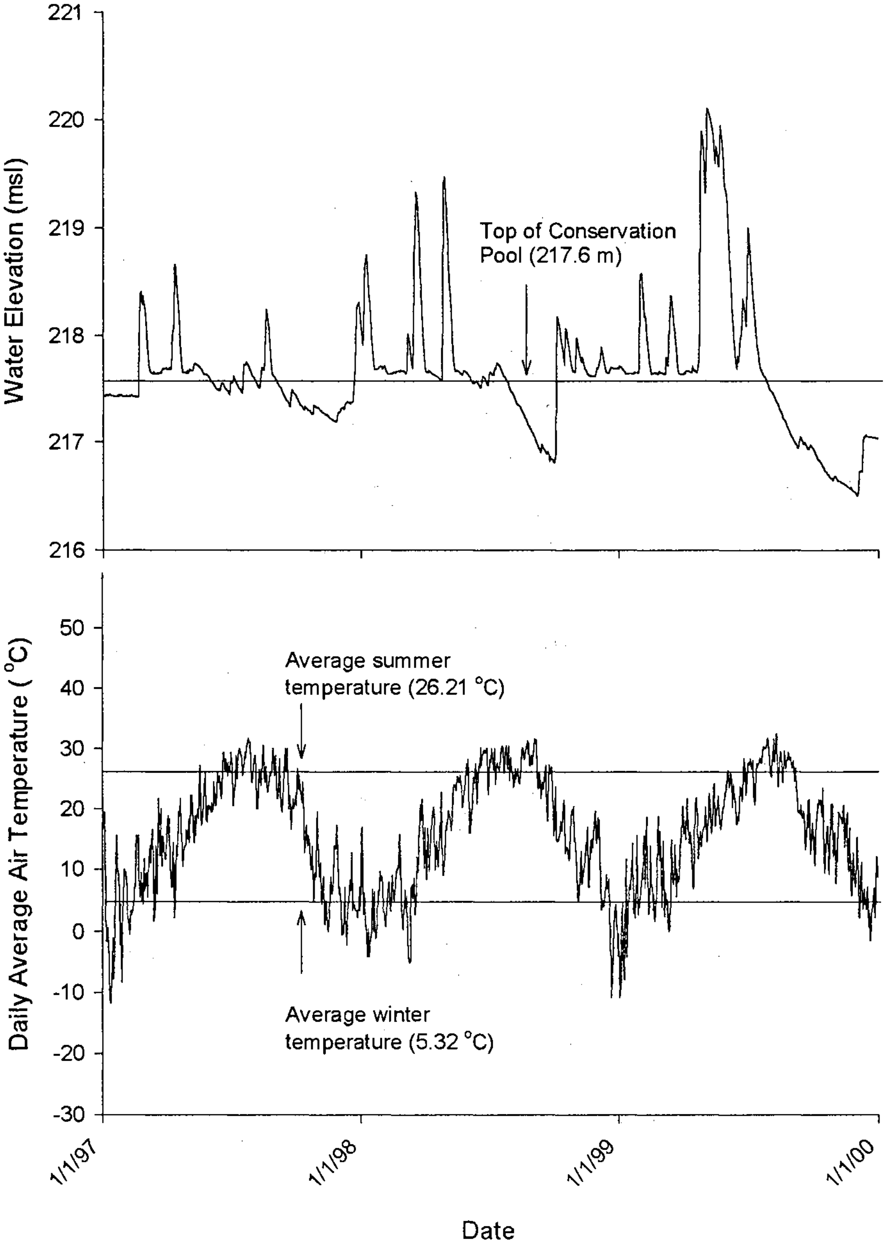
Figure 3.–Correlations between environmental variables during the spawning and post-spawning seasons and catch rates of young-of-year (YOY) and juvenile largemouth bass, juvenile smallmouth bass, and juvenile spotted bass in Skiatook Lake.

Figure 4.–Distribution of swim-up dates of young-of-year largemouth bass in Skiatook Lake, Oklahoma 1997 - 1999.

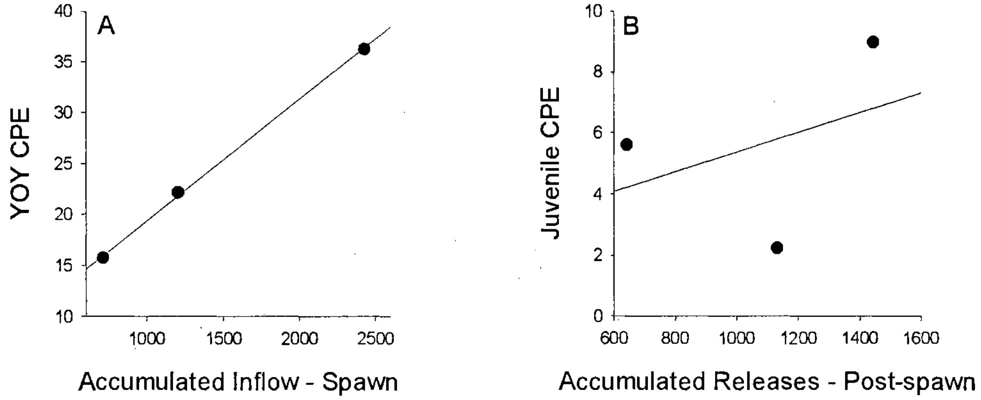
Figure 5.–Distribution of swim-up dates of young-of-year smallmouth bass in Skiatook Lake, Oklahoma 1997 - 1999.

Figure 6.–Distribution of swim-up dates of young-of-year spotted bass in Skiatook Lake, Oklahoma 1998 - 1999 (none were collected in 1997).

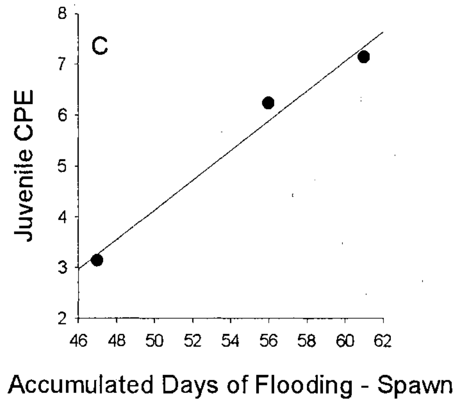

Bull Creek
Hominy Creek
Mid-lake
Lower-lake
1 km


Water Elevation (msl)
221
220
219
218
217
216
Top of Conservation Pool (217.6 m)
Daily Average Air Temperature (°C)
50
40
30
20
10
0
-10
-20
-30
Average summer temperature (26.21 °C)
Average winter temperature (5.32 °C)
1/1/97
1/1/98
1/1/99
1/1/00
Date

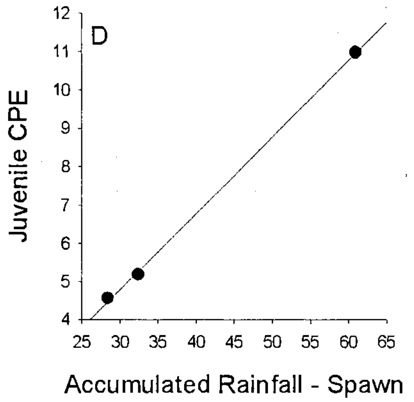
Largemouth bass

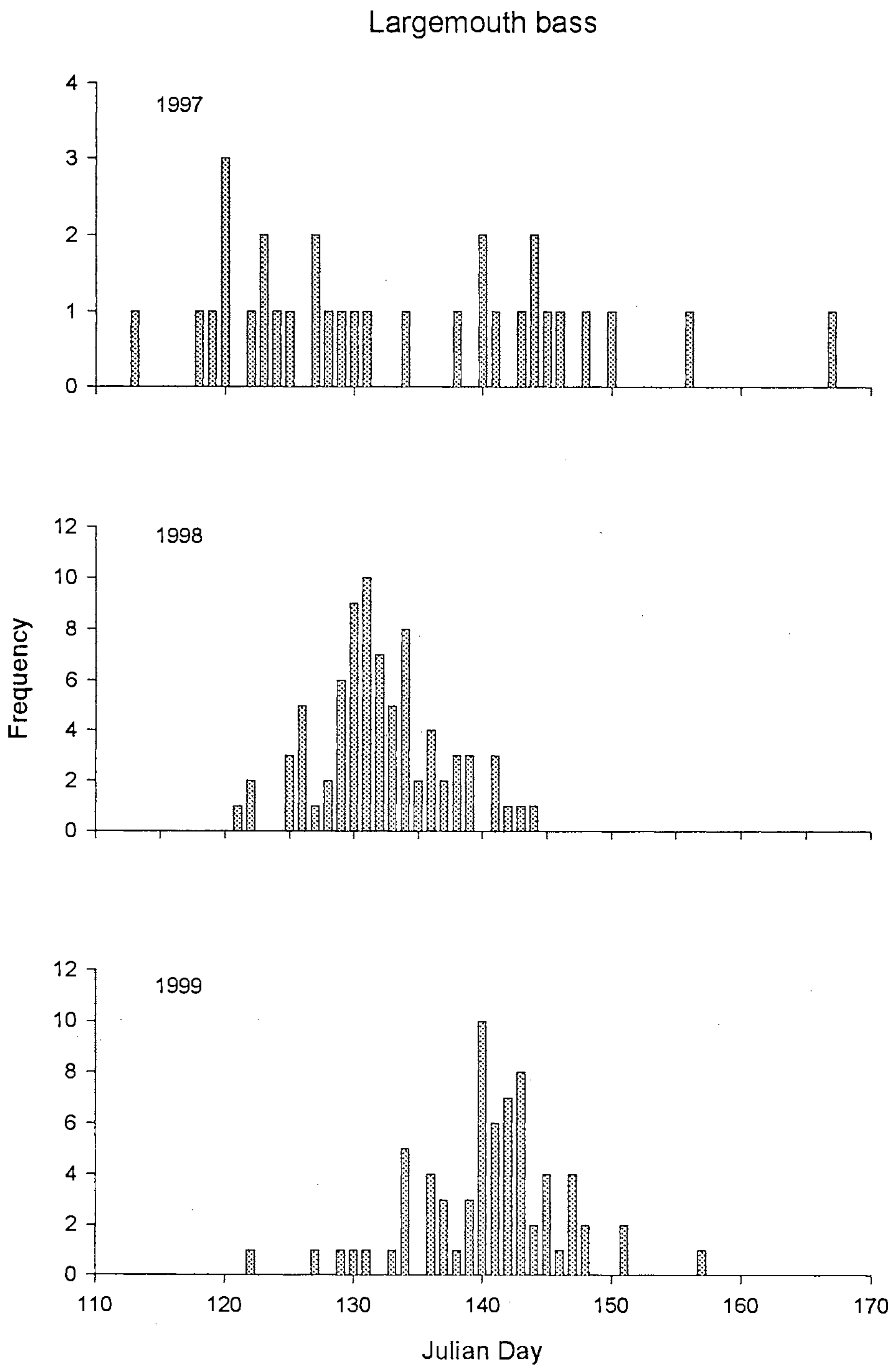


Smallmouth bass

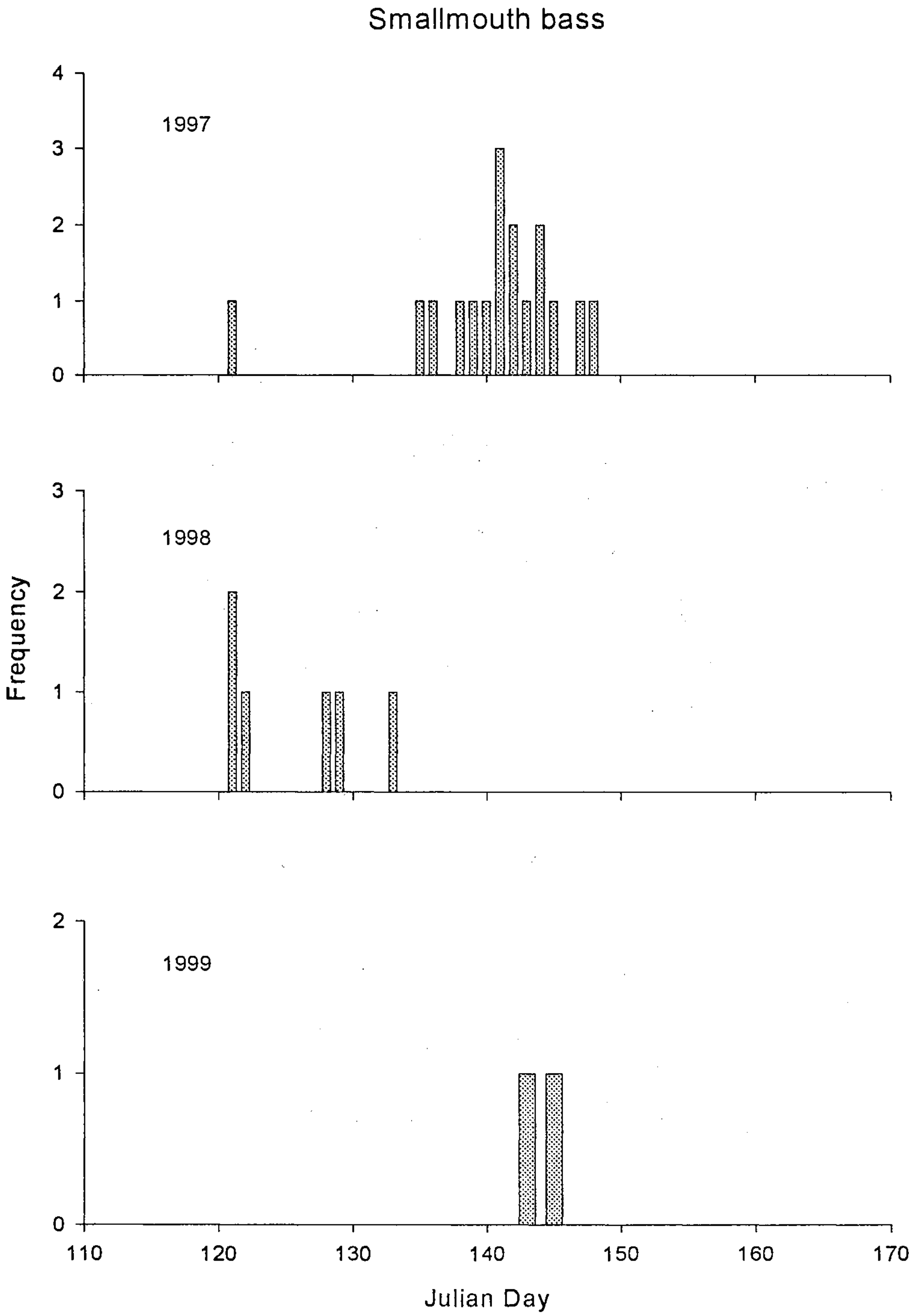


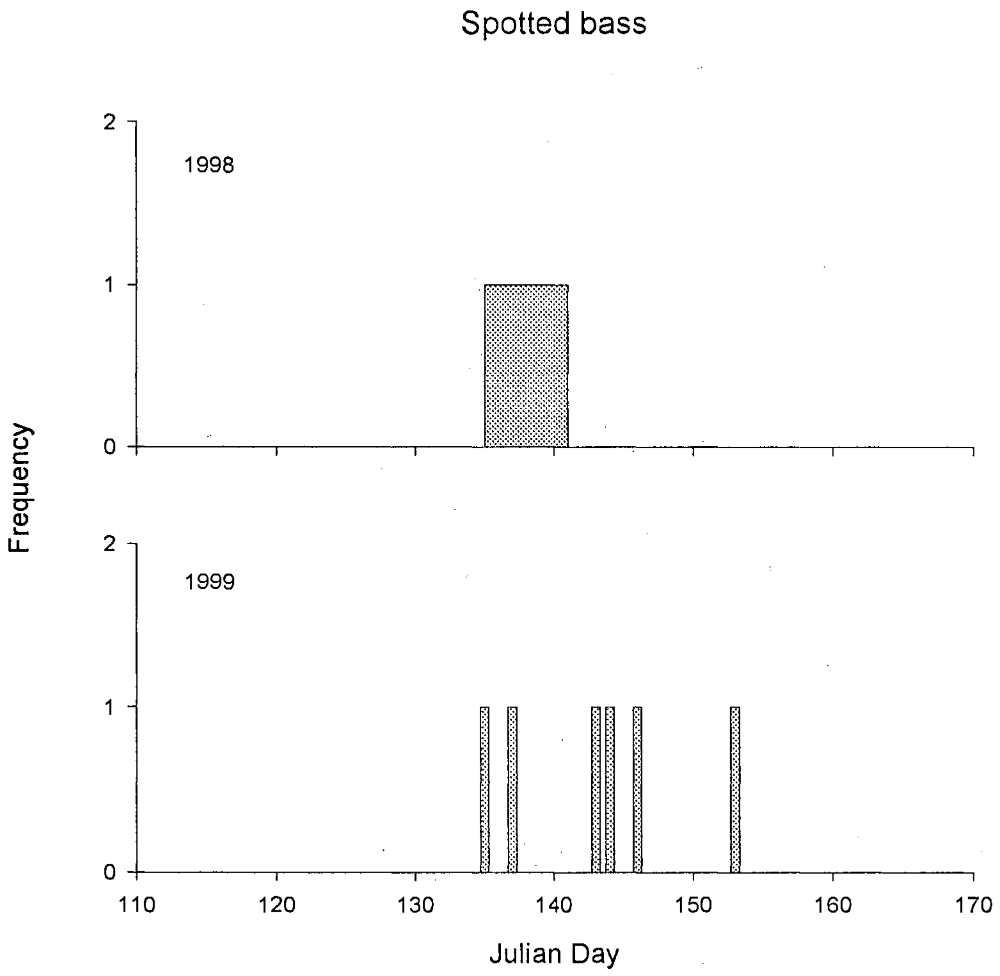
Spotted bass





Largemouth bass
1997
1998
1999
Frequency
Julian Day
0
1
2
3
4
0
2
4
6
8
10
12
0
2
4
6
8
10
12
110
120
130
140
150
160
170


Smallmouth bass
4
3
2
1
0
1997
3
2
1
0
1998
Frequency
2
1
0
1999
110
120
130
140
150
160
170
Julian Day


Spotted bass
1998
1999
Frequency
0
1
2
0
1
2
110
120
130
140
150
160
170
Julian Day

VITA

James Michael Long

Candidate for the Degree of

Doctor of Philosophy

Thesis: POPULATION DYNAMICS AND INTERACTIONS OF THREE BLACK BASS SPECIES IN AN OKLAHOMA RESERVOIR AS INFLUENCED BY ENVIRONMENTAL VARIABILITY AND A DIFFERENTIAL HARVEST REGULATION

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