Fisheries Management and Ecology, 2004, **11**, 345–352

Environmental influences on largemouth bass *Micropterus salmoides* populations in shallow Nebraska lakes

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Abstract The influence of environmental variables on largemouth bass *Micropterus salmoides* (Lacépède) populations in 22 shallow (mean depth 1.0–2.9 m) Nebraska lakes was evaluated. Largemouth bass exhibited density-dependent size structure and growth, but not condition. Total annual mortality averaged only 30%. Deeper lakes contained low density largemouth bass populations with a high proportion of fish >380 mm, whereas larger lakes with little submerged vegetation had faster growth. The proportion of largemouth bass >380 mm and relative abundance tended to increase with emergent vegetation coverage. More stable recruitment was evident in shallower lakes with increased emergent vegetation coverage. Strong year classes were associated with cooler September air temperatures. Largemouth bass populations exhibited density-dependent effects in lakes up to 332 ha. Lake depth, emergent vegetation and autumn air temperatures may influence largemouth bass populations more than previously suggested.

KEYWORDS: habitat, population dynamics, productivity, recruitment, vegetation.

Introduction

Largemouth bass *Micropterus salmoides* (Lacépède) population characteristics (e.g. abundance, size structure, condition, growth and mortality) in temperate lakes and reservoirs are influenced by both biotic and abiotic environmental factors. Growth and condition of largemouth and spotted bass *Micropterus punctulatus* (Rafinesque) have been linked to total alkalinity, chlorophyll *a*, conductivity and mean lake depth in southern US reservoirs (Miranda & Durocher 1986; DiCenzo, Maciena & Reeves 1995), whereas relative abundance has been linked to secchi disk transparency in small Midwestern impoundments (Guy & Willis 1991). Environmental variables may influence largemouth bass populations throughout life in lentic environments across a large geographic scale.

Increased density of largemouth bass typically leads to reduced growth, size structure and condition, particularly in water bodies <40 ha. Increased largemouth bass density was inversely related to condition (Wege & Anderson 1978; Schindler, Hodgson & Kitchell 1997), growth (Hill & Willis 1993) and size structure (Gabelhouse 1984; Hill & Willis 1993). In addition, largemouth bass populations with high total annual mortality had low size structure in small impoundments in the Midwestern US (Reynolds & Babb 1978). However, these relationships were documented in water bodies ranging from 0.5 to 27.9 ha. In larger Nebraska sandhill lakes, other fish species [i.e. bluegill *Lepomis macrochirus* Rafinesque and yellow perch *Perca flavescens* (Mitchill)] did not exhibit density-dependent growth, size structure and condition (Paukert, Willis & Klammer 2002a).

Vegetation coverage of lakes plays a vital role in the population dynamics of largemouth bass (Aggus & Elliot 1975). In impoundments, relative abundance of largemouth bass increased with increasing submerged vegetation coverage (Durocher, Province & Kraii 1984; Guy & Willis 1991). Wiley, Gorden, Waite & Powless (1984) estimated that largemouth bass production peaked near 52 g m^{-3} dry mass (36% coverage) of vegetation. Excessive vegetation coverage provides cover for largemouth bass prey (Colle & Shireman 1980), and too little coverage apparently is linked to low recruitment in some waters (Aggus & Elliot 1975). Growth has also been linked to submerged vegetation coverage. Reduced vegetation abundance resulted in

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increased growth of smaller largemouth bass because, after all submerged vegetation was removed, the bass became piscivorous at smaller sizes, thus increasing growth (Bettoli, Maceina, Noble & Betsill 1992). Although largemouth bass appear to be highly influenced by submerged vegetation, there has been little study on the effects of emergent vegetation coverage on largemouth bass populations.

The objective of this study was to evaluate the relationships between environmental factors and largemouth bass population dynamics in the shallow, exclusively littoral (< 4.5 m maximum depth) Nebraska sandhill lakes. It is thought fish communities in these lakes may function differently than in other lakes and reservoirs where previous largemouth bass research was focused. This study was implemented specifically to determine if relationships previously found for smaller water bodies (i.e. < 40 ha) were consistent with larger (i.e. up to 332 ha) natural lakes.

Materials and methods

Study site

Twenty-two natural lakes with largemouth bass were sampled in the sandhill region of north-central Nebraska in 1998 and 1999. These lakes varied in surface area from 15 to 332 ha, were shallow and entirely littoral (mean depth 1.0–2.9 m; Table 1). Submerged vegetation coverage ranged from 0 to 97%, whereas emergent vegetation coverage ranged from 0 to 24% of the lake surface. Twenty of the 22 lakes contained bluegill, 21 contained yellow perch, whereas black bullhead *Ameiurus melas* Rafinesque was collected in 17 lakes, and common carp *Cyprinus carpio* L. in only one lake. Northern pike *Esox lucius* L., a top predator, was found in 11 lakes.

Largemouth bass were sampled by night electric fishing during May and June of 1998 and 1999 using pulsed-DC current with 3–6 A and 200–250 V output at 12 randomly selected 10-min shoreline stations. Twelve of the 22 lakes were sampled in 1998, and the remaining 10 in 1999. Catch-per-unit-effort (CPUE) was expressed as the mean number of largemouth bass ≥ 200 mm total length collected per hour of night electric fishing. During each sampling period, scales were collected from up to 10 largemouth bass per one centimetre length group for age and growth analysis, and these fish were weighed (nearest g) and measured (total length nearest mm). All additional fish collected were categorised by centimetre length group by species.

Largemouth bass condition was quantified using mean relative weight (W_r) of 200–300 mm largemouth bass (Wege & Anderson 1978). Largemouth bass size structure was quantified using relative stock density of preferred-length fish [RSD-P; 100 × (the number of largemouth bass ≥ 380 mm/the number of largemouth bass ≥ 200 mm)] (Gabelhouse 1984). Growth was assessed using the time (in years) to reach 300 mm

Table 1. Largemouth population and environmental characteristics for 22 Nebraska sandhill lakes sampled for largemouth bass, 1998–1999

Parameter	Mean (SE)	Median	Range	*n*
Largemouth bass				
CPUE	67 (12)	49	7–159	22
RSD-P	25 (4)	27	0–61	19
W_r for 200–300 mm fish	112 (2)	115	95–124	21
Years to reach 300 mm	3.6 (0.1)	3.4	2.9–5.1	19
Total annual mortality (%)	30 (3)	26	10–56	18
Recruitment variability	0.50 (0.07)	0.45	0.09–0.92	19
Environment				
Total alkalinity (mg L^{-1})	149 (19)	119	85–447	22
Chlorophyll *a* (mg m^{-3})	5.1 (1.5)	2.5	0.7–28.7	22
Conductivity (μS)	324 (42)	274	177–1121	22
Mean lake depth (m)	1.8 (0.1)	1.8	1.0–2.9	22
Maximum lake depth (m)	2.9 (0.2)	3.0	1.5–4.3	22
Secchi depth (cm)	139 (16)	111	20–258	22
Lake area (ha)	110 (20)	80	15–332	22
Submerged vegetation (%)	46 (7)	40	0–97	22
Emergent vegetation (%)	10 (1)	10	0–24	22

CPUE, mean number of fish ⩾200 mm collected per hour of night-time electric fishing; RSD-P, relative stock density of preferred-length largemouth bass; mean W_r, mean relative weight for 200–300 mm largemouth bass; recruitment variability, recruitment coefficient of determination (RCD).

derived from the von Bertalanffy growth function (Ricker 1975), assessed from back-calculated length at age data from annuli counted on scales.

All physical and chemical habitat measurements, except vegetation coverage and mean and maximum lake depth, were collected at four sampling locations throughout the lake during July of the same year as the fish sampling. Phytoplankton community biomass was measured in each lake by chlorophyll *a* extraction. Secchi disk transparency was measured to the nearest cm, and water samples were collected to determine total alkalinity (using Hach kits). Conductivity was determined with an electronic metre. Vegetation, and mean and maximum lake depth were assessed on all lakes in July 1999. Five to seven evenly spaced transects across each lake were established (Paukert, Willis & Holland 2002b). At 50–200-m intervals along each transect (depending on lake size), vegetation was classified as either emergent or submerged in a 1-m^2 grid along side of the boat (Paukert *et al.* 2002b). Mean and maximum depth were calculated using measurements (nearest 0.1 m) taken at each of the vegetation sites. Mean depth was calculated by dividing the sum of all the depth measurements for each lake by the number of sites on each lake.

Regression analysis was used to determine if there were any density dependent relationships with largemouth bass CPUE and RSD-P, mean W_r, time to reach 300 mm, total annual mortality, and recruitment variability. Because northern pike can alter relationships with largemouth bass when these species are sympatric (Paukert & Willis 2003), the dummy variable of northern pike presence (yes or no) was included in the intraspecific density relationships. To reduce the dimensionality of the physical and chemical lake characteristics data, principal component analysis (PCA) was used (Johnson 1998). An environmental variable PCA was computed using conductivity, chlorophyll *a*, total alkalinity, mean and maximum lake depth, secchi dish transparency, lake area, and the proportion of the lake covered by emergent and submerged vegetation, and presence of northern pike as a dummy variable. Pearson correlations were used to determine bivariate relationships between largemouth bass population characteristics (CPUE, RSD-P, mean W_r, years to reach 300 mm, total annual mortality, and recruitment variability) and the environmental principal components (e.g. Paukert *et al.* 2002a).

Recruitment and year-class strength were assessed two different ways. First, the recruitment coefficient of determination (r^2; RCD) was used to assess variability in recruitment of largemouth bass for each population (Isermann, McKibbin & Willis 2002). This value is the coefficient of determination for the regression of a catch curve (i.e. regression of log abundance + 1 against age). Catch curve residuals were also used to assess relative year-class strength, with positive residuals being classified as strong year classes (i.e. higher than expected abundance for that age) and negative residuals classified as weak year classes (Maceina 1997). Stepwise logistic regression was used to detect the influence of temperature on year-class strength across all largemouth bass populations. In this analysis, the coded value of year class-strength (i.e. 1 = strong year class; 0 = weak year class) for each population and each year was used. The probability that a particular year has a strong year class based on mean monthly air temperatures taken from the National Oceanic and Atmospheric Administration weather station in Valentine, Nebraska, from 1990–1998 was then modelled. In addition, stepwise multiple regression was used to determine the relationship between mean residual from the catch-curve analysis (i.e. mean residual across all largemouth bass populations for each year) and mean monthly temperatures for that year.

Results

Largemouth bass population characteristics

Largemouth bass CPUE averaged 67 fish ≥ 200 mm per electric fishing hour, but varied from seven to 159 fish per hour (Table 1). Size structure typically was high: RSD-P values averaged 25 and ranged from 0 to 61. Mean W_r values indicated these fish had relatively high condition, averaging over 100 for 18 of the 21 populations. Growth was also fast, with an average of 3.6 years to reach 300 mm, a size desirable to anglers (Gabelhouse 1984). Total annual mortality estimates were typically low, averaging only 30%.

Largemouth bass populations in these lakes exhibited density-dependent size structure and growth, but not condition. Largemouth bass CPUE decreased with increased RSD-P values ($r^2 = 0.51$; d.f. = 2, 16; $P = 0.0035$) and decreased with time to reach 300 mm ($r^2 = 0.22$; d.f. = 2, 16; $P = 0.05$; Fig. 1). However, CPUE was not significantly related to mean W_r ($r^2 = 0.23$; d.f. = 2, 18; $P = 0.10$). Largemouth bass CPUE increased with increased total annual mortality estimates ($r^2 = 0.38$; d.f. = 2, 15; $P = 0.05$; Fig. 1). High density, low size structure largemouth bass populations typically had higher mortality.

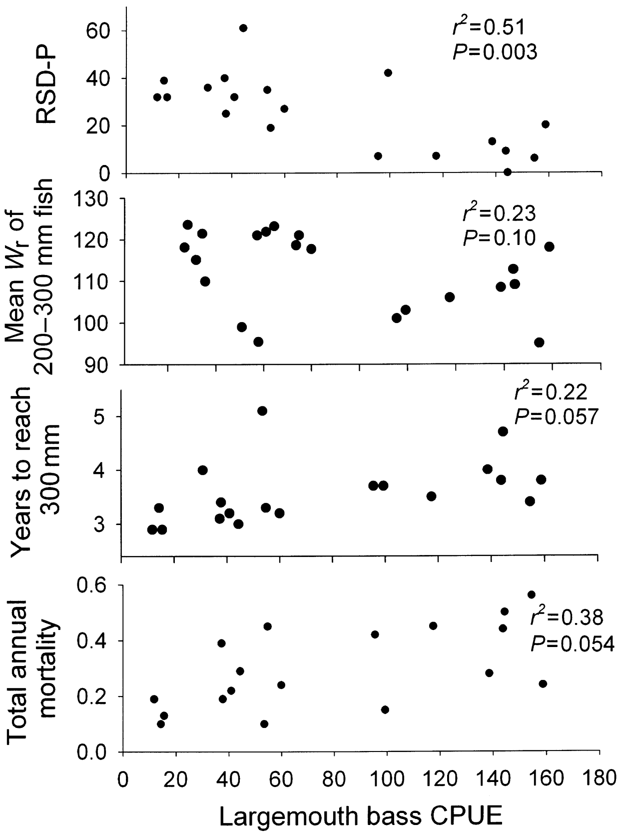

Figure 1. Relationship between the mean number of largemouth bass ≥200 collected per hour of electric fishing (CPUE) and largemouth bass relative stock density of preferred-length fish (RSD-P), mean relative weight (W_r), years to reach 300 mm, and total annual mortality (proportion) for fish collected in shallow Nebraska lakes during May and June, 1998–1999.

Physical and chemical relationships

The first three axes of the habitat principal components analysis explained 66% of the variation in the data set (Table 2). Larger lakes with low submerged vegetation coverage scored high on principal component 1 (PC1), whereas deeper lakes (both mean and maximum depth) with high secchi disk transparency readings and low emergent vegetation coverage with low chlorophyll *a* values scored high on principal component 2 (PC2). Principal component 3 (PC3), which explained 17% of the variation, was primarily an index of total alkalinity and conductivity.

Largemouth bass structure and dynamics were related to physical habitat and measures of productivity. Largemouth bass CPUE was inversely related to PC2 ($r = -0.67$; d.f. = 20; $P = 0.0006$), whereas RSD-P was positively related to PC2 ($r = 0.48$; d.f. = 17; $P = 0.039$; Fig. 2). Largemouth bass recruitment

Table 2. Component loadings for the first three principal components (PC) axes of the environmental principal components analysis (PCA) for 22 Nebraska sandhill lakes that contained largemouth bass sampled in 1998 and 1999. The eigenvalues and per cent variance explained by each axis are denoted at the bottom of the table

Parameter	PCA loadings		
	PC 1	PC 2	PC 3
Total alkalinity (mg L^{-1})	0.417	−0.106	0.460
Chlorophyll *a* (mg m^{-1})	−0.178	−0.372	−0.312
Conductivity (μS)	0.312	−0.158	0.567
Mean lake depth (m)	0.360	0.429	−0.234
Maximum lake depth (m)	0.347	0.392	−0.289
Secchi depth (cm)	−0.280	0.360	0.326
Lake area (ha)	0.380	−0.164	0.010
Submerged vegetation (%)	−0.468	0.167	0.294
Emergent vegetation (%)	−0.003	−0.464	−0.026
Presence of northern pike	−0.079	0.297	0.196
Eigenvalue	2.82	2.12	1.70
Variance explained (%)	28	24	17

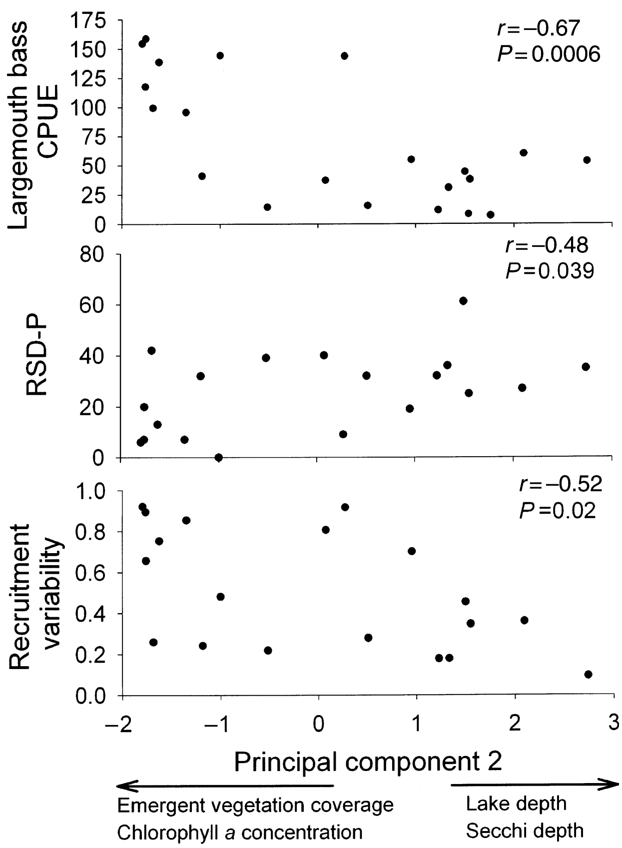

Figure 2. Relationship between mean number of largemouth bass ≥200 collected per hour of electric fishing (CPUE), largemouth bass relative stock density of preferred-length fish (RSD-P), largemouth bass recruitment variability index (RCD), and environmental principal component 2, which is an index of emergent vegetation coverage, chlorophyll *a*, mean lake depth, and secchi depth, for shallow Nebraska natural lakes sampled in 1998 and 1999.

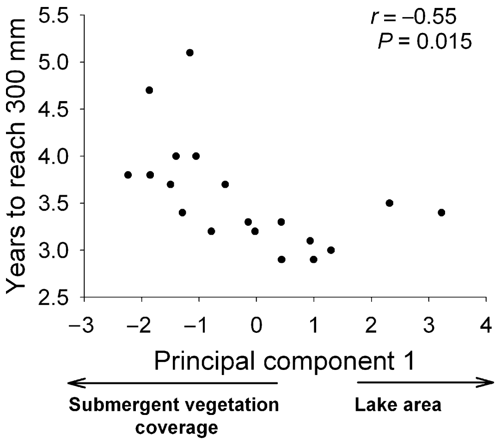

Figure 3. Correlation between largemouth bass years to reach 300 mm and environmental principal component 1, which was primarily and indicator of submerged vegetation coverage and lake area.

stability (RCD) increased with decreased PC2 scores ($r = -0.52$; d.f. = 17; $P = 0.02$). Low relative abundance and high size structure of largemouth bass populations with inconsistent recruitment were associated with increased mean lake depth and lower emergent vegetation coverage. The time needed for a largemouth bass to attain 300 mm was inversely related to PC1, an index of submerged vegetation and lake size ($r = -0.55$; d.f. = 17; $P = 0.015$), suggesting that larger lakes with low submerged vegetation coverage had faster growing largemouth bass (Fig. 3). Total annual mortality tended to increase with PC3 ($r = 0.46$; d.f. = 16; $P = 0.054$; Fig. 4). Populations with high total annual mortality were associated with increased total alkalinity and conductivity. However, this may be related more to largemouth bass population characteristics as size structure was also related to PC3. Mean W_r was not strongly related to PC1 ($r = 0.03$; d.f. = 19; $P = 0.918$), PC2 ($r = 0.34$; d.f. = 19; $P = 0.130$) or PC3 ($r = -0.41$; d.f. = 19; $P = 0.063$).

Largemouth bass year-class strength across all populations sampled appeared to be influenced by autumn air temperatures. Logistic regression revealed that the probability of having a positive catch-curve residual (indicating a strong year class) was influenced by September ($\chi^2 = 14.33$; $P = 0.0002$) and November ($\chi^2 = 4.45$; $P = 0.035$) air temperature; no other month was significant ($P > 0.10$). Lakes were more likely to have strong year classes with cooler September mean air temperatures and warmer November mean air temperatures. Stepwise multiple regression using the mean catch-curve residual across all lakes indicated higher (positive) residuals were inversely related to mean September air temperatures ($r^2 = 0.78$; d.f. = 1, 8; $P = 0.0015$; Fig. 5). No other month was significant ($P > 0.10$).

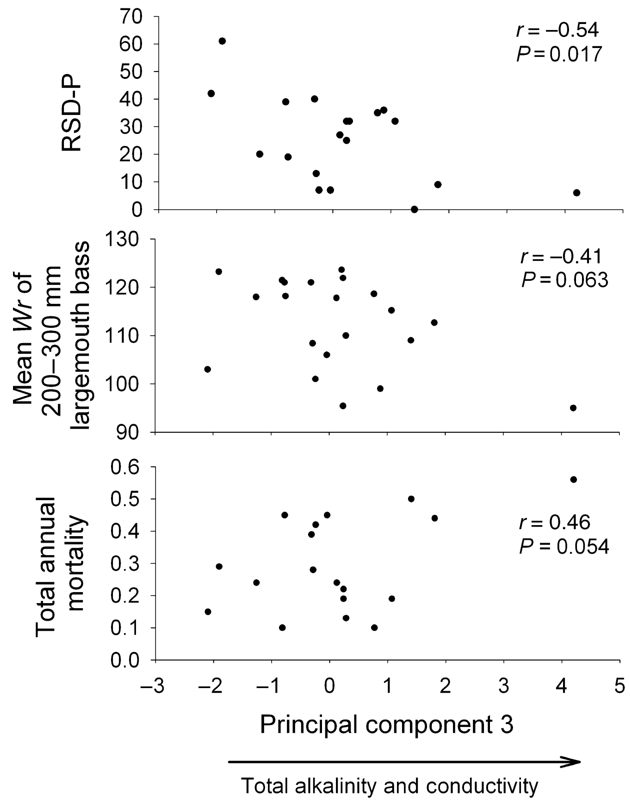

Figure 4. Relationship between largemouth bass relative stock density of preferred-length fish (RSD-P), mean W_r of 200–300 mm largemouth bass, largemouth bass total annual mortality, and environmental principal component 3, which is an index of total alkalinity and conductivity for shallow Nebraska natural lakes sampled in 1998 and 1999.

Discussion

Largemouth bass in these shallow, littoral lakes appeared to have density-dependent size structure and growth, but not condition. Density-dependent size structure, growth and condition have been documented in smaller water bodies (e.g. Wege & Anderson 1978; Guy & Willis 1991; Hill & Willis 1993; Schindler *et al.* 1997). Few studies have documented such relationships in water bodies of the size examined in the present study (i.e. up to 332 ha). However, largemouth bass size structure, growth and condition decreased in six South Dakota lakes up to 869 ha as bass CPUE increased (McKibbin 2002). The present study showed that there were no density-dependent effects on bass condition, which was similar to other species (e.g. bluegill, yellow perch and northern pike) in the shallow sandhill lakes (Paukert *et al.* 2002a;

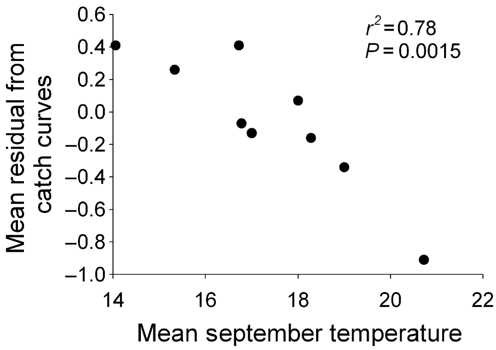

Figure 5. Relationship between mean residual from catch-curve regressions for 19 largemouth bass populations and mean September air temperature, 1990–1998. Each point represents the mean residual across all populations for each year.

Paukert & Willis 2003). Condition indices were relatively high and were never below 95, suggesting that food resources (i.e. bluegill and yellow perch) for predators (i.e. largemouth bass and northern pike) in these lakes were not limiting. The density-dependent relationship between largemouth bass CPUE and growth and size structure in these larger Nebraska lakes may be attributable to lake morphometry. The lakes studied were almost exclusively littoral (maximum depth range of 1.5–4.3 m) with vegetation throughout the entire lake area (Paukert *et al.* 2002b). Larger lakes and impoundments typically have a smaller littoral zone that is inhabited by largemouth bass. Therefore, the entire study lakes may be functionally similar to littoral zones of other lakes.

Largemouth bass total annual mortality was relatively low compared with other exploited populations (mean: 30%, range: 10–56%), and similar to other fish populations in these sandhill lakes (Paukert, Willis & Glidden 2001). Allen, Miranda and Brock (1998) summarised total annual mortality estimates for 34 largemouth bass population throughout the US and found an average of 64% (range 24–92%), with an average exploitation of 36% (range 9–72%). The total annual mortality in this study was lower, possibly because of the limited exploitation in these lakes (e.g. Paukert, Willis & Gabelhouse 2002c). In addition, high total annual mortality estimates were associated with reduced size structure in the sandhill lakes. Populations with high mortality typically do not have high proportions of larger fish, resulting in reduced size structure (Reynolds & Babb 1978).

Largemouth bass populations in the Nebraska sandhill lakes were influenced by submerged and emergent vegetation coverage within each lake. Growth rates were reduced with increased submerged vegetation coverage, whereas increased largemouth abundance and weak size structure were associated with increased emergent vegetation coverage. Increased submergent vegetation coverage has been associated with increase largemouth bass abundance (Durocher *et al.* 1984; Guy & Willis 1991), and decreased submerged vegetation has been related to increased growth of small largemouth bass because of an earlier onset of piscivory (Bettoli *et al.* 1992). Surprisingly, emergent vegetation appeared to be related to largemouth bass size structure and relative abundance, which is similar to other species (i.e. bluegill and yellow perch) in the sandhill lakes (Paukert *et al.* 2002a). In addition emergent vegetation was selected for bluegills in a telemetry study (Paukert & Willis 2002). Although the mechanisms are unclear, emergent vegetation appears to be important in the structure and dynamics of fish populations in these lakes.

There were few relationships between measures of productivity and largemouth bass population characteristics. However, deeper lakes (e.g. mean depth > 2 m) were typically associated with low density, high size structure largemouth bass populations with fast growth, although mean lake depth ranged only from 1.0 to 2.9 m. Similarly, largemouth bass growth in Texas reservoirs increased with mean lake depth (Miranda & Durocher 1986); however, Guy and Willis (1991) found no relationship between maximum depth and largemouth bass relative abundance. Other studies have suggested that growth and condition of black basses have been linked to measures of productivity (e.g. total alkalinity and chlorophyll *a*; Miranda & Durocher 1986; DiCenzo *et al.* 1995), but the current study found limited evidence of this relationship, which was similar to other fishes in these lakes (e.g. Heikes, Paukert & Willis 2001; Paukert *et al.* 2002a). Perhaps the limited range of condition and growth values for these largemouth bass populations explains the lack of significant relationships. Condition was typically high and growth was well above the South Dakota average (Willis, Milewski & Guy 1990). Therefore, most populations sampled were considered high quality with only slight differences in growth and condition.

Largemouth bass recruitment was related to autumn and early winter air temperatures and possibly lake size and emergent vegetation coverage. More consistent autumn air temperatures may indirectly influence largemouth bass recruitment in these shallow natural lakes. Temperature is critical for recruitment of juvenile largemouth bass (Garvey, Stein, Wright & Bremigan 2002), particularly during early spring

(Jackson & Noble 2000; Garvey *et al.* 2002). Warmer autumn water temperatures may increase food availability and therefore increase growth and/or reduce overwinter starvation (Parkos & Wahl 2002). This study indicated autumn and early winter temperatures were important in determining year class strength, although the mechanism for this relationship is unclear.

Acknowledgments

We thank P. Chvala, H. Fullhart, B. Heikes, J. Harrington, J. Klammer, A. Glidden and M. Wilson for field and laboratory help. D. Hartman and the Valentine State Fish Hatchery provided housing and logistic support. Valentine and Crescent Lake National Wildlife Refuges allowed access to refuge lakes. The project was funded by Nebraska Game and Parks Commission through Federal Aid in Sport Fish Restoration Project Number F-118-R and approved for publication by the South Dakota Agricultural Experiment Station as Journal Series 3308.

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