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Population Characteristics and Ecological Role of Northern Pike in Shallow Natural Lakes in Nebraska

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Abstract.—Northern pike *Esox lucius* were sampled in Nebraska's Sandhill lakes during 1998 and 1999 to determine population characteristics and their influence on the fish community in these shallow, warm lakes at the southwestern edge of this species' natural range. Density-dependent growth, size structure, and condition were not evident in the northern pike populations sampled. Relative abundance of largemouth bass *Micropterus salmoides* was positively related to size structure of yellow perch *Perca flavescens* and bluegills *Lepomis macrochirus* when northen pike were absent. When northern pike and largemouth bass populations were sympatric, these relationships were less evident. Population size structure of yellow perch was lower in lakes with northern pike, but decreased size structure was not evident for bluegills. Northern pike growth decreased with July bottom water temperature, which ranged from 20°C to 25°C. Recruitment patterns of northern pike in the Sandhill lakes appeared to be lake-specific, strong and weak year-classes occurring in the same year among different populations. Northern pike in these shallow, warm lakes act as a top-down predator and appear to structure fish communities predominated by largemouth bass and panfish. Biologists managing warmwater Midwestern lakes thus should consider the effect of northern pike on fish communities.

Northern pike *Esox lucius* are common throughout the northern United States and Canada; the southwestern edge of their natural range extends south to north-central Nebraska (Crossman 1996). Northern pike is a mesothermal coolwater species (Casselman 1996) that flourishes in shallow, productive environments (Casselman and Lewis 1996). Populations typically thrive in lakes with adequate flooded vegetation for spawning and recruitment, coolwater habitats for thermal refuge, and the presence of large-sized prey. When some or all of the conditions are not met, growth may slow and size structure may be reduced (Diana 1987). In addition, high population density may contribute to slow growth of northern pike (Casselman 1996).

Northen pike may alter fish communities, primarily through predation. Abundance and size structure of prey, typically yellow perch *Perca flavescens*, may be reduced with increased northern pike abundance (Margenau 1995). Northern pike were estimated to consume 50% of the annual production of Eurasian perch *P. fluviatilis* in Lake Windermere, England (Johnson 1966). In addition, northern pike may consume larger prey, such as largemouth bass *Micropterus salmoides* (Gurtin et al. 1996; Soupir et al. 2000), that serve as a predatory control on bluegills *Lepomis macrochirus* and yellow perch (Novinger and Legler 1978; Guy and Willis 1990, 1991a).

Lake characteristics and environmental factors appear to have substantial effects on northern pike populations. Optimal water temperatures for adult pike growth (8–18°C: Neumann et al. 1994) and juveniles (19–25°C: Casselman 1978; Bevelheimer et al. 1985) are often exceeded in lakes in the southern portion of the northern pike natural range. In addition, lakes with greater depth, which are typically associated with thermal refuges or more appropriate prey, typically produce larger northern pike (Jacobson 1992). Most studies of the population characteristics of northern pike involve more northerly populations (Diana 1987; Margenau et al. 1998); limited information exists for shallow, warmwater lakes, such as those in the Nebraska Sandhills.

The objectives of this study were to (1) describe the population characteristics of northern pike in shallow, warmwater lakes on the southwestern edge of their native range in North America; (2) evaluate the effects of the relatively harsh environment (i.e., shallow water, no thermal refuge)

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on northern pike recruitment, growth, and condition; and (3) evaluate the role of northern pike in structuring the fish community in lakes that typically have warmwater predators (i.e., largemouth bass).

Methods

Fish population assessments.—Northern pike, bluegill, yellow perch, and all other species except largemouth bass and common carp *Cyprinus carpio* were sampled at randomly selected shoreline sites where modified fyke nets, known as double-throated trap nets (16-mm-bar mesh, 1.1-m by 1.5-m frames, and 22-m leads), were set overnight. Total sampling effort was 10 trap-net nights in lakes less than 50 ha and 20 trap-net nights in lakes 50 ha or larger. Largemouth bass and common carp were sampled at night with pulsed DC (200–250 V, 3–6 A) electrofishing at 12 randomly selected shoreline stations fished for 10 min. All sampling was during May and June of 1998 and 1999, with 15 lakes being sampled each of the 2 years. Catch per unit effort (CPUE) was expressed as the number of stock-length (≥200 mm; Gabelhouse 1984) largemouth bass captured per hour of electrofishing and the number of stock-length bluegills (≥80 mm), yellow perch (≥130 mm), and northern pike (≥350 mm) per trap-net night.

Northern pike growth was assessed using mean back-calculated length at age 3 as determined from scales. Northern pike condition was quantified using mean relative weight (W_r) of 530- to 709-mm (i.e., quality to preferred length) northern pike; the standard weight equation was obtained from Anderson and Neumann (1996). Size structure of the fish populations was quantified using proportional stock density (PSD; Anderson and Neumann 1996).

Physical and chemical assessments.—Water temperature and dissolved oxygen (DO) profiles were taken in July during daylight hours at 0.5-m intervals at the deepest part of the lake. Alkalinity, chlorophyll *a*, total phosphorus, total dissolved solids (TDS), and Secchi disk transparency were measured at four locations in each lake during July and averaged. We then calculated the trophic state index (TSI; Carlson 1977) based on chlorophyll *a*, total phosphorus, and Secchi disk transparency. The morphoedaphic index (TDS/mean lake depth; Ryder 1965) was also used as an index of productivity.

We quantified vegetation at intervals of 50–200 m (depending on lake size) along five to seven evenly spaced transects across each lake. At each interval, vegetation within a 1-m^2 grid mounted on the side of the boat was classified as either emergent or submergent. Percent coverage of vegetation was calculated as the number of sites of that class divided by the total number of sites in that lake (Paukert et al. 2002a). Mean depth was calculated for each lake using measurements (nearest 0.1 m) taken at each of the vegetation sites and was calculated by dividing the sum of all the depth measurements for each lake by the numbers of sites on each lake.

Statistical analysis.—Principal components analysis (PCA; Johnson 1998) was used to reduce the dimensionality of the data set. We computed three different PCAs: (1) northern pike prey (mean bluegill and yellow perch CPUE and PSD), (2) lake productivity (chlorophyll *a* TSI, total phosphorus TSI, Secchi disk TSI, total alkalinity, and MEI), and (3) lake physical habitat (lake area, mean lake depth, emergent vegetation coverage, submergent vegetation coverage, temperature, and dissolved oxygen 0.5 m from the bottom). In these analyses, we only interpreted PCA axes with eigenvalues greater than 1.0 (Johnson 1998). Spearman rank correlations were used to relate PCA axis score with northern pike population characteristics (mean CPUE, PSD, mean length at age 3, mean W_r) and to relate panfish and largemouth bass population characteristics in lakes with and without northern pike. Logistic regression was used to determine if bluegill or yellow perch PSD was related to lake predator type (i.e., lakes with both northern pike and largemouth bass, neither northern pike nor largemouth bass, largemouth only, and northern pike only). An analysis of variance (ANOVA) was used to test for differences in mean bluegill and yellow perch CPUE among the four lake predator types. In these analyses, we used a mixed model that does not assume homogeneous variances (Littel et al. 1996). To reduce spurious conclusions, a Bonferroni correction was computed for each suite of statistical tests (Sokal and Rohlf 1995). For example, when we correlated largemouth bass CPUE and PSD with bluegill and yellow perch PSD for lakes with and without northern pike, we used a correction of 0.10/8 = 0.0125. All statistical analyses were performed using SAS (SAS Institute 1996) at $\alpha = 0.10$.

Results

We sampled 30 natural lakes in the Sandhill region in north-central Nebraska in 1998 and 1999. Lakes varied in surface area (mean, 133 ha; range, 15–907 ha), were shallow (maximum depth, 1.5–

4.0 m; mean, 1.0–2.9 m), and were almost entirely littoral, submergent vegetation coverage averaging 43% (range, 0–83%). Secchi disk transparency was highly variable (mean, 123 cm; range, 14–258 cm), and total alkalinity averaged 148 mg/L (range, 85–447 mg/L).

Sixteen lakes contained northern pike, and 29 contained yellow perch. Bluegills and largemouth bass were collected in 22 lakes (Table 1). Few other prey species were collected, although common carp were present in nine lakes. Because of the low common carp sample sizes (>5 carp in only five lakes), these fish were excluded from further analysis.

Northern Pike Population Characteristics

We collected northern pike from 16 lakes, but in only 7 lakes were we able to collect more than 25 fish (Table 1). Mean W_r values were all below 100, ranging from 74 to 99, and PSD values were high, ranging from 43 to 100 for lakes in which we were able to calculate PSD (Table 1).

Northern pike mean CPUE was not related to northern pike PSD (r = 0.50, P = 0.20, df = 6), mean W_r (r = 0.43, P = 0.15, df = 11), or mean length at age 3 (r = −0.14, P = 0.69, df = 9). The higher relative abundance of northern pike did not decrease their growth, size structure, or condition.

Northern pike condition increased with prey species size structure. Prey species principal component (PC1), which increased with increased bluegill and yellow perch PSD (Table 2), explained 43% of the variation in the prey species PCA. Northern pike W_r means of 530–709 mm increased with prey PC1 (r = 0.93, P = 0.003, df = 5; Figure 1) but were not related to prey PC2, which was an index of increased bluegill abundance (r = −0.44, P = 0.32, df = 5).

Lake productivity had little influence on northern pike populations in these lakes. Lake productivity PC1, an index of increased MEI and total alkalinity and decreased total phosphorus TSI, explained 44% of the variability in the lake productivity PCA, whereas PC2, primarily an index of Secchi disk and chlorophyll-*a* TSI, explained 27% of the variation (Table 3). Northern pike PSD increased with lake productivity PC2 (r = 0.82, P = 0.02, df = 5); thus higher northern pike size structure was related to higher measures of productivity (Figure 2). Northern pike mean CPUE and mean length at age 3 were not related to either lake productivity PC1 (P > 0.40) or PC2 (P > 0.80).

Physical lake habitat had limited influence on northern pike in these shallow natural lakes. Large lakes with low submergent vegetation coverage scored high on habitat PC1 (Table 4), whereas shallow lakes with higher emergent vegetation coverage and increased bottom DO scored high on PC2. Habitat PC3, an index of increased lake bottom water temperature, explained 17% of the variation of the habitat PCA. Habitat PC2 tended to increase with northern pike mean CPUE (r = 0.40, P = 0.06, df = 14) and PSD (r = 0.64, P = 0.09, df = 6) but was not related to mean length at age 3 (r = −0.15, P = 0.67, df = 9) or mean W_r (r = 0.17, P = 0.58, df = 11). Northern pike mean length at age 3 decreased with habitat PC3 (r = −0.62, P = 0.04, df = 9; Figure 3). No other northern pike population characteristic was related to habitat PC scores (P > 0.28).

Northern pike populations in the Nebraska Sandhills typically were young and exhibited among-lake recruitment variability. No population sampled contained fish older than 10 years. Of the 11 populations aged, only 2 had fish older than age 6. Catch-curve data from six populations revealed that strong year-classes (as indicated by positive residuals of the catch curve from ages 2–6) were not common across populations. Three of the six northern pike population samples for which catch curves could be computed had strong year-classes (1993, 1994, and 1996), whereas three populations had weak year-classes during the same years. Strong and weak year-classes occurred in the same year among lakes; however, a missing year-class (in 1996) apparently occurred in only one lake.

Fish Community Interactions

Sympatric northern pike and largemouth bass populations occurred in 11 Sandhill lakes, 11 lakes contained largemouth bass and no northern pike, 3 lakes contained no predators, and 5 contained northern pike only. Largemouth bass mean CPUE was negatively related to bass PSD (r = −0.66, P = 0.04, df = 8) in lakes without northern pike. However, in lakes that also contained northern pike, largemouth bass did not exhibit this intraspecific relationship (Figure 4). Largemouth bass mean CPUE was higher (mean = 105 bass/h) in lakes without northern pike compared with sympatric populations (mean = 38 bass/h; Wilcoxon's rank-sum test: z = 2.9, P = 0.004, df = 1). Largemouth bass CPUE for all study lakes ranged from 7 to 159 bass/h; the highest CPUE in lakes with sympatric populations was 144/h; however, we

TABLE 1.—Northern pike population characteristics for Nebraska Sandhill lakes sampled in May and June 1998 and 1999. Catch per unit effort (CPUE) is the mean number of stock-length and longer fish per trap net (northern pike, bluegill, and yellow perch) or per hour of electrofishing (largemouth bass and common carp). Mean relative weight (W_r) is for 350–710-mm northern pike. Standard errors (for CPUE, mean W_r, and mean length at age) or 95% confidence intervals (for proportional stock density [PSD]) are in parentheses. A minimum of 20 stock-length (350-mm) northern pike were used to calculate PSD, and three 530–709-mm northern pike were used to calculate mean W_r. Only two stock-length largemouth bass were collected in Hagan Lake. Other abbreviations are as follows: NWR = Valentine National Wildlife Refuge, N = total number of northern pike sampled.

Lake	Northern pike					Bluegill		Yellow perch	
	N	CPUE	PSD	Mean W_r	Mean length at age 3	CPUE	PSD	CPUE	PSD
Alkali						85.6 (23.4)	92 (1)	15.4 (4.2)	96 (2)
Big Alkali	19	0.8 (0.3)	84 (18)	84 (1.6)	542 (9)	0.1 (0.1)		0.1 (0.1)	
Cameron								82.6 (11.8)	63 (4)
Clear	21	1.1 (0.2)	43 (23)	99 (5.0)	668 (37)	11.3 (0.1)	79 (5)	0.2 (0.1)	53 (25)
Clear-NWR	7	0.4 (0.1)		98		11.4 (2.8)	52 (7)	20.2 (4.8)	12 (4)
Cottonwood	2	0.2 (0.1)		74 (0.1)		79.5 (17.8)	27 (3)	18.5 (3.3)	31 (7)
Cozad						232.5 (29.0)	55 (2)	5.7 (2.6)	49 (14)
DeFair								1.6 (0.7)	38 (27)
Dewey	51	2.6 (0.5)	94 (7)	89 (1.6)	628 (23)	19.9 (4.2)	61 (4)	6.4 (2.2)	33 (8)
Duck						21.3 (10.9)	23 (6)	3.6 (1.5)	58 (17)
Goose	31	1.4 (0.4)	96 (5)	93 (2.4)	594 (10)	11.8 (1.9)	67 (6)	12.8 (4.1)	11 (4)
Hackberry	26	1.3 (0.3)	92 (11)	82 (0.5)	758 (57)	15.3 (2.6)	54 (6)	4.4 (1.3)	36 (10)
Hagan								120.8 (63.1)	12 (3)
Home Valley								67.0 (10.3)	39 (3)
Island						20.5 (3.9)	99 (2)	11.4 (3.0)	90 (4)
Lackaff West	15	0.8 (0.2)	67 (37)	93 (4.1)	729 (23)	0.6 (0.2)	58 (33)	15.8 (3.4)	18 (5)
Marsh	8	0.6 (0.2)		97 (3.3)				17.1 (4.6)	47 (7)
Marsh-NWR								51.9 (9.6)	79 (3)
Medicine						58.4 (15.0)	70 (4)	24.7 (11.4)	60 (6)
Pelican	13	0.7 (0.2)	100 (100)	77 (3.1)		177.2 (24.9)	16 (2)	1.9 (0.4)	24 (15)
Roseberry	28	2.0 (0.8)	100 (100)	96 (1.6)	660			36.4 (12.8)	77 (5)
Round	21	1.9 (0.5)	84 (16)	93 (1.6)	514 (36)			25.7 (6.5)	11 (4)
Schoolhouse	15	1.5 (0.6)	87 (20)	77 (3.9)	655 (67)	3.2 (2.2)	41 (8)	12.4 (5.4)	14 (6)
Shell	30	1.5 (0.4)	76 (17)	88 (2.4)	531 (18)	12.0 (2.1)	40 (7)	1.8 (0.5)	54 (18)
Shoup						6.4 (1.3)	77 (11)		
Tower						13.1 (3.9)	49 (9)	1.0 (0.3)	50 (38)
Twin	35	1.7 (0.3)	79 (15)	84 (1.6)	743 (44)	7.3 (1.6)	66 (8)	0.1 (0.1)	
Watts						32.1 (4.1)	64 (3)	3.7 (0.9)	43 (11)
West Long	2	0.1 (0.1)				28.3 (4.5)	68 (6)	14.2 (2.9)	74 (7)
Willow						1.2 (0.6)	35 (21)	0.1 (0.1)	

only collected two northern pike in this lake (West Long), so pike density probably was low (Table 1). Northern pike mean CPUE (z = 0.34, P = 0.73, df = 1), PSD (z = 0.83, P = 0.40, df = 1), mean W_r (z = 1.32, P = 0.21, df = 1), and mean length at age 3 (z = −0.47, P = 0.64, df = 1) did not differ in lakes with and without largemouth bass, and all P-values were well above the Bonferroni corrected alpha level of 0.025.

In lakes without northern pike, bluegill PSD tended to increase with largemouth bass mean CPUE (r = 0.68, P = 0.02, df = 9) but was not significant after the Bonferroni correction ($P > 0.01$). However, bluegill PSD was negatively related to largemouth bass PSD (r = −0.80, P = 0.003, df = 9). In lakes containing both northern pike and largemouth bass, these relationships were not significant ($P \geq 0.21$; Table 5). Yellow perch PSD was positively related to largemouth bass CPUE in lakes without northern pike (r = 0.71, P = 0.01, df = 9) but was not significant after the Bonferroni corrections ($P > 0.01$) in sympatric northern pike and largemouth bass populations (r = 0.77, P = 0.04, df = 5).

Prey abundance and size structure was associated with presence of northern pike. Yellow perch mean CPUE was higher (67/trap net, SE = 9) in lakes without largemouth bass or northern pike compared than in lakes containing largemouth bass only (19/trap net, SE = 12), northern pike only (19/trap net, SE = 6), or both northern pike and largemouth bass (8/trap net, SE = 2; F = 14.2, P = 0.001, df = 3, 9). Logistic regression revealed that, compared with lakes containing both largemouth bass and northern pike, yellow perch PSD was 3.8 times greater in lakes with no predators,

TABLE 1.—Extended.

Lake	Largemouth bass	
	CPUE	PSD
Alkali	154.5 (21.0)	37 (6)
Big Alkali		
Cameron		
Clear	59.9 (10.5)	72 (10)
Clear-NWR	7.0 (2.4)	57 (30)
Cottonwood	53.5 (8.9)	73 (13)
Cozad	37.7 (4.3)	61 (11)
DeFair	144.4 (24.5)	44 (9)
Dewey	37.3 (8.5)	70 (11)
Duck	99.3 (12.0)	89 (6)
Goose	15.5 (3.1)	55 (19)
Hackberry	40.9 (7.4)	53 (12)
Hagan	0.0 (0.0)	
Home Valley		
Island	117.5 (20.1)	35 (6)
Lackaff West		
Marsh		
Marsh-NWR		
Medicine	138.6 (18.7)	27 (7)
Pelican	14.3 (3.4)	52 (18)
Roseberry		
Round		
Schoolhouse	8.3 (4.5)	31 (29)
Shell	30.8 (7.8)	76 (12)
Shoup	158.8 (28.9)	59 (9)
Tower	54.7 (14.2)	83 (8)
Twin	11.8 (2.7)	73 (20)
Watts	95.5 (12.7)	40 (7)
West Long	143.8 (32.1)	29 (8)
Willow	44.3 (8.5)	100 (99)

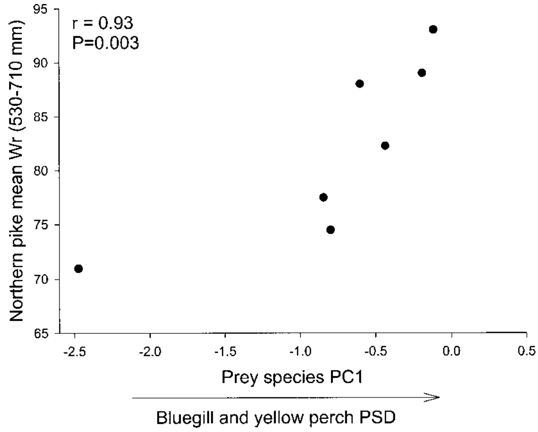

FIGURE 1.—Relationship between the mean relative weight (W_r) of 530–709-mm northern pike and prey species principal component (PC) 1 in Nebraska's Sandhill lakes, which increased with bluegill and yellow perch proportional stock density (PSD).

2.0 times greater in lakes with just northern pike, and 1.3 times greater in lakes with just largemouth bass ($\chi^2 = 684.23$, $P < 0.0001$, df = 3). However, differences among predator lake types were not significant for mean bluegill CPUE ($F = 0.39$, $P = 0.68$, df = 2,18) or PSD ($\chi^2 = 0.10$, $P = 0.95$, df = 2).

Discussion

Northern Pike Population Characteristics

Growth, size structure, and condition of northern pike in Nebraska's Sandhill lakes did not appear to be density dependent. Other studies have suggested that northern pike growth is reduced at higher densities (Diana 1987; Margenau et al. 1998), although this is not always the case (Mann 1980). Our contradictory results may result from

TABLE 2.—Component loadings for the first two principal component (PC) axes of the northern pike prey species principal components analysis for Nebraska Sandhill lakes sampled in 1998 and 1999. The eigenvalues and percent variance explained by each axis are denoted at the bottom of the table. Abbreviations are as follows: CPUE = mean number of stock-length (80-mm bluegills or 130-mm yellow perch) collected per trap-net night; PSD = proportional stock density.

Variable estimated	PC1	PC2
Bluegill CPUE	−0.19	0.73
Yellow perch CPUE	0.40	−0.45
Bluegill PSD	0.70	0.04
Yellow perch PSD	0.56	0.51
Eigenvalues	1.73	1.09
Percent variance	43	27

TABLE 3.—Component loadings for the first two principal component (PC) axes of the lake productivity principal components analysis for Nebraska Sandhill lakes sampled in 1998 and 1999. Variables are as follows: TSI = trophic state index; MEI = morphoedaphic index (total dissolved solids (mg/L)/mean lake depth). The eigenvalues and percent variance explained by each axis are denoted at the bottom of the table.

Variable estimated	PC1	PC2
Chlorophyll *a* TSI	−0.34	0.55
Total phosphorus TSI	−0.51	0.00
Secchi disk TSI	−0.04	0.75
Morphoedaphic index	0.58	0.04
Total alkalinity	0.53	0.37
Eigenvalues	2.20	1.37
Percent variance	44	27

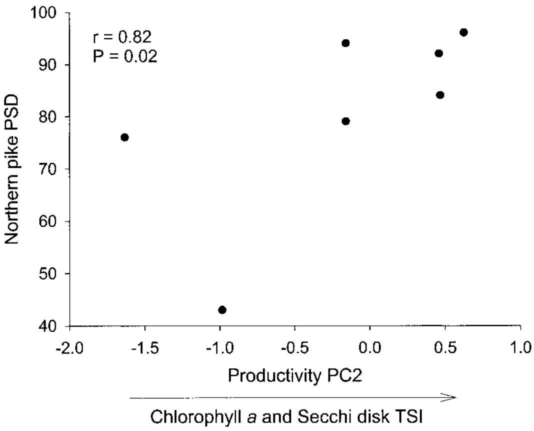

FIGURE 2.—Correlation between northern pike proportional stock density (PSD) and lake productivity principal component (PC) 2, which increased with chlorophyll-*a* and Secchi disk trophic-state indices (TSIs).

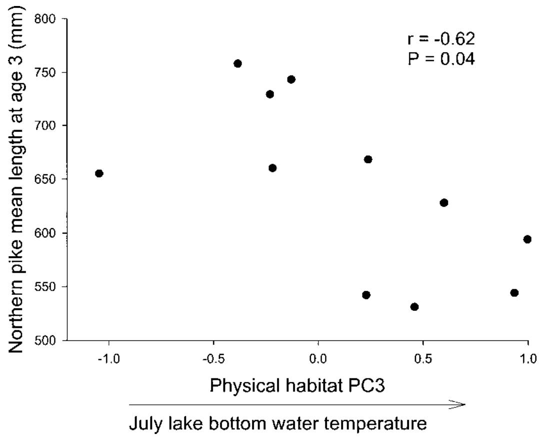

FIGURE 3.—Relationship between northern pike mean length at age 3 and physical habitat principal component (PC) 3, which increased with lake bottom water temperature.

the narrow range of northern pike abundance in our trap-net samples. If a wider range of CPUE was found at another time of year (e.g., spring; Guy and Willis 1991b) or with another gear (e.g., gill nets; Neumann and Willis 1995), we may have identified density-dependent growth. Although summer trap-netting may not be the most effective gear for northern pike population sampling, late summer gill-net and trap-net CPUE values in four Nebraska Sandhill lakes (U.S. Fish and Wildlife Service 1997, 1998, 1999, 2000) were positively related ($r = 0.52$, $P = 0.04$, df $= 14$), suggesting that our samples may reflect northern pike abundance.

Exploitation for all fish species was presumably minimal. Winter creel surveys on two of the more popular lakes indicated that northern pike harvest was 0.5–3.3 kg/ha, and angler effort was 5–8 angler-hours/ha (J. A. Klammer, Nebraska Game and Parks Commission, unpublished data). Little angling effort occurs during the summer because of extensive vegetation coverage. Two lakes that contained northern pike were closed to fishing, and most were either on private land or difficult to access.

Differences in the physical and chemical environment among the lakes apparently had little in-

TABLE 4.—Component loadings for the first three principal component (PC) axes of the physical habitat principal components analysis for Nebraska Sandhill lakes sampled in 1998 and 1999. The eigenvalues and percent variance explained by each axis are denoted at the bottom of the table.

Variable estimated	PC1	PC2	PC3
Lake area (ha)	0.57	−0.02	−0.34
Mean lake depth (m)	0.44	−0.43	0.40
Emergent vegetation coverage (%)	0.08	0.66	−0.34
Submergent vegetation coverage (%)	−0.68	−0.24	−0.03
Water temperature 1 m from bottom (°C)	0.09	0.32	0.71
Dissolved oxygen 1 m from bottom (mg/L)	−0.10	0.47	0.32
Eigenvalues	1.74	1.49	1.03
Percent variance	29	25	17

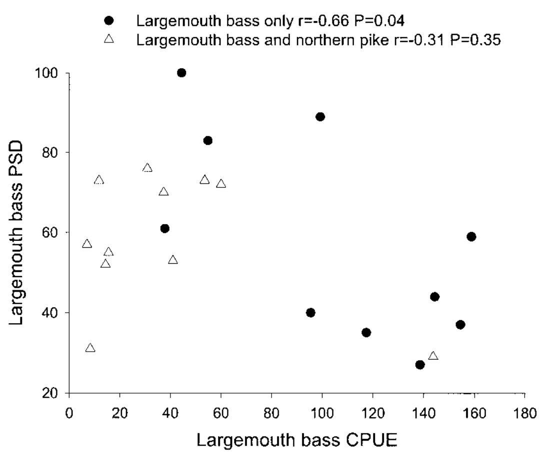

FIGURE 4.—Relationship between largemouth bass mean catch per unit effort (CPUE) and proportional stock density (PSD) for populations with sympatric largemouth bass and northern pike (triangles) and populations without northern pike (circles) in Nebraska's Sandhill lakes.

TABLE 5.—Correlations between (1) catch per unit effort (CPUE; mean number of 20-cm fish collected per hour of electrofishing) and (2) proportional stock density (PSD) of largemouth bass and PSD of bluegill and yellow perch in lakes with largemouth bass as the primary predator and lakes with sympatric northern pike and largemouth bass; *P*-values are in parentheses and were significant at $\alpha = 0.0125$ after Bonferroni corrections (0.10/8).

	Largemouth bass only		Northern pike and largemouth bass	
Correlate	Largemouth bass CPUE	Largemouth bass PSD	Largemouth bass CPUE	Largemouth bass PSD
Bluegill PSD	0.68 (0.02)	−0.80 (0.003)	0.46 (0.21)	0.43 (0.24)
Yellow perch PSD	0.71 (0.01)	−0.48 (0.17)	0.77 (0.04)	0.68 (0.09)

fluence on northern pike population characteristics. Similarly, Paukert et al. (2002b) found very little influence of physicochemical lake characteristics on bluegill and yellow perch populations in Nebraska Sandhill lakes. However, increased northern pike size structure was associated with increased measures of productivity. Although other studies have suggested that increased chlorophyll *a* is linked to increased growth (i.e., spotted bass *Micropterus punctulatus*; DiCenzo et al. 1995) or fish yield (Jones and Hoyer 1982), findings of our study and in Paukert et al. (2002b) suggest fish populations may not be strongly related to their physicochemical environment in the Nebraska Sandhill lakes. This may partially be due to the limited range for many of the physicochemical variables sampled in these lakes (Paukert and Willis 2000)

Northern pike population characteristics were linked to emergent or submergent vegetation coverage. Other fish species typically show reduced growth with increased submergent vegetation: yellow perch (Lott (1991), bluegill (Trebitz et al. 1997), black crappie (Paukert and Willis 2000). In Nebraska Sandhill lakes, increased emergent vegetation was associated with higher quality bluegill populations (Paukert et al. 2002b). Although common carp may reduce vegetation in lakes (Crivelli 1983), possibly altering the relationships between northern pike and aquatic vegetation, we were unable to ascertain the role of common carp in these lakes because we collected fewer than 5 common carp in only five of the study lakes. Further research on the effects of common carp in these Sandhill lakes may be needed to better understand fish community dynamics.

Water temperature was related to the growth of northern pike in the lakes we evaluated. Growth of northern pike decreased with increased July bottom water temperature. Optimum growth of subadult northern pike has been reported at 19°C (Casselman 1978) to 25°C (Bevelheimer et al. 1985), whereas adult northern pike in South Dakota grew fastest at 8–18°C (Neumann et al. 1994). In addition, Headrick and Carline (1993) noted that adult northern pike in southern Ohio selected cooler water when temperatures exceeded 25°C. July bottom water temperatures in our lakes ranged from 20–26°C, suggesting that these shallow (maximum depth 4.2 m) lakes lacked a thermal refuge, and thus growth may have been reduced. Diana (1987) suggested that stunting may be attributed to lack of thermal refuge, and his simulations suggested that water temperatures exceeding 27°C may reduce growth, which was similar to our observed maximum bottom water temperature.

Northern pike recruitment varied among water bodies in these shallow, natural lakes. Although strong and weak year-classes were evident, missing year-classes were nearly nonexistent. Our study lakes typically had flooded vegetation suitable for northern pike spring spawning (Bry 1996), so lack of spawning habitat is probably not limiting pike recruitment. Broad environmental factors did not appear to be related to northern pike recruitment in these lakes. Strong and weak year-classes occurred simultaneously across lakes. In contrast, year-class strength of northern pike has been attributed to broad environmental conditions in other waters. Year-class strength was positively related to water temperature in the Bay of Quinte, Ontario (Casselman 1996), and to water levels in Ball Club Lake, Minnesota (Johnson 1957). Our results suggest that relationships between northern pike recruitment and climatological factors in Nebraska Sandhill lakes were lake-specific.

Fish Community Interactions

Northern pike appear to play an important role in structuring the fish communities in Nebraska Sandhill lakes. In lakes with only largemouth bass as the primary predator, size structure of bluegills and yellow perch increased with increased largemouth bass abundance. These results were similar to other Midwestern studies in small impoundments (Novinger and Legler 1978; Guy and Willis 1990, 1991a), which suggested that abundant largemouth bass prey on smaller panfish, thus decreasing panfish intraspecific competition and increasing their size structure. However, in lakes with both northern pike and largemouth bass, this relationship was less evident. In addition, largemouth bass abundance was apparently reduced where northern pike were present. In sympatric northern pike and largemouth bass populations, northern pike act as an additional predator on yellow perch and bluegills, and they prey on largemouth bass, reducing their abundance. Northern pike typically consume yellow perch and bluegills when both species are present (Beyerle and Williams 1968; Margenau et al. 1998). Northern pike also consume largemouth bass (Gurtin et al. 1996; Soupir et al. 2000) and typically act as a top-down predator that influences fish communities (Casselman and Lewis 1996). Reduced abundance of bluegill and yellow perch in lakes containing northern pike suggests that pike prey on these panfish. Northern pike apparently reduced the size structure of the fusiform yellow perch but not the size structure of the compressiform bluegill. Finally, northern pike may alter the relationship between largemouth bass and panfish, even in larger (i.e., 300 ha) water bodies.

Management Implications

Northern pike populations in these shallow natural lakes on the southwestern edge of their natural range appeared to be self-sustaining. However, reduced condition and truncated age structure coupled with fast growth associated with higher total annual mortality indicate that trophy potential of northern pike may be limited, so management of northern pike in these lakes should not focus on trophy potential. In addition, environmental factors may not affect northern pike populations similarly across all Sandhill lakes. Recruitment patterns suggested that these lakes may need to be assessed and managed on a lake-specific basis. Predation on bluegills and yellow perch suggest that northern pike use the same food resources as largemouth bass in these lakes. Managers attempting to support a high-quality bluegill or yellow perch population need to consider the implications of northern pike as a predator on panfish and largemouth bass before implementing management strategies.

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