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Latitudinal Comparisons of Walleye Growth in North America and Factors Influencing Growth of Walleyes in Kansas Reservoirs

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Abstract.—We compared the growth of walleyes *Stizostedion vitreum* in Kansas to that of other populations throughout North America and determined the effects of the abundance of gizzard shad *Dorosoma cepedianum* and temperature on the growth of walleyes in Kansas reservoirs. Age was estimated from scales and otoliths collected from walleyes (N = 2,072) sampled with gill nets from eight Kansas reservoirs during fall in 1991–1999. Age-0 gizzard shad abundance was indexed based on summer seining information, and temperature data were obtained from the National Oceanic and Atmospheric Administration. Parameter estimates of von Bertalanffy growth models indicated that the growth of walleyes in Kansas was more similar to that of southern latitude populations (e.g., Mississippi and Texas) than to that of northern (e.g., Manitoba, Minnesota and South Dakota) or middle latitude (e.g., Colorado and Iowa) populations. Northern and middle latitude populations had lower mean back-calculated lengths at age 1, lower growth coefficients, and greater longevity than southern and Kansas populations. A relative growth index (RGI; $[L_t/L_s] \times 100$, where L_t is the observed length at age and L_s is the age-specific standard length derived from a pooled von Bertalanffy growth model) and standardized percentile values (percentile values of mean back-calculated lengths at age) indicated that the growth of walleyes in Kansas was above average compared with that of other populations in North America. The annual growth increments of Kansas walleyes were more variable among years than among reservoirs. The growth increments of age-0 and age-1 walleyes were positively related to the catch rates of gizzard shad smaller than 80 mm, whereas the growth of age-2 and age-3 walleyes was inversely related to mean summer air temperature. Our results provide a framework for comparing North American walleye populations, and our proposed RGI provides a simple, easily interpreted index of growth.

Growth, recruitment, and mortality regulate population dynamics and thereby influence the ecology and management of fish populations. Although population assessments require an understanding of all rate functions (i.e., growth, recruitment, and mortality), growth is especially important because it provides an integrated evaluation of environmental conditions (e.g., prey availability, thermal conditions) and genetic factors (Kitchell et al. 1977; Momot et al. 1977; Summerfelt and Hall 1987; Kocovsky and Carline 2001). Growth also has direct and indirect effects on recruitment dynamics and trophic interactions by altering the age of maturation and size structure of both predator and prey populations. In addition, growth may reflect potential problems (e.g., overfishing) or provide feedback on management practices (e.g., harvest regulations, prey manipulations). Thus, detailed information on growth rates are necessary for proper management of predator and prey populations.

Walleyes *Stizostedion vitreum* are one of the most popular sport fish in North America and form an integral component in aquatic food webs (Craig 2000). Numerous studies have described growth (i.e., length at age) of walleyes and have provided

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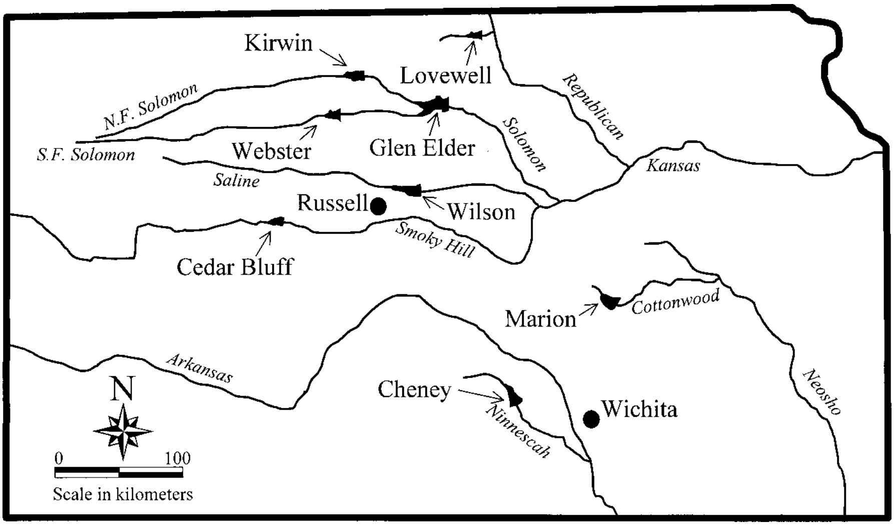

FIGURE 1.—Locations of the reservoirs used in evaluating the growth of walleyes in Kansas during 1991–1999. Major river names are given in italics.

several generalizations regarding growth, mortality, and longevity throughout the species' distribution (Carlander 1997). Walleyes from northern latitudes generally exhibit slower growth, lower natural mortality, and increased longevity compared to southern populations (Colby and Nepszy 1981; Beverton 1987; Carlander 1997; Craig 2000). Although temperature and length of the growing season undoubtedly influence latitudinal trends in walleye growth, large-scale growth trends are often confounded with changes in fish assemblage structure and prey availability (Santucci and Wahl 1993). For example, most aquatic systems from southern latitudes have higher species diversity, thereby increasing the number of potential prey species for walleyes in midwestern and southern systems (Matthews 1998). Most of these systems also contain gizzard shad *Dorosoma cepedianum*, which are often selected by walleyes over other available prey species (Einfalt and Wahl 1997). The presence of gizzard shad coupled with long growing seasons leads to fast growth of walleyes, especially during the first year (Santucci and Wahl 1993; Carlander 1997).

Historically, most walleye populations were limited to the natural lakes and large rivers of Canada and the northern United States (Carlander 1997). As a result of reservoir construction and extensive stocking programs, walleyes are now distributed throughout North America. Walleyes were first introduced into Kansas reservoirs in 1949 (Schademann 1987) and are currently one of the most popular sport fish in Kansas (Burlingame 1998). Kansas reservoirs are unique systems with respect to the ecology of walleyes because the highly variable climate of the southern Great Plains region results in frequent water-level fluctuations and high summer water temperatures (>30°C). Despite the importance of walleye fisheries and their potential role in structuring prey communities in Great Plains systems, little is known about how the growth of walleyes in Kansas compares with that of other North American populations or about the factors influencing growth in Kansas reservoirs. Therefore, the objective of this study was to gain an understanding of walleye growth in Kansas reservoirs. Specifically, we compared the growth of walleyes in Kansas to that of populations throughout North America using traditional techniques and by developing a standardized growth index. We also evaluated the relative importance of spatial and temporal variation in growth among Kansas populations. Lastly, we evaluated the influence of temperature and gizzard shad abundance on walleye growth rates.

Methods

Study area.—Walleyes were sampled from eight reservoirs across Kansas during 1991–1999 (Figure 1; Table 1). Typical of most Kansas reservoirs, the study reservoirs are relatively shallow (mean depth ± SE, 6.2 ± 0.5 m) and turbid and are seldom thermally stratified due to high, persistent winds. Most of the reservoirs are characterized by

TABLE 1.—Surface area (SA), mean depth, watershed area (WA), shoreline development index (SDI = shoreline length/[2 × $\{SA \times \pi\}^{1/2}$]), and years when scales and otoliths were collected for eight Kansas reservoirs used in the analysis of walleye growth.

Reservoir	SA (ha)	Depth (m)	WA (km^2)	SDI	Years
Cedar Bluff	1,327	7.7	14,323	6.2	1992, 1993, 1995, 1996
Cheney	3,864	5.2	1,719	4.9	1995, 1996
Glen Elder	5,093	5.8	17,702	3.9	1991–1993, 1995, 1996, 1998, 1999
Kirwin	2,055	5.9	3,540	3.7	1996, 1998
Lovewell	1,208	4.5	984	5.7	1991–1993, 1995, 1996
Marion	2,493	5.2	520	5.5	1995, 1996, 1998
Webster	1,513	6.6	2,978	5.8	1995, 1996
Wilson	3,642	8.8	4,965	7.5	1995, 1996

rocky shorelines with gradual slopes and little or no aquatic vegetation. Dead timber is abundant in the littoral areas and coves of Cedar Bluff, Cheney, Kirwin, and Webster reservoirs. Although watershed area is highly variable among reservoirs, all watersheds are dominated by grassland habitat. Livestock grazing and row-crop agriculture are the primary land uses within the watersheds. White crappies *Pomoxis annularis*, white bass *Morone chrysops*, channel catfish *Ictalurus punctatus*, hybrid striped bass (striped bass *M. saxatilis* × white bass), largemouth bass *Micropterus salmoides*, and walleyes are the dominant sport fish and gizzard shad is the primary prey species in all reservoirs.

Walleye and gizzard shad sampling.—Walleyes were sampled each fall (late October to early November) with gill-net compliments (one gill-net compliment = four separate monofilament gill nets, each 30.5 m long × 1.8 m deep, with 2.5-, 3.8-, 6.4-, or 10.2-cm bar-measure mesh). Total length (mm) was measured from all fish, and scales and otoliths were removed from five fish per 10-mm length-group. The number of years in which structures were collected for age and growth analysis varied from 2 to 7 years (Table 1). Scales were pressed onto 1.0-mm acetate slides and projected with a microfiche projector for age estimation. Otoliths were used to corroborate scale age and to estimate age when scales were difficult to read ($<5\%$ of the fish; Erickson 1983; Boxrucker 1986). The mean back-calculated length at age of walleyes in each reservoir and year was estimated with the Fraser–Lee method with an *a*-value of 55 mm (Carlander 1982), and the estimates were then weighted by the number of fish in each age-class to reduce the influence of older fish (DeVries and Frie 1996). Mean back-calculated lengths at age were summarized by reservoir (i.e., averaging over all years), and statewide means were estimated by averaging over all reservoirs. We also calculated the annual growth increment during the most recent year for each fish. Mean annual growth increments were estimated by calculating the mean increment for all fish in an age-class within each reservoir and year.

Age-0 gizzard shad were sampled with a ¼-arc shoreline seine haul (i.e., hauls began perpendicular to shore with a seine 15.2 m long × 1.8 m deep with 0.6-cm ace mesh). We only used seining data from samples collected from the last week in July to the second week in August to reduce the effect of gizzard shad growth on size structure and abundance estimates. These constraints resulted in the use of samples from Cedar Bluff Reservoir in 1992, 1993, and 1995; Glen Elder Reservoir in 1991, 1992, 1995, 1996, 1998, and 1999; and Lovewell Reservoir in 1991, 1995, and 1996. All gizzard shad were placed into 10-mm length-groups (total length) and counted. Catch per unit effort (CPUE) of age-0 gizzard shad was estimated as the number of fish per seine haul (Table 2).

Comparisons with North American populations.—Age and growth information were compiled for walleye populations throughout North America (see Appendix). Studies were selected to represent the geographical distribution of walleyes from a variety of habitats (i.e., natural lakes, reservoirs, and rivers) and were limited to those with 30 or more fish in a sample. If several studies were conducted on a single water body, we used the study with the largest sample size. However, we included replicate studies on large water bodies (e.g., Great Lakes) when fish were sampled from different regions. Male and female walleyes often exhibit different growth rates (Colby et al. 1979; Carlander 1997); therefore, we used three separate data sets in the analysis. The first data set (hereafter, the combined data set; $N = 74$ studies; Appendix 1) included studies in which individuals were not differentiated by sex. The other two data

TABLE 2.—Air temperature and age-0 gizzard shad variables used in the analysis of walleye growth for eight Kansas reservoirs during 1991–1999.

Variable	Description	Mean	SE
MNTSUM	Mean summer temperature (°C)	25.4	0.2
MNTFAL	Mean fall temperature (°C)	13.6	0.2
MAXSUM	Maximum summer temperature (°C)	40.2	0.3
MAXFAL	Maximum fall temperature (°C)	36.1	0.3
CPUEG70	Number of gizzard shad <70 mm per seine haul	53.3	17.1
CPUEG80	Number of gizzard shad <80 mm per seine haul	53.9	13.1
CPUEG90	Number of gizzard shad <90 mm per seine haul	60.1	13.2

sets included studies with separate growth estimates for males ($N = 42$ studies; Appendix 2) and females ($N = 38$ studies; Appendix 3). Because we did not determine sex of walleyes in Kansas, growth estimates for Kansas populations were only compared to the combined data.

Growth of walleyes from Kansas was compared with that of other North American populations included in the combined data set by first fitting a von Bertalanffy growth model to each population:

$$L_{\text{age}} = L_\infty(1 - e^{-K(\text{age}-t_0)}),$$

where L_{age} is the mean back-calculated length at age, L_∞ is the theoretical maximum length, K is the growth coefficient, and t_0 is the theoretical age when length equals zero. Growth models were fit to L_{age} data using nonlinear regression techniques (PROC NLIN) in the Statistical Analysis System (SAS; Freund and Littell 1991). Walleye populations were delineated into one of four regions, following Hubert (1999): (1) northern populations (Indiana, Manitoba, Maryland, Maine, Montana, North Dakota, New York, Ohio, Ontario, Pennsylvania, South Dakota, Saskatchewan, and Wisconsin), (2) middle populations (Colorado, Iowa, Nebraska, and Wyoming), (3) southern populations (Kentucky, Mississippi, North Carolina, Tennessee, Texas, and Virginia), and (4) Kansas populations. Canonical discriminant analysis (CDA) was used to determine which growth variables best discriminated among walleye populations by region. Growth variables included population-specific estimates of L_∞, K, mean back-calculated length at age 1, and maximum age (i.e., the oldest fish in the sample). Distances (i.e., Mahalanobis distances) between the centroids (based on mean canonical axis scores) for each region were compared via analysis of variance (ANOVA).

In addition to the CDA, we further compared walleye growth by developing a relative growth index (RGI) as follows:

$$\text{RGI} = (L_t/L_s) \cdot 100,$$

where L_t is the observed length at age t and L_s is the predicted age-specific standard length. In order to obtain L_s estimates, we estimated a von Bertalanffy growth model (i.e., a standardized growth model) for the North American populations used in the CDA. However, we truncated the data set to include only ages 1–10 because few populations ($N = 18$) contained walleyes older than age 10. The same procedure was used to develop standardized growth models for males and females, except data were limited to ages 1–8 because few populations (males, $N = 14$; females, $N = 16$) contained fish older than age 8. An RGI of 100 indicates that walleye growth is similar to growth of walleyes across their distribution. An RGI above 100 indicates that growth is above average, whereas an RGI below 100 indicates that growth is below average. Furthermore, the 5th, 10th, 25th, 50th, 75th, 90th, and 95th percentiles for mean total lengths at each age were estimated following the guidelines of Hubert (1999). Similar to our estimation of standardized growth models, percentile values were calculated for the combined, male, and female data sets.

Factors influencing Kansas populations.—We used methods described by Lewis (1978) and Meador and Matthews (1992) to investigate patterns in the spatial and temporal variability in walleye growth increments. First, we conducted a repeated-measures ANOVA (Littell et al. 1996). Partial variance components were then estimated using estimates from the ANOVA analysis following the methods of Meador and Matthews (1992):

$$S_R^2 = (\text{MS}_R - \text{MS}_I)/N_Y,$$

$$S_Y^2 = (\text{MS}_Y - \text{MS}_I)/N_R, \quad \text{and}$$

$$S_I^2 = \text{MS}_I,$$

where S^2 is the variance, MS is the mean square from ANOVA, N is the sample size, R represents the reservoir, Y represents the year, and I represents the interaction between reservoir and year. The percentage of variation (model variation) was estimated for each component and partitioned into a ratio to identify the relative importance of spatial and temporal variability on walleye growth increments.

The influence of specific biotic and abiotic factors on the growth of walleyes in Kansas reservoirs was investigated with an approach similar to that described by Michaletz (1998). We focused our analysis on age-0 to age-3 walleyes because they comprised 77% of the total sample. The influence of walleye density on growth was evaluated by correlation analysis of walleye CPUE (number per gill-net compliment) on mean growth increment for each age-class. Relationships between age-0 gizzard shad abundance (i.e., CPUE) and walleye growth increments were also assessed by use of correlation analysis.

Water temperature data were unavailable for the study reservoirs; therefore, the effect of temperature on walleye growth was investigated based on air temperature data collected from Russell and Wichita, Kansas, by the National Oceanic and Atmospheric Agency (Figure 1). Recent research on Glen Elder Reservoir suggests that prey consumption and seasonal growth of walleyes is more closely related to temperatures during summer and fall than during winter and spring; therefore, we limited our analysis of temperature effects to the summer and fall months (Table 2). Mean and maximum air temperatures were calculated for each month and then summarized separately by season: summer (June, July, August) and fall (September, October, November).

The effect of gizzard shad abundance and temperature on the annual growth increments of walleyes was examined by means of stepwise multiple regression analysis by age-class. The contribution of individual variables was tested via F-tests, and regressions were limited to variables that contributed significantly ($P \leq 0.05$) to the model. All statistical analyses were conducted with SAS (Littell et al. 1996) at $\alpha = 0.05$.

Results

Comparisons among North American Populations

The first two canonical axes explained 99% of the variation in walleye growth (Figure 2). Mean back-calculated length at age 1 (canonical correlation [r^*] = 0.97), maximum age ($r^* = -0.45$), and K ($r^* = 0.36$) were correlated with the first canonical axis, and maximum age ($r^* = 0.87$) was correlated with the second canonical axis. Northern populations were characterized by smaller lengths at age 1, higher maximum ages, and lower K values compared to walleyes in southern systems and Kansas reservoirs. Populations from middle latitudes were intermediate with respect to these variables. Distances between centroids for each region were significantly different ($F = 6.2$–19.9; df = 4, 66; $P = 0.0001$–0.0003), except for middle and northern populations ($F = 2.10$; df = 4, 66; $P = 0.08$) and southern and Kansas populations ($F = 0.57$; df = 4, 66; $P = 0.68$).

Standard growth models (Figure 3) indicated that males had a lower L_∞ and a higher K than females. The combined male and female standard growth models were intermediate with respect to L_∞ and K. Relative growth index values varied from 40 to 238 among all populations and ages (see Appendix). Similar to the CDA, RGI values were generally highest for southern and Kansas populations, and lowest for northern populations. The L_{age} values for Kansas populations (Table 3) were generally above the 90th percentile for each age (Table 4) and further illustrate the fast growth rates of walleyes in Kansas reservoirs.

Factors Influencing Kansas Populations

Although the growth of walleyes was relatively fast in Kansas reservoirs, growth estimates varied among reservoirs and years. Over 60% of the variation in mean growth increment of Kansas walleyes was attributed to the year × reservoir interaction (Table 5). Temporal variation exceeded spatial variation in growth for all ages.

Multiple regression techniques were used to evaluate the specific factors influencing the growth of walleyes, but models with more than one variable were not significant ($P > 0.05$). Abundance of gizzard shad was the most important factor influencing growth rates of age-0 and age-1 walleyes. Mean growth increments of age-0 and age-1 walleyes were positively correlated with all length-categories of age-0 gizzard shad abundance; however, CPUE of gizzard shad smaller than 80 mm explained the highest proportion of variation in growth increments of age-0 and age-1 walleyes (Figure 4). Mean growth increments of age-2 and age-3 walleyes were best explained by mean summer temperature (Figure 4). Although a linear model explained 59–77% of the variation in growth increments of age-2 and age-3 walleyes, the relationship appeared nonlinear, and reductions in growth increments were evident at mean air temperatures above 25°C. Mean annual growth increments were not related to CPUE of walleyes in

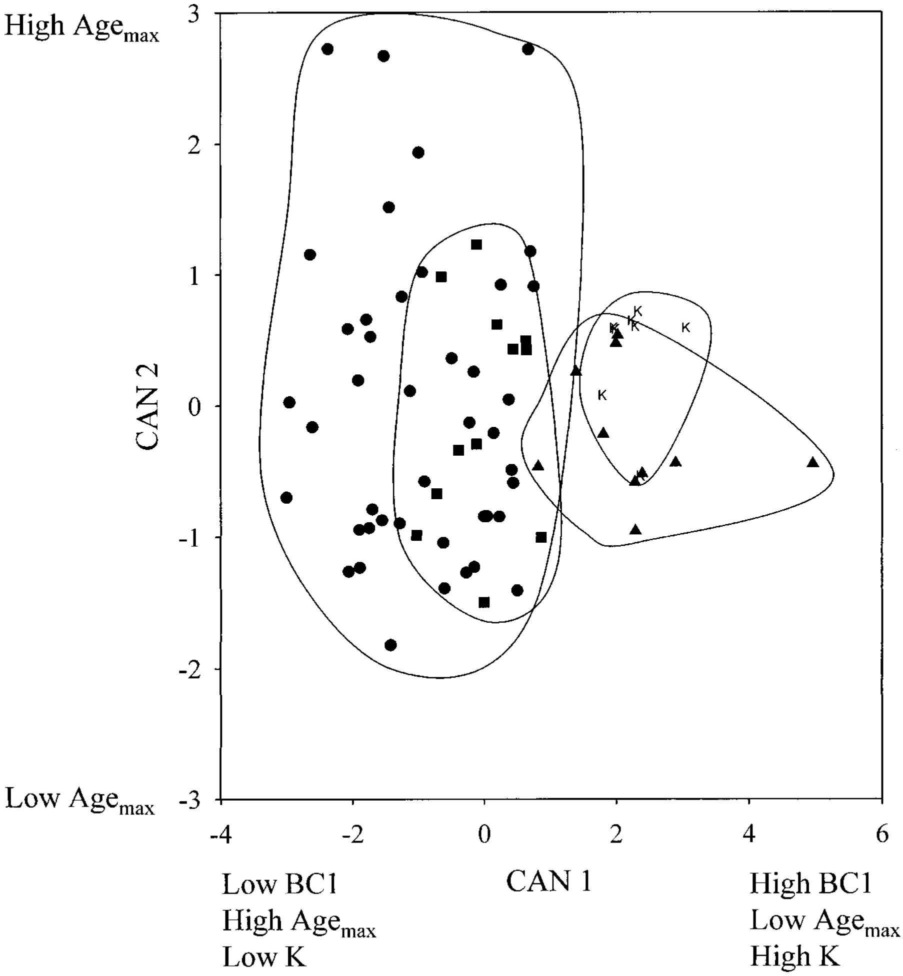

FIGURE 2.—Canonical discriminant analysis of northern (circles; Indiana, Manitoba, Maryland, Minnesota, Montana, North Dakota, New York, Ohio, Ontario, Pennsylvania, South Dakota, Saskatchewan, and Wisconsin), middle (squares; Colorado, Iowa, Nebraska, and Wyoming), southern (triangles; Kentucky, Mississippi, North Carolina, Tennessee, Texas, and Virginia), and Kansas K walleye populations. Canonical factor scores (CAN) represent mean back-calculated length at age 1 (BC1), maximum age (Age$_{max}$), and the growth coefficient (*K*) from von Bertalanffy growth models.

any of the study reservoirs (r = 0.50–0.23; $P >$ 0.05).

Discussion

Our results support previous research that has shown that fish from northern latitudes generally exhibit slower growth and higher longevity than more southerly populations (Colby et al. 1979; Colby and Nepszy 1981; Beverton 1987; Craig 2000). For example, Beverton (1987) compared walleye populations along a latitudinal gradient extending from Canada to Texas and found that fish from southern latitudes grew faster, matured later, and died at a younger age. Although previous research has suggested latitudinal trends in growth (Colby and Nepszy 1981; Beverton 1987), our results provide important information on how Kansas populations compare with other North American populations. Our initial expectation was that Kansas populations would be most similar to other populations in the Great Plains region (e.g., Nebraska, South Dakota). However, our results suggest that walleye populations in Kansas reservoirs are most similar to southern walleye populations, which is likely due to the extended growing season and high abundance of gizzard shad.

Walleye populations in Kansas reservoirs had RGI values above 100 for all ages, which indicates

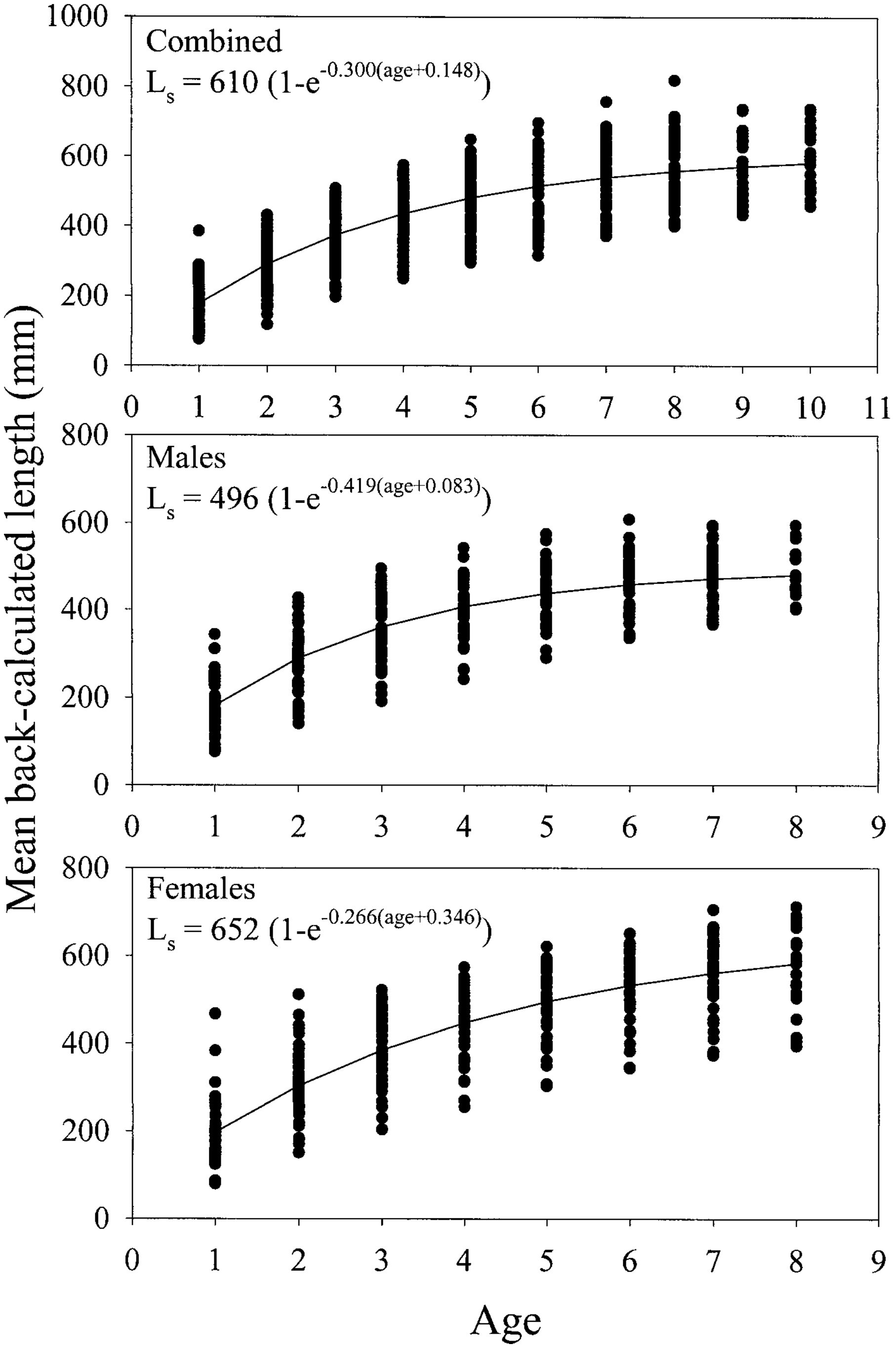

FIGURE 3.—Mean back-calculated lengths at age for walleye populations throughout North America. The line represents the best-fit von Bertalanffy growth model (i.e., the standardized growth model) and was used to estimate age-specific standard lengths (L_s).

TABLE 3.—Sample size (*N*), mean back-calculated length at age (±SE in parentheses), and relative growth index (below mean back-calculated lengths) for walleyes sampled from eight Kansas reservoirs during 1991–1999.

		Age						
Reservoir	*N*	1	2	3	4	5	6	7
Cedar Bluff	228	237 (3.3) 133	383 (4.8) 132	465 (12.4) 125	529 (14.7) 121	581 (14.7) 121	639 (13.4) 124	673 (1.4) 125
Cheney	66	255 (2.5) 143	375 (5.4) 129	433 (6.3) 116	510 (5.8) 117	567 (22.8) 118	597 (13.1) 116	617 (13.7) 114
Glen Elder	770	249 (4.5) 140	384 (7.0) 133	470 (8.2) 126	533 (5.6) 123	579 (6.5) 121	621 (10.4) 121	642 (11.8) 119
Kirwin	119	252 (15.0) 142	382 (8.6) 132	459 (16.1) 123	547 (8.4) 126	601[a] 125		
Lovewell	393	267 (2.3) 150	399 (8.4) 138	468 (5.2) 126	511 (7.2) 118	560 (7.1) 117	600 (8.6) 117	642 (31.7) 119
Marion	287	263 (2.7) 148	398 (3.1) 137	467 (5.9) 125	528 (3.3) 122	575 (9.2) 120	602 (6.5) 117	624 (15.4) 116
Webster	71	288 (4.5) 162	430 (17.0) 148	507 (12.6) 136	559 (19.8) 129	599 (14.2) 125	636 (20.5) 124	666[a] 124
Wilson	138	263 (1.4) 148	404 (1.9) 139	492 (0.2) 132	549 (5.1) 126	587 (3.8) 122	611 (4.4) 119	652[a] 121
Total	2,072	259 (5.3) 146	394 (6.2) 136	470 (7.7) 126	533 (6.2) 123	581 (5.1) 121	615 (6.5) 120	645 (7.7) 120

[a] Only one fish sampled.

that the growth of these walleyes was faster than that of most North American populations. Similar results were obtained by examining percentile values, which indicated that mean back-calculated lengths were generally above the 90th percentile for all ages. Hubert (1999) recommended using percentile values as the standard method for comparing among populations. We suggest using both percentile values and the RGI to compare growth estimates. Percentile values are generally more descriptive than RGI values, but the RGI allows for more refined analyses. For example, RGI values can be calculated by age-class, standard length-categories (e.g., stock- to quality-length; Anderson and Neumann 1996), or length-categories defined by research questions. Moreover, the RGI not only provides a simple index for comparisons within

TABLE 4.—Sample size (*N*) and percentile distributions of mean lengths (mm) of walleyes sampled across North America. Combined estimates represent studies in which walleyes were not differentiated by sex.

Age	*N*	5%	10%	25%	50%	75%	90%	95%
Combined								
1	74	91	109	130	170	213	259	276
2	74	170	198	234	289	351	394	404
3	74	224	254	320	372	442	467	487
4	73	267	315	363	434	511	534	554
5	68	307	338	400	475	558	587	599
6	59	340	366	435	526	584	636	640
7	51	373	400	457	555	618	673	683
8	38	409	414	478	569	650	703	715
9	27	432	442	472	546	643	676	732
10	22	457	475	508	583	665	706	729
Males								
1	42	84	91	140	173	226	254	267
2	42	168	185	233	287	368	406	427
3	42	224	259	305	358	428	456	466
4	41	264	311	351	409	462	483	485
5	41	307	356	384	452	498	513	528
6	36	338	368	406	460	505	544	580
7	31	371	386	424	476	520	571	594
8	19	394	401	434	470	528	572	594
Females								
1	38	84	86	141	178	234	278	383
2	38	170	183	253	301	371	434	464
3	38	229	267	323	395	454	502	506
4	36	269	315	400	455	508	544	551
5	36	307	361	443	499	566	578	594
6	34	345	399	480	548	592	624	628
7	33	381	427	508	582	627	660	665
8	26	414	455	515	611	671	687	691

TABLE 5.—Percent of the variation in mean annual growth increments by year (temporal), reservoir (spatial), and interaction components, and ratio of spatial variation ($S_R{}^2$) to temporal variation ($S_Y{}^2$). Analyses were conducted by age-class for walleyes sampled from eight Kansas reservoirs during 1991–1999.

	Variation component			
Age	Year	Reservoir	Interaction	$S_R{}^2/S_Y{}^2$
0	21	13	66	0.6
1	23	13	64	0.6
2	3	1	96	0.3
3	15	3	82	0.2
4	6	5	89	0.8
5	10	9	81	0.9

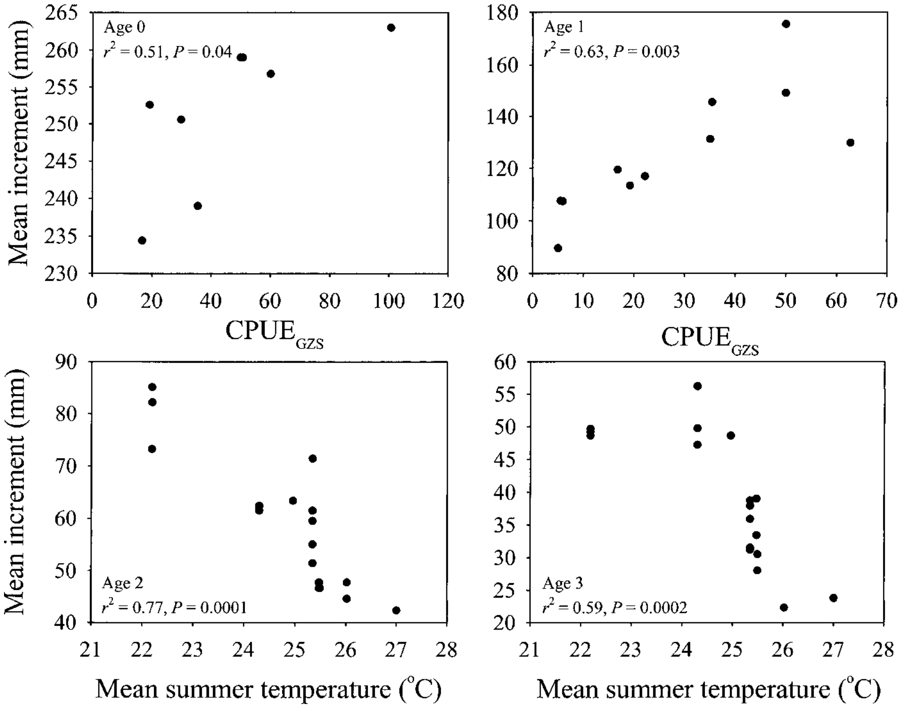

FIGURE 4.—Relationships between the mean annual growth increments (mm) of (1) age 0–1 walleyes and catch per unit effort of age-0 gizzard shad (CPUE$_{GZS}$ = number of fish <80 mm per seine haul; top panels) and (2) age 2−3 walleyes and mean summer temperature (bottom panels) in Kansas reservoirs during 1991–1999.

and among populations, but statistical analyses are more easily conducted than with percentile values.

Although walleyes in Kansas exhibited fast growth, we found that growth was variable among and within populations. Most studies of walleye growth have been limited to a specific population or have focused on the early life history to elucidate factors influencing growth or recruitment (Colby et al. 1979; Ball and Brown 1987; Fielder 1992; McWilliams and Larscheid 1992; Mitzner 1992). Our analysis of partial variance components indicated that the effect of reservoir on growth varied from year to year (i.e., interaction term). This is not surprising, given the variable climate and dynamic nature of reservoir systems in the southern Great Plains. An understanding of this trend is especially important for resource managers because management activities often occur on a statewide basis. For example, the high proportion of variance in the interaction term suggests that the effectiveness of management practices (e.g., harvest regulations) will likely vary depending on both the reservoir and year. These results also suggest that yearly variation is more influential on walleye growth than are differences among reservoirs. Thus, management practices may show higher variation in success within a reservoir than among reservoirs, at least over time periods like those used in our study. Interestingly, most of this variation was attributed to factors that also explained broad latitudinal trends in walleye growth (i.e., temperature, gizzard shad).

Studies relating growth to temperature in specific systems have varied in their conclusions. For example, Priegel (1970) and Smith and Pycha (1960) found that growth of walleyes was unrelated to temperature in Minnesota and Wisconsin. Forney (1966) and Madenjian (1991) found that temperature was related to growth of walleyes in Oneida Lake. Similarly, Staggs and Otis (1996) investigated the effects of temperature on growth of age-0 walleyes, sauger *S. canadense*, yellow perch *Perca flavescens*, white bass, freshwater drum *Aplodinotus grunniens*, and trout-perch *Percopsis omiscomaycus* in Lake Winnebago and found that growth was positively associated with summer temperature. Our results suggest that summer temperature explained little variation in annual growth of age-0 and age-1 walleyes, but was related to growth of age-2 and age-3 fish. Walleyes generally reach sexual maturity by ages 2–3 (males) or ages 3–4 (females) in Glen Elder Reservoir (M. C. Quist, unpublished data). High summer water temperatures may result in reduced activity and condition of walleyes during summer (Momot et al. 1977; Kocovsky and Carline 2001). Therefore, high summer temperatures likely stress adult walleyes and may particularly influence mature fish that are allocating energy to both gonadal and somatic growth (Beverton 1987). Although we used air temperature instead of water temperature in our analysis, we believe that our approach is valid because a current study on Glen Elder Reservoir indicates that water and air temperatures are highly correlated ($r^2 = 0.89$; $P = 0.0001$). Similar methods were used by Staggs and Otis (1996) to investigate the effects of temperature on growth of walleyes in Lake Winnebago.

Our results confirm that the dynamics of age-0 gizzard shad populations are an important factor influencing the growth of piscivores (DeVries and Stein 1992). Hartman and Margraf (1992) found a significant relationship between walleye growth and gizzard shad abundance in Lake Erie. Similar results have been reported by Knight et al. (1984), Johnson et al. (1988), and Santucci and Wahl (1993). Michaletz (1997) found that growth of crappies *Pomoxis* spp., largemouth bass, and white bass was related to age-0 gizzard shad dynamics in two Missouri reservoirs. The size structure of age-0 gizzard shad populations most strongly influenced growth of small predators due to gape-limited predation, while growth of large predators was most highly influenced by gizzard shad abundance. Our findings suggest that summer catch rates of gizzard shad smaller than 80 mm may provide an index of growth for age-0 and age-1 walleyes.

The results of this study have important implications for the management of walleye populations. Latitudinal gradients in growth indicate that expectations of walleye growth must be realistic with respect to regional dynamics. The proposed RGI, in conjunction with standardized percentile values, provides a simple index of growth that allows for rapid communication of walleye growth rates. Our detailed analysis of Kansas populations indicates that growth of walleyes is more variable among years than among reservoirs. Therefore, evaluations of management practices related to growth should encompass relatively long time periods. Although temperature and prey availability undoubtedly influence latitudinal trends in walleye growth, these same factors were also important on a regional scale, the growth of walleyes being positively related to age-0 gizzard shad abundance and inversely related to summer temperature.

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Appendix: Populations Used for Growth Comparisons and Relative Growth Index Values

TABLE A.1.—Water body, von Bertalanffy parameter estimates (theoretical maximum length [L_∞], growth coefficient [K], theoretical age when length equals zero [t_0]), mean relative growth index (RGI_{mean}), maximum age (Age_{max}), minimum RGI (RGI_{min}), maximum RGI (RGI_{max}), and source for studies that did not differentiate between male and female walleyes. Numbers in parentheses represent one SE.

Water body	L_∞	K	t_0	Age_{max}	RGI_{mean}	RGI_{min}	RGI_{max}	Source
Colorado								
Unidentified reservoir	712	0.213	−0.575	5	105 (2.5)	101	115	Carlander (1997)
Indiana								
Brookville Reservoir	610	0.489	−0.047	7	123 (4.0)	112	136	Ball and Brown (1987)
Iowa								
Black Hawk Lake	532	0.336	0.130	6	86 (2.1)	77	91	Carlander (1997)
Clear Lake	853	0.142	−0.786	12	104 (2.2)	95	118	Carlander (1997)
Des Moines River	678	0.206	−0.769	9	102 (2.3)	95	120	Carlander (1997)
Lake Macbride	682	0.241	0.003	7	95 (2.8)	82	103	Carlander (1997)
Mississippi River	689	0.333	0.253	11	110 (2.9)	85	115	Colby et al. (1979)
Spirit Lake	833	0.175	−0.381	10	108 (2.6)	97	122	Carlander (1997)
Kansas								
Cedar Bluff Reservoir	779	0.259	−0.462	7	126 (1.9)	119	113	Current study
Cheney Reservoir	681	0.307	−0.522	8	121 (3.7)	111	144	Current study
Glen Elder Reservoir	712	0.319	−0.368	8	125 (2.6)	119	140	Current study
Kirwin Reservoir	817	0.240	−0.554	5	129 (3.4)	123	142	Current study
Lovewell Reservoir	726	0.263	−0.827	11	125 (4.4)	117	150	Current study
Marion Reservoir	705	0.304	−0.593	8	126 (4.0)	116	148	Current study
Webster Reservoir	705	0.361	−0.493	7	135 (5.6)	123	162	Current study
Wilson Reservoir	711	0.334	−0.429	8	129 (3.6)	119	148	Current study
Manitoba								
West Blue Lake	603	0.233	−0.218	5	86 (1.4)	81	90	Carlander (1997)
Maryland								
Deep Creek Lake	746	0.258	−0.016	8	110 (3.1)	90	120	Moss et al. (1985)
Michigan								
Lake Gogebic	532	0.293	0.105	10	83 (1.9)	66	87	Colby et al. (1979)
Lake Huron	541	0.276	−0.445	14	89 (1.1)	86	96	Carlander (1997)
Minnesota								
Lake of the Woods	670	0.156	−0.725	12	86 (1.9)	78	95	Colby et al. (1979)
Mille Lacs Lake	604	0.223	−0.005	11	86 (2.9)	71	101	Carlander (1997)
Red Lake	456	0.335	0.172	6	73 (2.3)	61	77	Carlander (1997)
Mississippi								
Tombigbee River	717	0.311	−0.307	6	124 (2.3)	119	133	Carlander (1997)
Montana								
Frenchman Lake	474	0.252	0.343	5	106 (3.7)	94	117	Colby et al. (1979)
Hauser Lake	814	0.266	0.122	4	110 (5.7)	95	121	Colby et al. (1979)
Milk River	900	0.257	0.404	5	110 (10.3)	73	129	Colby et al. (1979)
Rainbow Lake	670	0.264	0.331	7	90 (5.6)	61	103	Colby et al. (1979)
Westrope Lake	546	0.357	0.387	4	81 (7.9)	61	91	Colby et al. (1979)
Unidentified lake	757	0.198	0.159	7	90 (5.1)	66	103	Carlander (1997)
Nebraska								
Box Butte Reservoir	693	0.302	0.131	4	105 (5.0)	88	111	Carlander (1997)
Lake McConaughy	804	0.254	−0.119	9	121 (2.4)	104	129	Carlander (1997)
Minature Reservoir	731	0.381	0.368	7	119 (5.8)	84	127	Carlander (1997)
New York								
Black Lake	454	0.382	−0.285	9	84 (2.3)	77	99	Carlander (1997)
Oneida Lake	443	0.335	−0.276	7	79 (1.6)	75	87	Carlander (1997)
North Carolina								
Apalachia Lake	591	0.218	−1.953	5	115 (11.1)	97	156	Carlander (1997)
Fontana Reservoir	748	0.230	−0.107	6	103 (2.4)	94	111	Moss et al. (1985)
Lake Hiwassee	451	0.587	0.046	5	100 (3.8)	89	109	Carlander (1997)
Lake James	760	0.246	−0.693	5	127 (5.0)	119	146	Carlander (1997)

TABLE A.1.—Continued.

Water body	L_∞	K	t_0	Age_{max}	RGI_{mean}	RGI_{min}	RGI_{max}	Source
North Dakota								
Lake Oahe	775	0.221	0.144	6	97 (5.2)	77	113	Carlander (1997)
Ohio								
Lake Erie	808	0.201	−0.678	11	118 (1.3)	109	125	Carlander (1997)
Ontario								
Attawapiskat Lake	896	0.074	−0.321	14	64 (3.9)	46	82	Colby et al. (1979)
Big Trout Lake	764	0.116	−0.704	17	82 (3.4)	68	104	Colby et al. (1979)
Deer Lake	898	0.079	−0.302	12	67 (4.4)	40	86	Colby et al. (1979)
Lake Huron	705	0.222	−0.242	11	102 (1.9)	96	112	Colby et al. (1979)
Lake of the Woods	802	0.084	−1.387	14	75 (2.1)	68	86	Colby et al. (1979)
Lake Ontario	748	0.232	−0.565	15	116 (1.2)	112	126	Carlander (1997)
Lake St. Joseph	897	0.084	−0.441	12	72 (3.7)	55	91	Colby et al. (1979)
Makoop Lake	590	0.153	−0.012	9	65 (3.6)	43	78	Colby et al. (1979)
North Caribou Lake	878	0.065	−1.229	18	66 (2.4)	58	79	Colby et al. (1979)
Sakwasoon Lake	619	0.128	−0.347	11	65 (2.8)	47	79	Colby et al. (1979)
Sandy Lake	601	0.188	0.079	10	75 (3.5)	51	88	Colby et al. (1979)
Savanne Lake	982	0.091	−0.449	10	84 (4.1)	67	105	Colby et al. (1979)
Pennsylvania								
Conneaut Lake	588	0.514	0.354	7	109 (2.9)	97	120	Colby et al. (1979)
Pymatuning Lake	799	0.264	−0.104	10	123 (1.5)	113	128	Colby et al. (1979)
Saskatchewan								
Wollaston Lake	786	0.112	−1.692	11	93 (2.6)	86	113	Carlander (1997)
South Dakota								
Elm Lake	757	0.239	0.007	6	105 (3.2)	92	115	Wolf et al. (1994)
Herman Lake	555	0.446	0.158	5	104 (2.3)	96	110	Wolf et al. (1994)
Lake Francis Case	702	0.251	−0.120	9	104 (1.6)	97	110	Carlander (1997)
Lewis and Clark Lake	931	0.134	−0.523	8	101 (2.7)	94	115	Carlander (1997)
Sinai Lake	694	0.325	0.102	6	111 (2.5)	101	117	Wolf et al. (1994)
Thompson Lake	686	0.188	−0.521	6	93 (1.2)	88	97	Wolf et al. (1994)
Tennessee								
Center Hill Reservoir	787	0.272	−0.501	8	131 (2.7)	121	143	Carlander (1997)
Dale Hollow Reservoir	893	0.226	−0.350	4	128 (2.3)	123	134	Carlander (1997)
Texas								
Canyon Reservoir	504	0.298	−3.805	3	125 (4.4)	117	150	Colby et al. (1979)
Twin Buttes Reservoir	577	0.455	−0.414	4	131 (8.7)	114	155	Colby et al. (1979)
Virginia								
Claytor Lake	981	0.206	−0.258	8	134 (3.4)	116	147	Carlander (1997)
Wisconsin								
Clear Lake	443	0.348	0.186	6	72 (3.0)	57	78	Carlander (1997)
Lake Winnebago	548	0.280	0.202	7	79 (3.5)	60	87	Carlander (1997)
Lake Poygon	559	0.260	0.103	7	85 (3.8)	64	97	Carlander (1997)
Trout Lake	598	0.345	0.399	11	96 (2.9)	76	103	Carlander (1997)
Wolf River	523	0.348	0.279	7	83 (3.6)	62	90	Colby et al. (1979)
Wyoming								
Semino Reservoir	652	0.144	−1.249	8	85 (2.2)	79	99	Marwitz and Hubert (1995)
Grayrocks Reservoir	597	0.256	−0.774	9	101 (3.3)	94	122	Marwitz and Hubert (1995)

TABLE A.2.—Water body, von Bertalanffy parameter estimates (theoretical maximum length [L_∞], growth coefficient [K], theoretical age when length equals zero [t_0]), mean relative growth index (RGI_{mean}), maximum age (Age_{max}), minimum RGI (RGI_{min}), maximum RGI (RGI_{max}), and source for male walleyes. Numbers in parentheses represent one SE.

Water body	L_∞	K	t_0	Age_{max}	RGI_{mean}	RGI_{min}	RGI_{max}	Source
Georgia								
Barton Reservoir	514	0.621	−0.029	5	123 (2.0)	113	136	Colby et al. (1979)
Iowa								
Clear Lake	634	0.288	−0.238	7	110 (2.2)	104	121	Colby et al. (1979)
East Okoboji	667	0.189	−0.245	9	89 (4.2)	77	119	Carlander (1997)
Lake Macbride	563	0.271	−0.576	8	102 (1.2)	98	108	Carlander (1997)
Mississippi River	557	0.496	0.340	5	108 (5.4)	87	115	Carlander (1997)
West Okoboji	535	0.279	0.035	7	86 (3.8)	70	97	Carlander (1997)
Kansas								
Glen Elder Reservoir	668	0.397	−0.038	6	130 (1.3)	125	133	Current study
Kentucky								
Lake Cumberland	587	0.398	−0.399	8	123 (2.1)	114	136	Carlander (1997)
Michigan								
Lake Gogebic	465	0.382	0.249	10	73 (3.9)	62	92	Carlander (1997)
Lake Michigan	543	0.275	−0.446	14	95 (0.4)	94	100	Colby et al. (1979)
Minnesota								
Lake of the Woods	594	0.181	−0.499	10	82 (1.9)	74	94	Carlander (1997)
Red Lake	460	0.252	−0.446	9	78 (1.1)	73	84	Carlander (1997)
Missouri								
Current River	479	0.567	0.043	8	105 (1.8)	98	111	Colby et al. (1979)
New York								
Black Lake	454	0.383	−0.279	9	92 (0.8)	89	96	Colby et al. (1979)
Lake Erie	630	0.342	−0.161	9	118 (2.0)	111	125	Carlander (1997)
Scriba Creek	457	0.304	−0.279	7	83 (1.1)	79	87	Colby et al. (1979)
Oneida Lake	443	0.334	−0.279	7	84 (0.7)	81	86	Colby et al. (1979)
North Dakota								
Lake Oahe	595	0.343	0.056	6	97 (2.9)	89	115	Carlander (1997)
Spiritwood Lake	666	0.216	−0.333	7	95 (1.4)	89	115	Carlander (1997)
Ohio								
Ferguson Lake	711	0.181	−0.595	7	101 (2.9)	90	112	Carlander (1997)
Hoover Reservoir	501	0.563	−0.277	7	117 (4.9)	106	140	Carlander (1997)
Lake Erie	622	0.375	−0.343	7	125 (2.0)	119	134	Carlander (1997)
Oklahoma								
Canton Reservoir	604	0.439	−0.665	5	141 (8.2)	128	171	Colby et al. (1979)
Ontario								
Attawapiskat Lake	601	0.134	0.041	12	51 (3.3)	42	84	Colby et al. (1979)
Lake Erie	557	0.496	−0.115	6	122 (2.0)	116	129	Carlander (1997)
Petownikip Lake	517	0.250	0.302	10	65 (5.3)	46	93	Colby et al. (1979)
Sakwaso Lake	584	0.139	−0.272	11	57 (3.8)	45	82	Colby et al. (1979)
Sandy Lake	590	0.197	0.117	10	63 (4.1)	50	98	Colby et al. (1979)
Wunnummin Lake	592	0.139	−0.184	11	57 (2.5)	50	85	Colby et al. (1979)
South Dakota								
Lake Sharpe	597	0.284	0.027	9	94 (4.2)	77	110	Colby et al. (1979)
Tennessee								
Center Hill Reservoir	534	0.634	−0.066	7	129 (4.3)	114	142	Carlander (1997)
Norris Reservoir	531	0.673	0.027	8	142 (8.3)	128	171	Colby et al. (1979)
Texas								
Ft. Phantom Hill Reservoir	580	0.647	0.046	3	143 (2.9)	137	148	Colby et al. (1979)
Lake Meredith	483	0.560	−1.218	7	125 (11.8)	103	189	Colby et al. (1979)

TABLE A.2.—Continued.

Water body	L_∞	K	t_0	Age$_{\text{max}}$	RGI$_{\text{mean}}$	RGI$_{\text{min}}$	RGI$_{\text{max}}$	Source
Utah								
Utah Lake	484	0.653	0.154	6	110 (2.4)	105	121	Carlander (1997)
Wisconsin								
Lake Michigan	589	0.344	−0.406	5	123 (1.0)	111	124	Carlander (1997)
Lake Winnebago	469	0.374	−0.017	8	89 (2.1)	78	100	Carlander (1997)
Pike Lake	491	0.431	−0.016	6	98 (0.7)	96	100	Carlander (1997)
Puckaway Lake	536	0.403	−0.152	9	107 (0.7)	105	112	Carlander (1997)
Ripley Lake	452	0.755	0.251	5	108 (2.3)	100	114	Carlander (1997)
Washington County Lake	565	0.327	0.130	7	97 (2.2)	73	111	Carlander (1997)
Wolf River	427	0.485	0.414	7	81 (3.0)	59	89	Carlander (1997)

TABLE A.3.—Water body, von Bertalanffy parameter estimates (theoretical maximum length [L_∞], growth coefficient [K], theoretical age when length equals zero [t_0]), mean relative growth index (RGI$_{\text{mean}}$), maximum age (Age$_{\text{max}}$), minimum RGI (RGI$_{\text{min}}$), maximum RGI (RGI$_{\text{max}}$), and source for female walleyes. Numbers in parentheses represent one SE.

Water body	L_∞	K	t_0	Age$_{\text{max}}$	RGI$_{\text{mean}}$	RGI$_{\text{min}}$	RGI$_{\text{max}}$	Source
Georgia								
Barton Reservoir	643	0.367	−0.427	7	118 (2.2)	104	133	Colby et al. (1979)
Iowa								
Clear Lake	692	0.290	−0.055	7	105 (1.9)	96	110	Colby et al. (1979)
East Okoboji	703	0.221	0.124	12	88 (4.3)	64	99	Carlander (1997)
Lake Macbride	716	0.212	−0.589	8	101 (0.6)	99	104	Carlander (1997)
Mississippi River	683	0.338	0.239	10	100 (4.4)	80	111	Carlander (1997)
West Okoboji	633	0.294	0.240	10	86 (4.7)	65	101	Carlander (1997)
Kansas								
Glen Elder Reservoir	702	0.373	−0.101	7	121 (1.4)	117	128	Current study
Kentucky								
Lake Cumberland	816	0.221	−0.613	9	118 (2.2)	104	113	Carlander (1997)
Michigan								
Lake Gogebic	571	0.266	0.043	10	81 (2.7)	63	86	Carlander (1997)
Lake Michigan	644	0.213	−0.580	15	91 (0.3)	89	92	Colby et al. (1979)
Minnesota								
Lake of the Woods	715	0.139	−0.631	13	78 (1.7)	72	87	Carlander (1997)
Red Lake	613	0.145	−0.848	9	72 (1.0)	69	78	Carlander (1997)
Missouri								
Current River	814	0.224	−0.433	8	115 (1.2)	110	119	Colby et al. (1979)
Montana								
Killens Reservoir	844	0.175	0.511	5	71 (10.0)	40	91	Colby et al. (1979)
New York								
Lake Erie	754	0.304	0.103	11	113 (2.0)	91	118	Carlander (1997)
Scriba Creek	491	0.326	−0.307	7	83 (2.7)	78	99	Colby et al. (1979)
Oneida Lake	524	0.259	−0.399	7	80 (0.2)	80	81	Colby et al. (1979)
North Dakota								
Lake Oahe	817	0.217	0.101	8	96 (3.1)	76	116	Carlander (1997)
Spiritwood Lake	874	0.182	−0.090	8	102 (4.4)	82	117	Carlander (1997)
Ohio								
Ferguson Lake	798	0.226	−0.370	9	112 (1.5)	106	118	Carlander (1997)
Hoover Reservoir	548	0.392	−0.714	10	110 (5.7)	89	132	Carlander (1997)
Lake Erie	677	0.395	−0.124	8	120 (2.2)	112	131	Carlander (1997)
Oklahoma								
Canton Reservoir	866	0.196	−1.298	7	132 (4.8)	122	158	Colby et al. (1979)

TABLE A.3.—Continued.

Water body	L_∞	K	t_0	Age_{max}	RGI_{mean}	RGI_{min}	RGI_{max}	Source
Ontario								
Attawapiskat Lake	733	0.099	−0.297	15	58 (3.4)	43	71	Colby et al. (1979)
Lake Erie	790	0.254	−0.348	10	116 (2.0)	108	128	Carlander (1997)
Petownikip Lake	565	0.210	0.189	11	68 (4.1)	43	78	Colby et al. (1979)
Sakwaso Lake	599	0.134	−0.762	11	61 (2.7)	44	69	Colby et al. (1979)
South Dakota								
Lake Sharpe	851	0.171	−0.058	9	95 (4.5)	71	108	Colby et al. (1979)
Tennessee								
Center Hill Reservoir	751	0.242	−1.156	10	123 (4.7)	111	143	Carlander (1997)
Norris Reservoir								Colby et al. (1979)
Texas								
Belton Reservoir	524	1.480	−0.498	3	180 (30.1)	135	238	Colby et al. (1979)
Ft. Phantom Hill Reservoir	541	0.998	−0.307	3	138 (4.2)	131	146	Colby et al. (1979)
Lake Meredith	567	0.554	−1.036	7	131 (12.7)	100	195	Colby et al. (1979)
Utah								
Utah Lake	610	0.385	−0.115	6	108 (2.1)	104	118	Carlander (1997)
Wisconsin								
Lake Winnebago	616	0.246	−0.169	8	88 (1.7)	77	92	Carlander (1997)
Pike Lake	820	0.164	−0.583	10	99 (1.8)	91	108	Carlander (1997)
Puckaway Lake	669	0.333	−0.100	9	109 (1.5)	101	114	Carlander (1997)
Ripley Lake	576	0.399	−0.016	5	102 (1.6)	100	108	Carlander (1997)
Washington County Lake	611	0.311	0.147	8	90 (3.8)	67	100	Carlander (1997)