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Seasonal variation in condition, growth and food habits of walleye in a Great Plains reservoir and simulated effects of an altered thermal regime

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Catch rates in gillnets and relative weight (W_r) of walleye *Stizostedion vitreum*, in Glen Elder Reservoir, Kansas, were lowest during the summer (June–August) and highest during the autumn (September–November). Approximately 80% of their annual growth in length and mass was attained during late summer and autumn. Growth was minimal during winter (January–February) and spring (March–May). The number of walleye with empty stomachs was highest during the summer. Invertebrates (Cladocera, Chironomidae) were common in walleye stomachs during the summer and spring, but contributed little to the ingested biomass. Gizzard shad *Dorosoma cepedianum* dominated walleye diets (per cent by mass) throughout the year. A bioenergetics model predicted that the proportion of maximum consumption (P_c) was highest during the autumn and was probably due to spatial overlap of walleye and gizzard shad once water temperatures were <22° C. The bioenergetics model predicted that walleye would lose up to 65% of their body mass during the summer if water temperature increased by 10% (as predicted by some global warming models). Growth during the autumn, winter and spring was enhanced up to 150% by increased temperatures. The results of this study indicate that lower condition, reduced consumption and slow growth are a generalized response of walleye to extreme temperatures. Elevated temperatures may have a net positive effect on walleye growth if they can survive the high thermal stress during summer.

Key words: Percidae; Great Plains; bioenergetics; population characteristics; global warming.

INTRODUCTION

The native distribution of walleye *Stizostedion vitreum* (Mitchill) is generally limited to the natural lakes and rivers of Canada and the northern United States (Carlander, 1997). After the completion of large-scale reservoir construction during the 1950s–1970s, introductions greatly expanded their distribution (Colby *et al.*, 1979; Carlander, 1997). Introductions to systems west of their native range have shown variable success, while introductions in the Great Plains were highly successful and now provide important recreational opportunities (Carlander, 1997; Burlingame, 1998; Craig, 2000).

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Kansas is located in the Great Plains region of the central U.S.A., an area characterized by high seasonal variability in temperature and precipitation (Matthews, 1988). Consequently, reservoirs in this region are exposed to a wide range of environmental conditions including dramatic changes in water levels, water quality and temperature (Willis, 1986). These conditions are magnified by flood control activities and municipal and agricultural water demands. Although walleye are able to tolerate a wide variety of environmental conditions (Colby *et al.*, 1979), the thermal regime can have a substantial influence on their population dynamics (Beverton, 1987; Hansen *et al.*, 1998).

Temperature has been shown to affect all aspects of walleye life history including spawning (Collette *et al.*, 1977), recruitment (Busch *et al.*, 1975; Momot *et al.*, 1977; Hansen *et al.*, 1998), behaviour (Reynolds, 1977), growth (Kelso, 1972; Momot *et al.*, 1977), condition (Kocovsky & Carline, 2001) and summer survival (Momot *et al.*, 1977). Summer water temperatures in Great Plains reservoirs often exceed 30° C and provide an excellent opportunity to examine the influence of extreme water temperatures on walleye growth and feeding ecology. These systems also allow for comparisons across their distribution and provide insight on the mechanisms that influence population characteristics (Beverton, 1987; Kocovsky & Carline, 2001). Changes in water temperature may result from several mechanisms, including low water levels, discharge from power facilities, or global warming (Matthews & Zimmerman, 1990). The effects of increased water temperature due to global warming are especially important in the Great Plains region where fish community structure and population dynamics are predicted to change with elevated temperatures (Matthews & Zimmerman, 1990; Carpenter *et al.*, 1992). One method to evaluate the effects of temperature on fishes is with bioenergetics models (Kitchell *et al.*, 1977; Hanson *et al.*, 1997). The objectives of this study were to investigate seasonal changes in population characteristics (i.e. abundance, condition and growth) and food habits of walleye in a typical Kansas reservoir. A bioenergetics modelling approach was used to evaluate seasonal trends in consumption and growth and to evaluate the potential effects of an altered thermal regime (as predicted from global warming models) on walleye growth.

MATERIALS AND METHODS

STUDY AREA

This study was conducted at Glen Elder Reservoir, Kansas, U.S.A. (39°29′ N; 98°18′ W). Glen Elder Reservoir is a 5093 ha impoundment on the Solomon River that was completed in 1969 for flood control. In addition to flood control, impounded water also serves irrigation, municipal and recreational needs. The watershed is comprised of mixed-grass prairie pastureland and row-crop agriculture. Similar to other Great Plains reservoirs, Glen Elder Reservoir is relatively shallow, turbid and does not thermally stratify due to persistent, high winds. Mean depth in the reservoir is 5·8 m and water temperatures often exceed 26° C throughout the summer and may reach 28° C during August [Fig. 1(a)]. Although there is some indication of chemical stratification [Fig. 1(b)], dissolved oxygen remained >4·5 mgl^{-1} throughout the water column all year.

Even though a few walleye were reportedly collected from Kansas during the mid-nineteenth century, walleye are characterized as an introduced species in Kansas (Cross & Collins, 1995). These early specimens were collected from the large rivers of

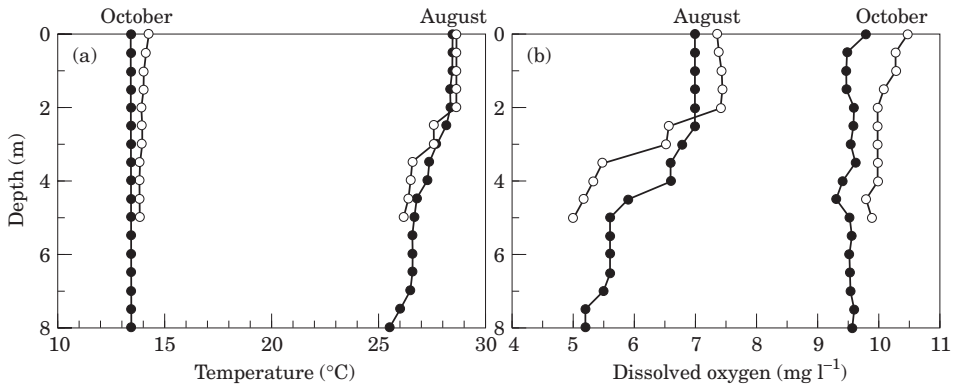

FIG. 1. Temperature (a) and dissolved oxygen (b) profiles from the pelagic (●) and littoral (○) areas of Glen Elder Reservoir during August and October 1999.

eastern Kansas (e.g. Missouri River). Abundant walleye populations were only established after reservoir construction and extensive stocking programmes during the 1960s and 1970s. Similar to other Kansas impoundments, abundant sport fishes include white crappies *Pomoxis annularis* Rafinesque, channel catfish *Ictalurus punctatus* (Rafinesque), white bass *Morone chrysops* (Rafinesque), and walleye. Gizzard shad *Dorosoma cepedianum* (Lesueur) are highly abundant and form the dominant prey species. Although natural reproduction occurs in the study reservoir, walleye larvae are annually stocked (*c.* 500 fry ha^{-1}) to supplement natural reproduction.

WALLEYE SAMPLING

Juvenile and adult walleye were sampled monthly from six fixed sites using 45·7 × 1·8 m experimental gillnets (9·2 m panels with 25·4, 38·1, 50·8, 63·5 and 76·2 mm bar measure mesh) from June 1999 to May 2000. Samples were not collected during December 1999 because of unstable ice cover. Gillnets were deployed at sunset and retrieved at 1–2 h intervals to limit digestion and regurgitation of stomach contents (Bowen, 1996). Nets were set and retrieved one to three times per night depending on the number of fish sampled. In response to low catch rates, an attempt was made to collect walleye throughout the reservoir during June and July. These samples included gears that were either not used during other seasons (i.e. electrofishing) or were not sampled at fixed locations (i.e. gillnets); therefore, these data were excluded from catch rate and condition analyses.

Lengths (mm, total length, L_T) and masses (g, total mass and gonad mass) were measured from all fish. Scales and otoliths were removed from each fish for age and growth analysis (DeVries & Frie, 1996). Scales were pressed onto 10 mm acetate slides and aged using a microfiche projector. Otoliths were used to corroborate scale age and to determine ages when scales were difficult to read (<5% of scale samples; Erickson, 1983; Boxrucker, 1986). Stomachs were removed from each walleye by cutting at the junction with the oesophagus and connection with the small intestine. Stomach contents were fixed in 10% formalin and transferred to 95% ethanol prior to analysis. Prey items were identified to species for fishes, genus or species for crustacean zooplankton (later aggregated by order), and family for Insecta. All taxa were measured to the nearest 0·01 mm using an image analysis system and prey fishes and insects were weighed to the nearest 0·001 g. Total lengths and masses of partially digested prey fishes were estimated from published equations for standard length and L_T (Minton & McLean, 1982), backbone length and L_T (Minton & McLean, 1982; Knight *et al.*, 1984), and mass–length relationships (Carlander, 1969, 1997). Masses of invertebrate taxa were estimated using length–mass relationships provided by Dumont *et al.* (1975) and Smock (1980).

Data from monthly samples were pooled by season based on water temperature: summer (June, July, August; mean ± S.E., 25·6° C ± 1·3), autumn (September, October,

November; 14·6° C ± 4·2), winter (January, February; 47° C ± 0·3), and spring (March, April, May; 12·4° C ± 2·5). Seasonal condition of walleye was assessed using relative weight (W_r; Murphy *et al.*, 1990). All data were summarized by year class for those year classes represented by at least five individuals in each season (year classes: 1995–1998). Food habits were assessed by calculating frequency of occurrence, per cent by number and per cent by mass (Bowen, 1996). Per cent by number and per cent by mass were determined for each individual and averaged to obtain seasonal estimates. The analysis of per cent by mass refined the interpretation of dietary habits and provided estimates for application of a bioenergetics model. Only fish with identifiable prey items in their stomach were used in the food habits analyses (i.e. unidentified prey taxa and walleye with empty stomachs were excluded; Isaak *et al.*, 1993; Jackson *et al.*, 1993; Bryan *et al.*, 1995; Slipke & Duffy, 1997). Most unidentified prey were fishes, but these were relatively uncommon in the samples ($\leq$2% by mass in the stomachs examined).

Mixed-model, repeated-measures ANOVA was used to determine whether seasonal differences existed in catch per unit effort (CPUE; number of walleye h^{-1}) and W_r. Degrees of freedom were estimated using the Kenward–Roger approximation (Kenward & Roger, 1997) and the variance-covariance matrix was assumed to be compound symmetric (Littel *et al.*, 1996). Repeated-measures ANOVA was also used to assess differences in mean length and mass among seasons for each year class. A Bonferroni adjustment was used to reduce the probability of a Type-I error associated with multiple *F*-tests (Kuehl, 1994). Linear regression analysis was used to test for relationships between walleye L_T and number and L_T of consumed gizzard shad. All statistical analyses were conducted using SAS (Littel *et al.*, 1996; SAS, 1996) and α=005.

BIOENERGETICS MODELLING

A bioenergetics model (Hewett & Johnson, 1992; Hanson *et al.*, 1997) was used to estimate walleye consumption and growth from site-specific data collected from Glen Elder Reservoir. The model describes energy intake and use by an individual fish with the generalized equation: $C=(R+S)+(F+U)+\Delta B$, where, C=consumption, R=respiration, S=specific dynamic action, F=egestion, U=excretion and ΔB=change in mass or growth. All growth and consumption computations were in grams of prey per gram of predator per day (Hanson *et al.*, 1997). The species-specific variables used in the model are described in Kitchell *et al.* (1977) and Hanson *et al.* (1997).

Modelling simulations were conducted for the 1995–1998 year classes using a daily time step over 365 days from 10 June 1999 to 9 June 2000. Each age class was divided into four successive periods to better represent seasonal trends in consumption and growth. These periods were summer (days 1–100), autumn (days 101–190), winter (days 191–280) and spring (days 281–365). Mean L_T at the beginning and end of each interval was estimated using equations derived from length by date regressions and were converted to mass using season-specific length–mass relationships (Bryan, 1995). The estimated L_T and masses were similar to observed monthly values. Dietary information was categorized by year class and entered into the bioenergetics model as the proportion by mass of prey taxa on individual sampling dates. Caloric densities of vertebrate prey items were obtained from Minton & McLean (1982) and Wissing (1974). Caloric densities of invertebrate prey were obtained from Cummins & Wuycheck (1971) and caloric density of walleye was taken as 17 514 kJ g^{-1} (Hanson *et al.*, 1997).

The first spawning cohort was designated as 1996 and the date of spawning was input as 5 April, the peak of walleye spawning in Glen Elder Reservoir (K. Austin, pers. comm.). Female walleye were not sampled immediately before and after spawning, therefore the proportion of body mass lost during spawning (9·28%) was obtained from Bryan (1995). Water temperatures were measured at 0·5 m depth intervals from two sites each month to coincide with monthly walleye sampling. Mean water temperatures were obtained by averaging across all depth intervals for a site and then averaging the two sites [temperatures were similar between sites; Fig. 1(a)].

After all species- and site-specific data were entered, the proportion of maximum consumption (P_c) was calculated as: $P_c=C\cdot(C_{max}\cdot r_c)^{-1}$ where, C is the estimated

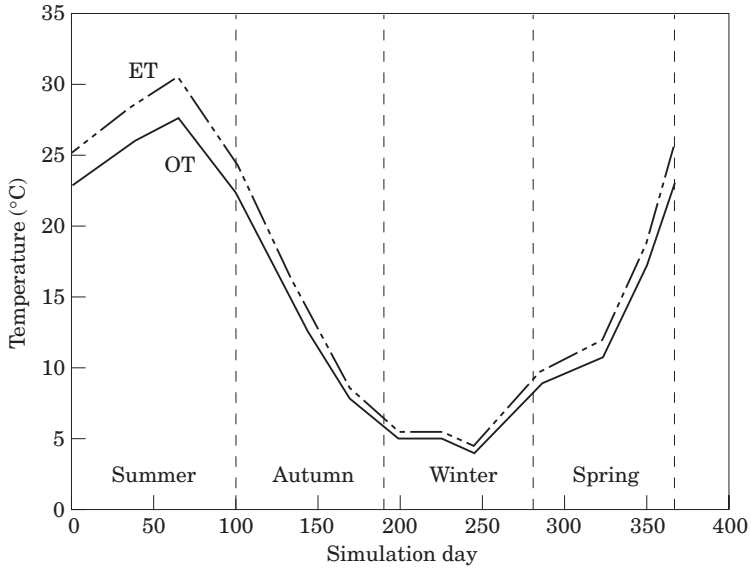

FIG. 2. Observed (OT) and elevated (ET) water temperatures used in the bioenergetics model for walleye from Glen Elder Reservoir, Kansas. Observed temperatures represent monthly measurements during June 1999 to May 2000. Elevated temperatures represent a 10% increase in temperature. Vertical lines represent the end of each season used in the analysis.

consumption, C_{max} is maximum consumption of a specific ration at a given temperature and r_c is a temperature-dependent proportional adjustment of consumption rate (Kitchell *et al.*, 1977; Hanson *et al.*, 1997). In the present model, P_c was estimated by solving the equation with observed growth and temperature data.

The model developed for walleye in Glen Elder Reservoir (hereafter considered as the baseline model) can be used to address certain reservoir management questions. For example, it allows the simulation of walleye growth response to situations such as altered thermal regimes (Kitchell *et al.*, 1977; Rice *et al.*, 1983; Bryan, 1995). A similar approach to that of Kitchell *et al.* (1977) and Bryan (1995) was taken and the effects of increased temperatures on growth of walleye modelled by assuming that water temperature was elevated by 10%, resulting in a 1·3–2·8° C increase during the spring, summer and autumn and <1° C during the winter (Fig. 2). The elevated temperatures used in the study were similar to current global warming predictions (Webb & Nobilis, 1994; Hogg & Williams, 1996; Kacholia & Reck, 1997). Growth responses of fish were estimated by varying P_c from 0·2 to 1·0 (0·2 increments). Proportionality constants were varied across a large distribution of values because the response in walleye consumption with elevated temperatures was unknown, and P_c values were highly variable among year classes and seasons. All other variables remained equal to those in the baseline model. Per cent mass gain or loss was estimated for each year class and compared to the baseline model.

RESULTS

POPULATION CHARACTERISTICS AND FOOD HABITS

Two hundred and eighty walleye were collected varying from 221 to 707 mm L_T and from 86 to 4068 g. Most walleye were collected during the autumn when CPUE was significantly higher ($P \leq 0{\cdot}0001$; $8{\cdot}27 \pm 3{\cdot}45$) than during summer

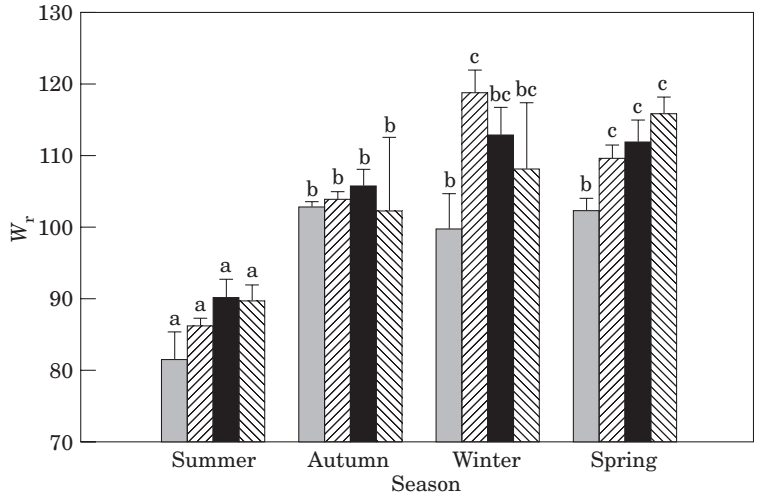

FIG. 3. Mean ± S.E. relative mass (n=280) of four year classes (▨, 1995; ■, 1996; ▨, 1997; □, 1998) of walleyes sampled from Glen Elder Reservoir, Kansas, during June 1999 to May 2000. Bars with different letters indicate a significant difference (P<0·001; comparisons are among seasons by year class). Months were grouped into seasons based on water temperature: summer (June, July, August), autumn (September, October, November), winter (January, February) and spring (March, April, May).

(0·16 ± 0·04), winter (0·26 ± 0·08) and spring (2·03 ± 0·53). Catch rates were significantly ($P \leq 0{\cdot}0001$) lower during the summer compared to all other seasons. Similar to CPUE, mean W_r was lowest during the summer for all year classes (Fig. 3).

Most year classes increased in mean L_T and mass between the end of summer and autumn (Fig. 4). Because the study was not started until June, it was not possible to directly determine the proportion of annual growth accumulated throughout the year. The initial L_T and mass at the beginning of the growing season, however, was estimated using mean back-calculated lengths at age and length-mass regressions. Based on this analysis, it was estimated that 61–80% of the annual growth in length was attained between the end of August and October. Similar results were found for annual growth in mass, where 70–82% of the annual growth was completed between late summer and autumn, generally between August and October.

The largest proportion of empty stomachs was observed during early and mid summer for all year classes (Table I). Frequency of occurrence and per cent by number of cladocerans were highest during the summer for the 1998 and 1997 year classes. Chironomidae, freshwater drum *Aplodinotus grunniens* Rafinesque, and gizzard shad were the most common prey items in the stomachs of walleye from the 1996 and 1995 year classes during the summer. Gizzard shad were the most common and numerically abundant prey item during the autumn and winter for all ages. During the spring, gizzard shad were the most common prey species, but diets were generally dominated (numerically) by chironomids and cladocerans.

Per cent by mass was dominated by freshwater drum and gizzard shad during the summer for all ages. Similarly, gizzard shad were the most important prey

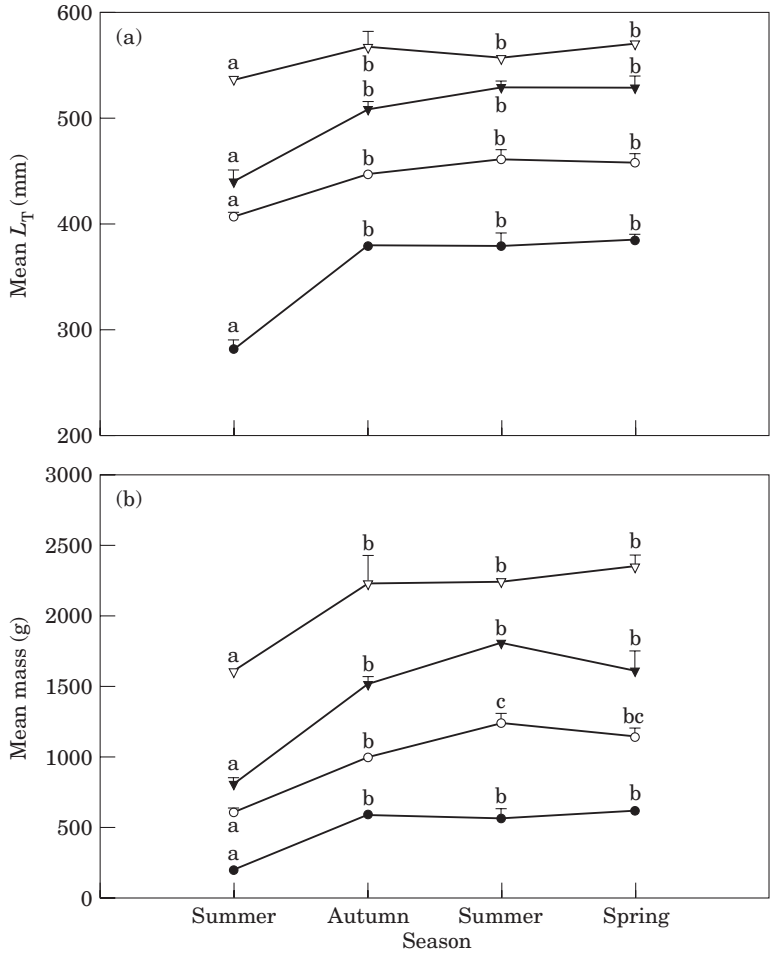

FIG. 4. Mean ± S.E. length (a) and mass (b) of four year classes (▽, 1995; ▼, 1996; ○, 1997; ●, 1998) of walleyes sampled from Glen Elder Reservoir, Kansas, during June 1999 to May 2000. Values with different letters indicate a significant difference ($P<0{\cdot}001$; comparisons are among seasons within year classes). Months were grouped into seasons based on water temperature: summer (June, July, August), autumn (September, October, November), winter (January, February) and spring (March, April, May).

for all year classes during autumn, winter and spring. Chironomids and cladocerans were often common and numerically important during the summer and spring, but contributed little to the ingested biomass.

Most walleye consumed small gizzard shad (<90 mm) from the 1999 year class, however, several large walleye (>650 mm) consumed gizzard shad up to 200 mm. Most walleye stomachs contained one or two gizzard shad during the summer and spring. During the autumn and winter, nearly all walleye (>80%) had three or more gizzard shad in their stomach and several fish had consumed up to 12 gizzard shad. There was a significant relationship between walleye L_T and the number ($r^2=0{\cdot}11$, $P=0{\cdot}0001$) and L_T ($r^2=0{\cdot}19$, $P=0{\cdot}0001$) of consumed gizzard shad. Although these relationships were significant, the low r^2 values

TABLE I. Frequency of occurrence (% *O*), per cent by number (% *N*), and per cent by mass (% *M*) of prey items sampled from four year classes of walleye in Glen Elder Reservoir, Kansas (June 1999 to May 2000). Sample size (*n*) and the proportion of empty stomachs are provided for each year class and season. Months were grouped into seasons based on water temperature: summer (June, July, August), autumn (September, October, November), winter (January, February) and spring (March, April, May)

Season and prey	1998			1997			1996			1995		
	% *O*	% *N*	% *M*	% *O*	% *N*	% *M*	% *O*	% *N*	% *M*	% *O*	% *N*	% *M*
Summer	*n*=16			*n*=16			*n*=9			*n*=5		
Empty	38			19			11			20		
Copepoda	6	5	1	0	0	0	0	0	0	0	0	0
Chironomidae	6	5	1	20	17	2	50	8	2	0	0	0
Cladocera	52	55	10	50	54	4	0	0	0	20	50	1
Freshwater drum	6	10	10	15	17	56	25	52	60	0	0	0
Gizzard shad	24	20	38	15	12	38	25	40	38	80	50	99
White bass	6	5	40	0	0	0	0	0	0	0	0	0
Autumn	*n*=32			*n*=43			*n*=17			*n*=6		
Empty	0			8			0			7		
Copepoda	0	0	0	0	0	0	0	0	0	0	0	0
Chironomidae	0	0	0	2	1	a	0	0	0	0	0	0
Cladocera	0	0	0	2	1	a	0	0	0	0	0	0
Freshwater drum	0	0	0	7	4	2	0	0	0	17	7	1
Gizzard shad	100	100	100	89	94	98	100	100	100	83	93	99
White bass	0	0	0	0	0	0	0	0	0	0	0	0
Winter	*n*=11			*n*=12			*n*=22			*n*=5		
Empty	18			8			9			0		
Copepoda	0	0	0	0	0	0	0	0	0	0	0	0
Chironomidae	0	0	0	0	0	0	0	0	0	0	0	0
Cladocera	0	0	0	0	0	0	0	0	0	0	0	0
Freshwater drum	0	0	0	0	0	0	0	0	0	0	0	0
Gizzard shad	100	100	100	91	96	89	100	100	100	100	100	100
White bass	0	0	0	9	4	11	0	0	0	0	0	0
Spring	*n*=18			*n*=13			*n*=10			*n*=12		
Empty	11			8			0			17		
Copepoda	0	0	0	0	0	0	0	0	0	0	0	0
Chironomidae	22	54	11	8	14	12	0	0	0	0	0	0
Cladocera	11	10	1	15	59	1	20	57	7	0	0	0
Freshwater drum	0	0	0	0	0	0	0	0	0	0	0	0
Gizzard shad	67	36	88	77	27	87	80	43	93	100	100	100
White bass	0	0	0	0	0	0	0	0	0	0	0	0

[a]Frequency <0·001%.

TABLE II. Proportionality constants (P_c; proportion of maximum consumption) from a bioenergetics model used to estimate consumption and growth of four year classes of walleyes in Glen Elder Reservoir, Kansas. Initial and final masse represent masses at the beginning and end of each simulation. Months were grouped into seasons based on water temperature: summer (June, July, August), autumn (September, October, November), winter (January, February) and spring (March, April, May)

Year class or season	Simulation days	Initial mass (g)	Final mass (g)	P_c
1998				
Summer	1–100	178	178	0·71
Autumn	101–190	178	589	0·88
Winter	191–280	589	591	0·23
Spring	281–365	591	601	0·35
1997				
Summer	1–100	545	550	0·55
Autumn	101–190	550	1100	0·66
Winter	191–280	1100	1239	0·40
Spring	281–365	1239	1250	0·35
1996				
Summer	1–100	1000	1016	0·59
Autumn	101–190	1016	1600	0·57
Winter	191–280	1600	1798	0·41
Spring	281–365	1798	1850	0·34
1995				
Summer	1–100	1600	1620	0·44
Autumn	101–190	1620	2221	0·48
Winter	191–280	2221	2250	0·27
Spring	281–365	2250	2337	0·35

indicated high variability in both the number and length of gizzard shad consumed by large walleye.

BIOENERGETICS MODELLING

The proportion of maximum consumption (P_c) consumed by walleye was generally highest during the autumn and lowest during the winter and spring for all year classes (Table II). Manipulative simulations suggested that growth of walleye during summer would be lower with elevated temperatures compared to the observed thermal regime (Fig. 5). Growth of walleye would be enhanced during the autumn, winter and spring relative to the baseline model except at low levels of consumption. The youngest year classes experienced the least mass gain during the summer and highest gain during the autumn compared to the other year classes, while the oldest fish experienced opposite trends. Changes in P_c generally had the greatest influence on walleye growth estimates during the autumn.

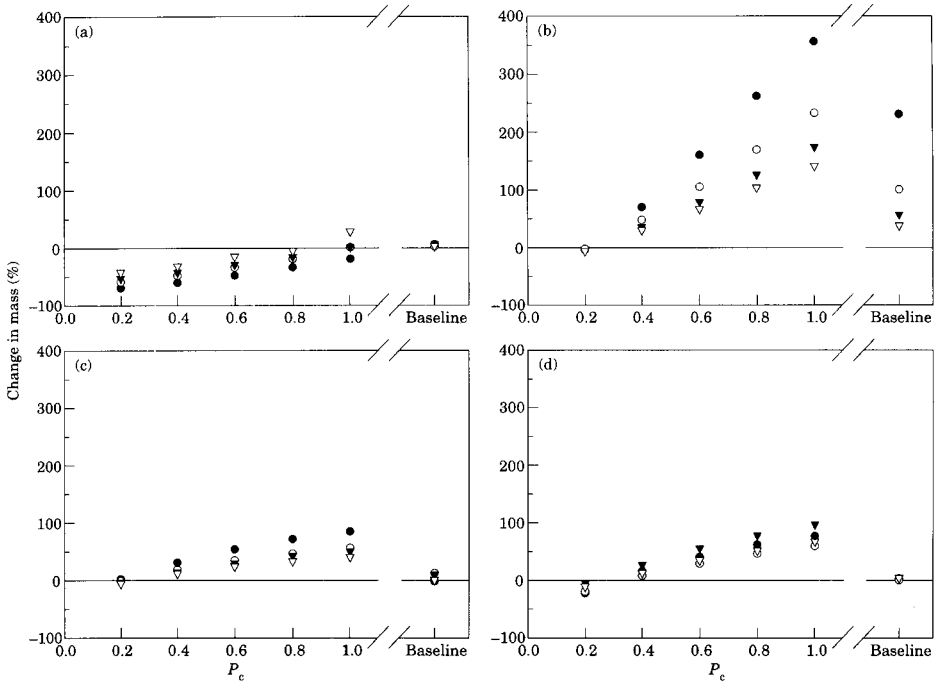

FIG. 5. Per cent change in mass of walleye with an elevated thermal regime (10% temperature increase). Simulations were conducted by year class (▽, 1995; ▼, 1996; ○, 1997; ●, 1998) and season: (a) summer (days 1–100); (b) autumn (101–190); (c) winter (191–280), and (d) spring (281–365) at different proportions of maximum consumption (P_c). Baseline values represent observed changes in mass of walleye from Glen Elder Reservoir, Kansas, during June 1999 to May 2000.

DISCUSSION

The food habits of walleye have been extensively studied throughout their native distribution. Several studies on walleye from natural lakes in South Dakota and Minnesota indicate that invertebrates are an important component of their diet (Johnson & Hale, 1977; Isaak *et al.*, 1993; Slipke & Duffy, 1997). In larger systems such as Lake Oahe (South Dakota), the Great Lakes and Oneida Lake (New York), cyprinids, rainbow smelt *Osmerus mordax* (Mitchill), yellow perch *Perca flavescens* (Mitchill), and clupeids are often the dominant prey (Forney, 1974; Swenson, 1977; Knight *et al.*, 1984; Jackson *et al.*, 1993; Bryan *et al.*, 1995). In the present study, invertebrate prey were common and numerically abundant in walleye diets during the summer and spring, but contributed little to the total biomass consumed. Rather, gizzard shad were generally the most important prey item throughout the year. In systems with soft-rayed and spiny-rayed prey fishes, walleye diets are usually dominated by soft-rayed fishes such as cyprinids and clupeids (Range, 1973; Goddard & Redmond, 1978; Johnson *et al.*, 1988). Relative abundance of these prey species probably influenced consumption, but several studies have shown that walleye will selectively prey on soft-rayed fishes, even when they are less abundant (Parsons, 1971; Knight *et al.*, 1984).

The importance of gizzard shad for growth of sport fishes is well documented. Wahl & Stein (1988) found that growth of esocids was higher in systems that

contained gizzard shad compared to lakes with only centrarchids. Santucci & Wahl (1993) summarized growth of walleye and found that length increments of walleye averaged 60 mm year^{-1} higher for systems that contained gizzard shad compared to systems with a centrarchid or cyprinid as the main prey. The selection of gizzard shad by predators is probably due to increased predation success on gizzard shad (e.g. reduced handling time and capture per strike) relative to spiny-rayed prey (Wahl & Stein, 1988; Einfalt & Wahl, 1997)

In southern and mid-western lakes, walleye generally occupy deep water during the summer and move inshore during the autumn and spring once water temperatures reach *c.* 15° C (Ager, 1977; Williams, 1997). Activity of walleye decreased once water temperatures exceeded 23° C in Center Hill Reservoir, Tennessee (Ager, 1977). Similar results have been reported in laboratory studies where walleye sought thermal refugia and reduced feeding activity at temperatures >22° C (Kelso, 1972; Hokanson, 1977). Temperatures throughout the water column were well above the thermal optimum of 22° C for most of June, July and August in Glen Elder Reservoir. Catch rate of walleye in Glen Elder Reservoir was lowest during the summer and probably reflects changes in habitat selection as well as reduced activity. Attempts were made to sample additional walleye throughout the reservoir with increased effort during the summer months, but few walleye were collected (n<10). Although changes in habitat use undoubtedly influenced the catch rates, these results suggest that low CPUE was most likely due to reduced activity during the summer. The effects of warmer temperatures during summer were also reflected in lower condition, reduced growth and a high proportion of empty stomachs.

Juvenile gizzard shad primarily feed on zooplankton and invertebrates in littoral zones of lentic systems and prefer the warmest water available during summer (Jester & Jensen, 1972). In systems where the upper few metres of water are >22–25° C, gizzard shad may be relatively unavailable to walleye. For example, Momot *et al.* (1977) found that high water temperatures (>25° C) in Hoover Reservoir, Ohio, effectively segregated walleye and gizzard shad during the summer. The authors suggested that this resulted in poor growth and high summer mortality. Kocovsky & Carline (2001) suggested a similar explanation for growth and mortality of walleye in Pymatuning Sanctuary, Pennsylvania. Water temperatures in Glen Elder Reservoir were often 2–3° C higher in the upper few metres of the water column during summer. If walleye altered their distribution to avoid high water temperatures, temperature-mediated spatial segregation of walleye and gizzard shad may have influenced consumption of gizzard shad during summer.

Growth of walleye generally occurs from mid-June to August in northern populations (Forney, 1966; Kelso & Ward, 1972; Carlander, 1997). Most annual growth in populations from southern latitudes, however, occurs during late summer and autumn (Carlander, 1997). For example, Stroud (1949) found that 76% of the annual growth (in length) of walleye in a Tennessee reservoir was accomplished by mid-August, and 99% was completed by September. In the current study, up to 82% of the annual growth in mass and 80% of the growth in length was achieved between August and October when water temperatures were between 12–15° C.

Percentages of maximum consumption (P_c) reflect prey availability as well as predatory intensity (Rice *et al.*, 1983). Seasonal P_c values in Glen Elder Reservoir were highest during the autumn, but were also relatively high during summer. High P_c values during the autumn probably reflect the availability of age 0 year gizzard shad and suitable water temperatures for feeding activity and growth of walleye. Conversely, most walleye had empty stomachs and exhibited little growth during the summer. The high proportion of empty stomachs appears to contrast the estimated P_c values during the summer. The model, however, does not include information on the proportion of walleye with empty stomachs. Furthermore, maximum consumption (C_{max}) for walleye is lower at temperatures >25° C relative to lower temperatures (Kitchell *et al.*, 1977; Hanson *et al.*, 1997), indicating that P_c can be high at temperatures above optimum even though total consumption declines.

Simulation of the effects of elevated temperatures indicated that growth of walleye during summer would be substantially less than that observed during the present study. These effects were especially evident for the younger year classes and low levels of consumption. Although the bioenergetics model predicted growth after the summer months, it is unknown whether fish would survive such a dramatic mass loss. Direct mortality of walleye may also occur if water temperatures rise above 32° C (Carlander, 1997; Hanson *et al.*, 1997) and fish are unable to find thermal refugia. No thermal stratification was measured in Glen Elder Reservoir, but fish probably find refugia in isolated habitats (*i.e.* underwater springs and tributaries). Whether or not these same refugia would be available with an elevated thermal regime is unknown. Increased water temperatures may also have indirect effects. For example, increased temperatures may result in faster growth of gizzard shad and reduced prey availability for walleye. Although it would be interesting to model the effects of elevated temperatures on prey populations, the data are insufficient to assess these complex effects. Such analyses would require a detailed analysis of prey availability, response of prey population dynamics (*i.e.* growth and mortality), and response of walleye to these changes. Even though the data cannot directly address these interactions, P_c values reflect prey availability (Rice *et al.*, 1983; Bryan, 1995) and modelling across a wide range of P_c values provides insight to the potential influences of prey availability.

Reservoir systems in the Great Plains and southern U.S.A. are characterized by high summer temperatures (McCarraher *et al.*, 1971; Turner & Summerfelt, 1971; Dodds *et al.*, 1993; Thornton, 1990). Thus, the results of this study are not limited to reservoir systems in Kansas. Unlike walleye populations previously studied with regard to extreme temperatures (Momot *et al.*, 1977; Kocovsky & Carline, 2001), walleye have little or no evolutionary history with the environmental conditions or fish communities characteristic of reservoir systems (Ryder & Kerr, 1978; Carlander, 1997). Reduced activity, consumption, condition and summer growth, however, appear to be a generalized response of walleye to high summer water temperatures across their distribution. The results of the bioenergetics simulations suggest that further increases in water temperature would have disparate effects on growth of walleye depending on the season. If walleye are able to find thermal refugia or subsist on energy reserves during the summer, elevated temperatures would have a net positive effect on growth

throughout the year. Because the effects of elevated water temperatures may cause complex interactions between walleye and prey populations, further investigations are required to assess the importance of altered prey communities on walleye growth.

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