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Factors related to growth and survival of larval walleyes: implications for recruitment in a southern Great Plains reservoir

M.C. Quist[a,*], C.S. Guy[a,1], R.J. Bernot[a], J.L. Stephen[b]

[a] *US Geological Survey, Biological Resources Division, Kansas Cooperative Fish and Wildlife Research Unit,*
205 Leasure Hall, Manhattan, KS 66506, USA
[b] *Kansas Department of Wildlife and Parks, Box 1525, Emporia, KS 66801, USA*

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Abstract

Larval fishes, limnological characteristics, and zooplankton populations were sampled from Glen Elder Reservoir, Kansas, during 1999–2001 to determine factors associated with growth and survival of larval walleyes (*Stizostedion vitreum*). Ichthyoplankton populations were sampled weekly from April to June during all years using paired conical nets. Water temperature and zooplankton populations were sampled at each ichthyoplankton sampling site. Approximately, 70% of all larval fishes and 80% of the larval walleyes were sampled in the upper reservoir during all years. Cyprinidae and Centrarchidae were the only taxa that were more abundant in the main reservoir than the upper reservoir. Despite similarities in zooplankton abundance between years, recruitment of walleyes in 1999 was the lowest in nearly 20 years, while moderate year classes were produced in 2000 and 2001. During 1999, low, variable spring temperatures resulted in poor growth of larval walleyes. Poor growth of walleyes, coupled with high densities of larval gizzard shad (*Dorosoma cepedianum*), resulted in poor recruitment during 1999. Walleyes grew faster in 2000 and 2001 and were able to consume larval gizzard shad resulting in moderate recruitment. These results suggest that abiotic conditions mediate biotic interactions and that both abiotic and biotic characteristics are important for regulating walleye recruitment dynamics.

Keywords: Walleye; Larvae; Growth; Survival; Recruitment; Reservoir; Kansas

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1. Introduction

High variability in recruitment of walleyes (*Stizostedion vitreum*) is widely recognized, especially in reservoirs (Colby et al., 1979; Fielder, 1992). Each cohort is subject to a unique set of environmental conditions; thus, determining the mechanisms underlying recruitment is difficult. This is especially important considering that environmental conditions at each ontogenetic stage can have different effects on growth, survival, and subsequent recruitment to the adult population.

Growth during the early life stages often regulates recruitment of larval fishes to the adult population (Werner and Gilliam, 1984). Survival through ontogeny depends on becoming sufficiently large to consume increasingly larger prey items, avoid predation, and survive competitive interactions (Paine, 1976; Werner and Gilliam, 1984). Consequently, food limitation during the larval stage has been hy-

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[*] Corresponding author. Present address: Wyoming Cooperative Fish and Wildlife Research Unit, University of Wyoming, Laramie, WY 82071-3166, USA. Tel.: +1-307-766-5415.
E-mail address: mcquist@uwyo.edu (M.C. Quist).

[1] Present address: Montana Cooperative Fishery Research Unit, Department of Ecology, 301 Lewis Hall, Montana State University, Bozeman, MT 59717, USA.

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pothesized as the primary factor influencing survival of larval fishes. The critical-period hypothesis suggests that availability of food to first-feeding fishes (i.e., exogenous feeding) controls year-class strength (Hjort, 1914, 1926). Recently, the match–mismatch hypothesis has expanded the critical-period hypothesis to include not only the first-feeding stage, but the entire larval period (Cushing, 1990). Specifically, the hypothesis states that temporal and spatial overlap between peaks in food resources (e.g., zooplankton) and larval abundance regulates survival of larval fishes (Cushing, 1990; Chick and Van Den Avyle, 1999). Because the ability to reach a large size is important for piscivores, hatching chronology should be matched to the availability of suitable food resources at each ontogenetic stage (Li and Mathias, 1982). In natural systems, ontogeny of piscivorous fishes has been patterned by the long evolutionary history with the physical, chemical, and biological characteristics of the system (Werner and Gilliam, 1984). Therefore, deriving broad generalizations regarding the growth and subsequent survival of larval fishes in dynamic reservoirs is difficult.

Despite the inability to make universal predictions regarding recruitment of piscivores in impounded systems, the timing and abundance of prey items are important factors influencing growth and survival of naturally produced and stocked walleyes (Mathias and Li, 1982). Shortly after yolk-sac absorption, larval walleyes feed on crustacean zooplankton (Colby et al., 1979; Mathias and Li, 1982); however, if food resources are unavailable, mortality may result from depleted energy reserves for maintenance, decreased foraging efficiency, or increased susceptibility to predation (Jonas and Wahl, 1998). Piscivorous species must not only pass through a planktivorous feeding stage when they are small, but their ability to compete for zooplankton is hindered by their morphology (Werner and Gilliam, 1984). Additionally, species that are specialized planktivores as adults can have competitive effects on species that are only planktivorous during early ontogeny (Davies et al., 1981). Competitive interactions are poorly understood for most reservoir fish assemblages, but it is likely that gizzard shad (*Dorosoma cepedianum*) interact with larval walleyes. Gizzard shad are not only important as potential competitors for zooplankton resources, but are themselves an important prey item for juvenile and adult walleyes (Momot et al., 1977). Thus, the switch to piscivory must occur when larval prey are available to walleyes for optimum growth and survival (Colby et al., 1979). The effects of such interactions may be exacerbated if stocking or timing of the walleye hatch is delayed (e.g., by abiotic factors) such that predator and prey resources are mismatched.

Despite the recreational and ecological importance of walleyes in Kansas reservoirs (Quist et al., 2002), little is known about factors that influence growth and survival during their early life history. Although factors influencing juvenile walleyes during their first year (e.g., post-larvae, fingerlings) may be important for walleye recruitment dynamics in some systems, first year growth and survival is high in Kansas reservoirs (Quist, 2002; Quist et al., 2002), suggesting that factors influencing larval walleye are most important for walleye recruitment. Therefore, the purpose of this study was to determine the abiotic and biotic factors influencing growth and survival of larval walleyes in a Great Plains reservoir. Specifically, we examined the influence of temperature, zooplankton densities, and larval gizzard shad on larval walleyes in Glen Elder Reservoir, Kansas.

2. Methods

2.1. Study area

Glen Elder Reservoir is a 5093 ha reservoir on the Solomon River, Mitchell County, Kansas. Glen Elder dam was completed in 1969 for flood control, and in conjunction with Webster and Kirwin reservoirs, provides flood protection to the lower Solomon River valley. In addition, impounded water serves over 8000 ha of irrigable croplands and provides municipal water, recreational, and fish and wildlife conservation benefits. The watershed (approximately 18,000 km^2) is comprised of mixed-grass prairie pastureland and row-crop agriculture, and the shoreline is dominated by limestone boulders and cobble. Similar to other reservoirs in the southern Great Plains, Glen Elder Reservoir is relatively shallow and turbid, and persistent high winds during most of the year prevent thermal stratification. Mean depth in the reservoir is 5.8 m and water temperatures often approach 30 °C during summer (Quist et al., 2002).

Table 1
Mean depth (m), number of sampling sites, and number of samples collected by habitat type in Glen Elder Reservoir, Kansas, during 1999–2001[a]

Habitat type	Depth (m)	Number of sample sites			Number of samples		
		1999	2000	2001	1999	2000	2001
Cove	4.2 (0.4)	4	3	0	45	22	0
Dam	12.0 (2.0)	2	3	3[b]	24	31	6[b]
Littoral	3.8 (0.7)	8	6	0	89	58	0
Pelagic	9.2 (0.8)	8	4	0	91	30	0
Upper reservoir	2.5 (0.1)	2	4	4	22	33	126

[a] Numbers in parenthesis represent one standard error.

[b] Samples were only collected when weather permitted.

Abundant sport fish include white crappies (*Pomoxis annularis*), channel catfish (*Ictalurus punctatus*), white bass (*Morone chrysops*), and walleyes. Gizzard shad are highly abundant and form the dominant prey species (Quist et al., 2002). Walleyes are annually stocked (approximately, 500 larvae/ha) into Glen Elder Reservoir to supplement natural reproduction and may contribute up to 90% of the year class (Quist, 2002).

2.2. Ichthyoplankton sampling

Larval fishes were sampled from April until June (1999–2001) from five habitat types (Table 1). Larval fish were sampled during the day at all sites using paired conical nets (bongo nets; 0.5 m diameter × 1.5 m long, 500 μm mesh). Ichthyoplankton were also sampled using a meter net (1.0 m diameter, 3.0 m long, 500 μm mesh) at all sites except those in the upper reservoir due to shallow depths (≤2.5 m). Bongo nets were pushed just below the surface from the bow of the boat, and the meter net was towed behind the boat using an aluminum depressor to maintain the top of the net at a depth of 0.5 m from the surface. Nets were deployed for 5–20 min at a rate of 1.5 m/s. Sample volume was determined from flow meters (General Oceanics, Inc., model 2030R) fixed to the mouth of all nets.

During 1999 and 2000, ichthyoplankton samples were collected from all five habitat types (Table 1). However, the sampling design was modified to more efficiently sample larval walleyes in 2001. Specifically, sampling was restricted to the upper reservoir in 2001. Samples from sites near the dam were also collected during 2001 when weather permitted, but no larval fishes were collected. In addition to limiting samples to the upper reservoir, the frequency of sampling was also increased in 2001. In 1999 and 2000, samples were collected weekly from the first week in April until the first week in June. During 2001, samples were collected daily in the upper reservoir for the first week after walleyes were stocked and then weekly thereafter. One additional sample was collected during the end of June in all years.

Several supplemental samples were also collected in 2000 and 2001 in an attempt to collect larval walleyes. These samples included bongo net samples near the shoreline (5–15 m from shore, approximately 1.0 m deep) and samples collected at night. During 2001, quatrefoil light traps (see Secor et al. (1992) for light trap dimensions) were set at three sites near the dam and three sites in the upper reservoir. Two light traps (one at the surface and one on the bottom) were set daily at each site at dusk and retrieved the next morning for 1 week following walleye stocking. Despite additional sampling efforts (i.e., near-shore samples, night samples, light traps), larval walleyes were not collected in any of the supplemental samples and were excluded from the analysis.

Ichthyoplankton samples were immediately preserved in 90% ethanol (Stevenson and Campana, 1992) and transported back to the lab for processing. Larval fishes were identified using keys provided by May and Gassaway (1967), Taber (1969), and Auer (1982). All larvae were identified to species except for cyprinids, catostomids, and centrarchids which were identified to family. Total length of larval walleyes was measured to the nearest 0.1 mm using an image analysis system. Saggital otoliths were removed from larval walleyes and mounted on glass slides using thermoplastic cement. Age in days was determined following the guidelines of Stevenson and Campana (1992). Two independent counts (i.e., re-randomized after the first count) of growth rings were made for each otolith by one observer. If the counts differed by more than two rings, the otolith was read once more by the observer. If the last count differed from the previous counts, the otolith was removed from the analysis; otherwise, the modal age was used in subsequent analyses.

All larval walleyes stocked into Glen Elder Reservoir were marked with oxytetracycline (OTC) and a subsample ($N = 25$) of larval walleye otoliths were assessed for OTC marks by staff at Southern Illinois University. All walleyes from the upper reservoir were marked; therefore, walleyes collected in the upper reservoir were assumed to be of hatchery origin. Because larval catch rates did not provide an adequate index of walleye recruitment, recruitment was assessed using catch per unit effort (CPUE = number of walleyes per gill net complement night [NCN]) of age-0 walleyes sampled with gill nets during the fall. Previous analyses indicated that CPUE of age-0 walleyes provides an index to recruitment of walleyes to later ages (Quist, 2002).

2.3. Thermal regime and zooplankton sampling

Water temperature (°C) was measured on each sampling date from four fixed sites using a multi-probe (Yellow Springs Instruments, Inc., model 85). Full-water column zooplankton samples were collected at each ichthyoplankton sampling site with a conical plankton net (0.1 m diameter × 0.4 cm long; 80 μm mesh) and preserved in 70% ethanol. Zooplankton were identified to species using keys provided in Pennak (1978) and enumerated by counting all organisms in a 5 ml subsample (Wetzel and Likens, 1991).

2.4. Statistical analyses

The analysis of larval densities was restricted to estimates from the bongo net samples because this was the only gear used in the upper reservoir and few fish were sampled using meter nets (i.e., <10% of those collected). Repeated-measures analysis of variance (ANOVA; Milliken and Johnson, 1992; Littell et al., 1996) was used to determine whether larval fish densities differed over spatial and temporal scales. Comparisons of larval fish densities were conducted only for walleyes and gizzard shad because other taxa were seldom abundant. Preliminary analyses included total larval densities, but the results are not presented because trends in total larval abundance were identical to those for gizzard shad (i.e., gizzard shad dominated the larval fish assemblage). Mean walleye and gizzard shad densities from the first week in April until the last week in June were compared between habitats for each year and sampling date. Similar statistical techniques were used to compare total zooplankton and *Daphnia* spp. densities. Preliminary analyses indicated that larval fish and zooplankton densities from sites in the main reservoir (i.e., dam, cove, littoral, and pelagic habitat types; Table 1) were not significantly different during 1999 or 2000 ($F_{3,15} = 0.6$–27.0, $P = 0.06$–0.64). Therefore, samples from the main reservoir were combined and then compared to density estimates from the upper reservoir. When significant interactions (i.e., habitat by date) occurred, least-square means were used to examine differences between habitats on individual sampling dates (Milliken and Johnson, 1992).

Growth of larval walleyes was estimated using a linear growth model (Stevenson and Campana, 1992). Differences in growth rate (i.e., slope estimates) and water temperature among years were compared using analysis of covariance (ANCOVA) and comparisons of yearly slope estimates were compared using linear contrasts. All analyses were conducted using SAS (Littell et al., 1996).

3. Results

3.1. Spatial and temporal distribution of larval fishes

We collected 93,736 individuals representing seven families (Table 2). Gizzard shad dominated the ichthyoplankton samples and represented 95.5% of all fishes collected. Despite only a few sampling sites in the upper reservoir ($N = 2$ sites in 1999, $N = 4$ sites in 2000), nearly all fishes were sampled in the upper reservoir. Logperch (*Percina caprodes*) were sampled

Table 2
Number of larval fish collected from main reservoir (MR; includes cove, dam, littoral, and pelagic habitats) and upper reservoir (UR) sites samples on Glen Elder Reservoir, Kansas, during 1999–2001

Taxa	1999		2000		2001	Percent from UR	
	MR	UR	MR	UR	UR	1999	2000
Gizzard shad	21167	50439	3247	9764	4971	70.4	75.0
Cyprinidae	16	8	8	2	247	33.3	20.0
Catostomidae	4	7	0	7	854	63.6	100.0
White bass	6	242	3	18	1574	97.6	75.0
Centrarchidae	124	54	16	14	89	30.3	46.7
Walleye	2	14	2	16	68	83.3	84.6
Log perch	0	4	0	3	12	100.0	100.0
Freshwater drum	4	2	0	1	743	33.3	100.0
Total	21323	50759	3276	9820	8558	70.4	74.9

only from the upper reservoir during 1999 and 2000, and catostomids and freshwater drum (*Aplodinotus grunniens*) were collected only from the upper reservoir in 2000. The only taxa that were more abundant in the main reservoir than the upper reservoir during 1999 and 2000 were larval cyprinids and centrarchids. Although few larval walleyes were collected during 1999 and 2000 from either habitat type, most (>80%) were sampled in the upper reservoir.

Due to differences in spawning dates and availability of fish for stocking between years, walleye were stocked (all fish were 3–4-day-old at time of stocking and all were stocked in the upper reservoir) at different times during the study (Fig. 1). In 1999, larval walleyes were stocked during the third week in April. Walleyes were stocked a week earlier in 2000 and 2 weeks earlier in 2001 relative to 1999. Larval walleyes were collected 2 days following walleye stocking in 1999 and 2000 and throughout the first week in 2001 (Fig. 1). Due to a significant habitat by date interaction during 1999 ($F_{10,204} = 3.59$, $P = 0.002$) and 2000 ($F_{8,125} = 3.22$, $P = 0.004$), mean walleye densities were not compared across all dates or habitat types. Although walleye densities were highly variable and most habitat by date combinations were not statistically significant ($P > 0.05$), densities were almost always higher in the upper reservoir (Fig. 1). The duration of larval walleyes in the samples also varied between years. In 1999, larval walleyes were sampled until the end of May, but during 2000, walleyes were only sampled until the first week in May. All larval walleyes were collected during April in 2001. Despite low sample sizes in 1999 and 2000, growth rates dif-

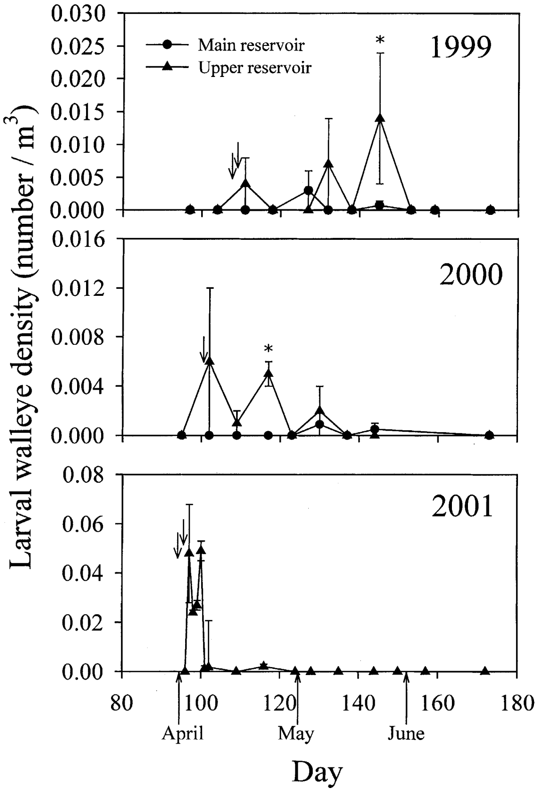

Fig. 1. Mean larval walleye density (number/m^3) by day of the year and habitat type (main reservoir and upper reservoir) collected in Glen Elder Reservoir, Kansas. Error bars represent one standard error. Arrows represent the date of larval walleye stocking in the upper reservoir and asterisks represent a significant difference ($P < 0.05$) between habitat types. Arrows on the *x*-axis represent the first day of each month.

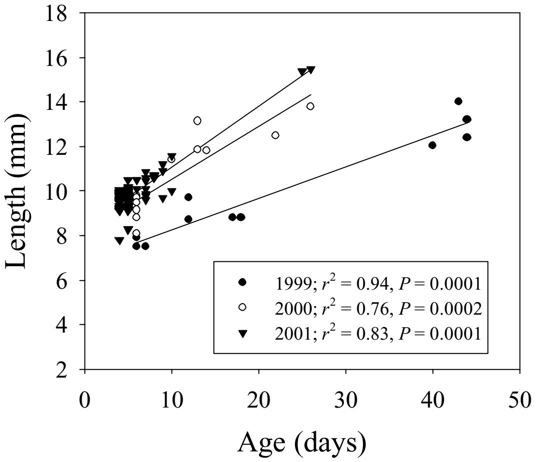

Fig. 2. Length (mm) at age (days) for larval walleyes collected in the upper reservoir of Glen Elder Reservoir, Kansas. Regression lines represent growth models for 2001 (uppermost line; length = 8.32+0.27[age]), 2000 (middle line; length = 8.10+0.24[age]), and 1999 (lowermost line; length = 6.85 + 0.14[age]).

fered between years (ANCOVA; $F_{2,86} = 22.70$, $P = 0.0001$). The slowest growth occurred during 1999, where growth rates were significantly lower than in 2000 and 2001 ($P < 0.0001$). Growth estimates were similar ($P = 0.24$) for walleyes collected in 2000 and 2001 (Fig. 2).

Gizzard shad first appeared in the ichthyoplankton during the middle of May in all 3 years (Fig. 3). Similar to larval walleye densities, the habitat by sampling date interaction for larval gizzard shad density was significant in 1999 ($F_{10,201} = 33.5$, $P = 0.0001$) and 2000 ($F_{8,139} = 19.6$, $P = 0.0001$). On individual sampling dates, larval gizzard shad densities in the upper reservoir were significantly higher ($P = 0.0001$–0.03) than in the main reservoir after their first occurrence in the samples (Fig. 3). Statistical comparisons between years were not conducted due to significant interactions, but larval gizzard shad densities in the upper reservoir were 10-fold higher in 1999 relative to 2000 and 2001 (Fig. 3). Densities in 2001 were generally the lowest of the 3 years and was the only year that exhibited a bimodal distribution in gizzard shad density.

Catch rates of age-0 walleyes during the fall varied between years and was the lowest in 1999 (0 walleyes/NCN) followed by 2000 (5.6 walleyes/NCN) and 2001 (2.1 walleyes/NCN). Historically, catch rates have varied from 0.4 to 36.5 walleyes/NCN in Glen Elder Reservoir (mean ± S.E., 9.8 ± 2.2 walleyes/NCN; 1980–1998). Thus, recruitment of walleyes during 1999 was the lowest observed in almost 20 years, while moderate year classes were produced during 2000 and 2001.

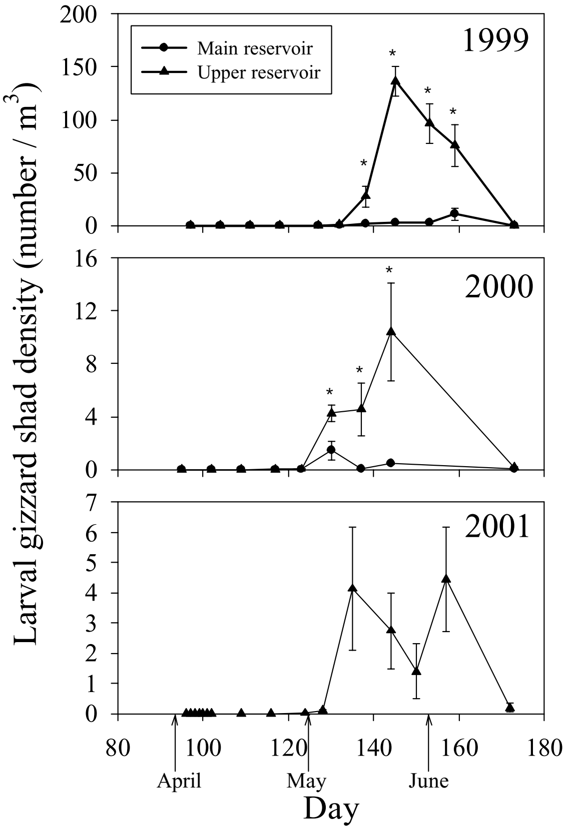

Fig. 3. Mean larval gizzard shad density (number/m^3) by day of the year and habitat type (main reservoir and upper reservoir) collected in Glen Elder Reservoir, Kansas. Error bars represent one standard error and asterisks represent a significant difference ($P < 0.05$) between habitat types. Arrows on the x-axis represent the first day of each month.

3.2. Thermal regime and zooplankton abundance

Temperatures in the upper reservoir were usually 1–2 °C higher than those in the main reservoir (Fig. 4), but differences were not statistically significant between habitats ($P = 0.29$–0.60 by year). During early spring (i.e., April–May), mean water temperatures in the upper reservoir were significantly lower in 1999

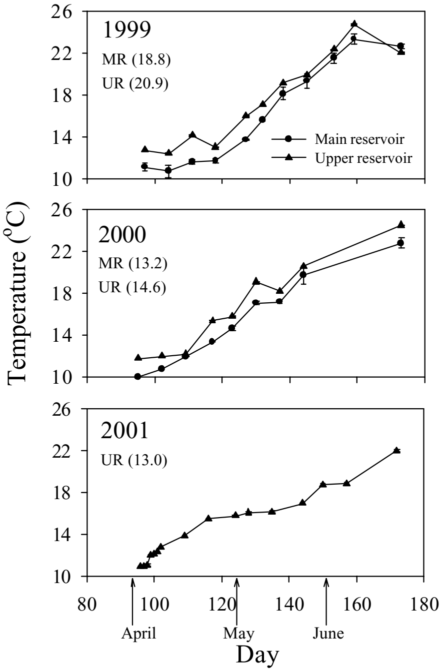

Fig. 4. Mean water column temperature (°C) by day of the year and habitat type (main reservoir [MR] and upper reservoir [UR]) sampled in Glen Elder Reservoir, Kansas. Error bars represent one standard error and numbers in parenthesis represent the coefficient of variation (CV = 100 × standard deviation/mean) of temperature during the time walleyes were collected in the upper water column. Arrows on the *x*-axis represent the first day of each month. Temperature data were not collected in 2001 in the main reservoir.

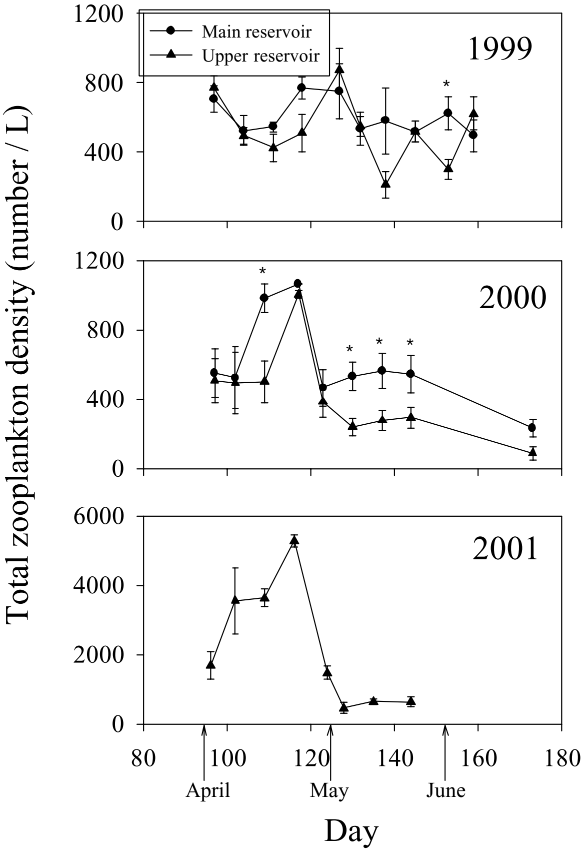

Fig. 5. Total zooplankton density (number/L) by day of the year and habitat type (main reservoir and upper reservoir) collected in Glen Elder Reservoir, Kansas. Error bars represent one standard error and asterisks represent a significant difference ($P < 0.05$) between habitat types. Arrows on the *x*-axis represent the first day of each month.

relative to 2000 and 2001 ($P = 0.02$). Temperatures in the upper reservoir were not different during 2000 and 2001 ($P = 0.64$). During April, the slowest rate of warming occurred in 1999 (0.01 °C/day) followed by 2000 (0.16 °C/day) and 2001 (0.25 °C/day). In addition to lower temperatures and reduced rate of warming, water temperatures were more variable in 1999 compared to 2000 and 2001 (Fig. 4). Moreover, 1999 was the only year that experienced a reduction in temperature prior to 1 May (Fig. 4).

Zooplankton communities were dominated by *Daphnia pulicaria*, *D. mendotae*, *Diaptomis* spp., and *Acanthocyclops* spp. in the main reservoir, and *D. mendotae*, *Acanthocyclops* spp., and Rotifera in the upper reservoir. *D. pulicaria* and *D. mendotae* were the primary daphnids in both habitats across all years. Similar to walleye and gizzard shad densities, total zooplankton and *Daphnia* spp. densities exhibited a significant habitat by date interaction in 1999 (total, $F_{12,264} = 9.5$, $P = 0.001$; *Daphnia* spp., $F_{12,264} = 4.1$, $P = 0.03$) and 2000 (total, $F_{10,180} = 3.7$, $P = 0.04$; *Daphnia* spp., $F_{10,180} = 6.4$, $P = 0.001$). Trends in total zooplankton density were similar between the main and upper reservoir during both years, especially for samples collected prior to May (Fig. 5). Although total zooplankton densities were similar in 1999 and 2000, total zooplankton densities in the upper reservoir were much higher in 2001 due to high densities of rotifers (>3000/l).

Patterns of *Daphnia* spp. abundance were different between the main and upper reservoir in 1999 and 2000 (Fig. 6). *Daphnia* spp. densities were similar

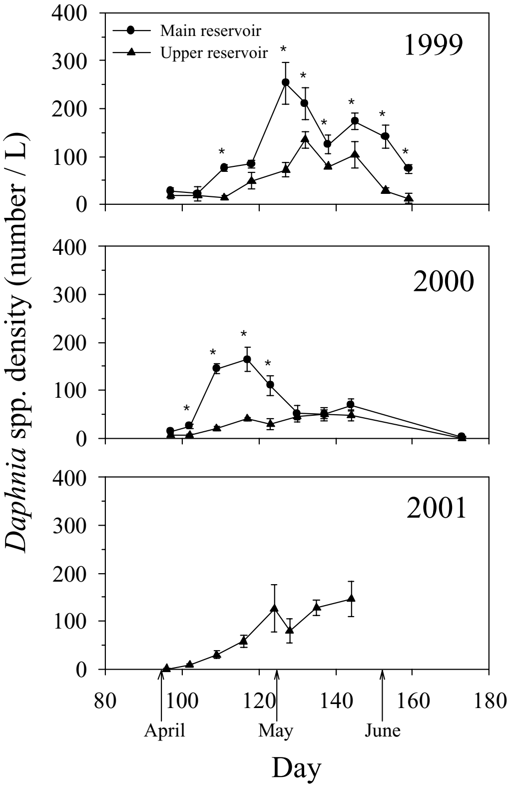

Fig. 6. *Daphnia* spp. density (number/L) by day of the year and habitat type (main reservoir and upper reservoir) collected in Glen Elder Reservoir, Kansas. Error bars represent one standard error and asterisks represent a significant difference ($P < 0.05$) between habitat types. Arrows on the *x*-axis represent the first day of each month.

between the main and upper reservoir during early and mid-April, but then rapidly diverged thereafter. In the main reservoir, *Daphnia* spp. densities increased to over 150 daphnids/l, while increases were more gradual in the upper reservoir. During 2001, *Daphnia* spp. densities in the upper reservoir exhibited a pattern similar to 1999.

4. Discussion

Densities of larval walleyes in Glen Elder Reservoir were substantially lower (<0.1 larvae/m^3) than those reported in other systems (commonly ≥0.3 larvae/m^3) despite similar gears, tow rates, and sampling times (Noble, 1972; Jude, 1992; Mion et al., 1998). Noble (1972) reported that walleye fry were commonly located at depths ≥0.5 m from the surface on windy days and near the surface on calm days. During this study, winds commonly exceeded 40 km/h and may have altered the vertical distribution of walleyes. However, few walleyes were collected even on calm days. Larval walleyes may also move to greater depths during the day or when turbidity is low (Colby et al., 1979). The lack of walleyes collected at night in Glen Elder, and generally high turbidity, suggests that vertical movement due to light penetration was probably not the cause of our low catch rates. Recent investigations suggest that Glen Elder Reservoir supports a low density adult population, which may partially explain the low density of naturally produced walleyes (J. Stephen, Kansas Department of Wildlife and Parks, unpublished information). Larval walleyes are also stocked at a low rate (approximately 500 larvae/ha) relative to other systems which are often stocked at rates exceeding 2500 larvae/ha (Fielder, 1992; Koppelman et al., 1992; Mitzner, 1992). Thus, the density of larval walleyes is probably low in Glen Elder Reservoir due to a low density adult population and low stocking rates. During 2001 when walleyes were sampled daily for 1 week following stocking, larval walleyes were sampled for 5 days after stocking, but were not collected thereafter (except for one fish sampled during the end of April), suggesting high mortality or a change in habitat use. Thus, low densities, coupled with potential changes in the vertical distribution of larval walleyes and high mortality rates, likely resulted in low catch rates during our study. Despite low catch rates of larval walleyes, this study provides important insight on factors influencing walleye recruitment in southern Great Plains reservoirs.

The larval period is considered critical in the life history of many fish species (Blaxter, 1986), especially walleyes (Colby et al., 1979). Similar to other piscivores, walleyes must pass through a planktivorous feeding stage before they can consume fishes (Colby et al., 1979; Carlander, 1997). Thus, the influence of zooplankton abundance on recruitment dynamics of walleyes has been the focus of numerous studies (Li and Mathias, 1982; Graham and Sprules, 1992). Peterson (1997) found a positive relationship between cladoceran zooplankton density (primarily *Daphnia* spp.) and walleye recruitment in several Pennsylvania lakes. Similarly, Fielder (1992) found that low

Daphnia spp. abundance ($\leq$10 daphnids/l) was related to poor recruitment of larval walleyes in Lake Oahe, South Dakota. Although these and other studies (Spykerman, 1974; Colby et al., 1979; Jennings and Philipp, 1992) have found a positive relationship between zooplankton abundance and survival of larval walleyes, others suggest that walleye recruitment is unrelated to zooplankton dynamics. For example, Priegel (1970) found that recruitment of walleyes was not related to crustacean zooplankton abundance in the Lake Winnebago system, Wisconsin. Rather, abiotic conditions (e.g., water level characteristics) explained most of the variation in recruitment. During all 3 years of this study, *Daphnia* spp. densities were less than 50 daphnids/l in the upper reservoir at the time of stocking, well below the 100 daphnids/l recommended by Li and Mathias (1982). In the upper reservoir, Daphnia spp. densities never reached 100 daphnids/l during 2000, but recruitment in 2000 was the highest of the 3 years. Conversely, *Daphnia* spp. densities were often above 100 daphnids/l in 1999, but recruitment was the lowest in 20 years. Main reservoir *Daphnia* spp. densities were almost always above 100 daphnids/l. Although recruitment of naturally produced walleyes may benefit from higher zooplankton densities in the main reservoir, no age-0 fish were collected during the fall of 1999 and 88% of the age-0 walleyes collected during the fall of 2000 were stocked fish (J. Stephen, Kansas Department of Wildlife and Parks, unpublished information). Because walleye survival is often dependent on the composition of zooplankton communities (Mathias and Li, 1982), one hypothesis for explaining these trends is that zooplankton community composition varied between years. However, detailed analysis of zooplankton community characteristics indicated that species composition and size structure were similar among years (R. Bernot, Kansas State University, unpublished information).

In northern systems, yellow perch (*Perca flavescens*) are the primary prey for larval walleyes and relatively predictable predator–prey relationships have evolved (Forney, 1980). Conversely, gizzard shad are highly abundant in reservoirs throughout the midwestern US (Cramer and Marzolf, 1970; Noble, 1981) and are often the most important prey species for age-0 walleyes (Momot et al., 1977; Carlander, 1997). Despite the generally positive influence of age-0 gizzard shad on growth of adult piscivores (Carlander, 1997), gizzard shad commonly have negative effects on members of the larval fish community (Dettmers and Stein, 1992; DeVries and Stein, 1992; Stein et al., 1995; Roseman et al., 1996; Donovan et al., 1997).

Larval gizzard shad can influence zooplankton populations directly by predation or indirectly through competitive herbivory (DeVries and Stein, 1992). Because zooplankton is an important prey item for most larval fishes, competition with age-0 gizzard shad may reduce growth and survival of larval walleyes. However, competition for zooplankton resources is probably important only for walleyes that are stocked or hatch near the time of peak larval gizzard shad abundance. Rather, the availability of larval gizzard shad during the ontogenetic switch to piscivory often influences recruitment of walleyes (Momot et al., 1977; Carlander, 1997). When suitable resources are unavailable or when larval walleyes are unable to switch to piscivory, they will continue to feed on zooplankton or macroinvertebrates, resulting in poor growth and recruitment (Colby et al., 1979; Forney, 1980). Donovan et al. (1997) found that late spawning and low densities of gizzard shad resulted in poor saugeye (*Stizostedion vitreum* × *S. canadense*) survival in Ohio reservoirs. Similarly, Momot et al. (1977) reported that poor survival of naturally produced walleyes was related to the absence of gizzard shad during the ontogenetic shift to piscivory. In Glen Elder Reservoir, gizzard shad densities were over 100 fish/m^3 in 1999. Despite an abundance of larval prey, no age-0 walleyes were collected during fall sampling, suggesting that larval walleyes were unable to prey on larval gizzard shad. Larval walleyes generally switch to piscivory at a length of 20–30 mm (Priegel, 1970; Colby et al., 1979). In 1999, walleyes were relatively small (<20 mm) when gizzard shad were available. Conversely, walleyes would have been large enough (approximately 25–30 mm) to consume larval gizzard shad when they became available during 2000 and 2001. Thus, larval walleyes in Glen Elder Reservoir likely experienced high mortality and reduced growth in 1999 as a direct result of a later stocking date and low spring temperatures, and as an indirect result of competition for prey resources and an inability to consume larval gizzard shad. In addition, the effects of a smaller size in 1999 were likely exacerbated by competitive interactions with highly abundant larval gizzard shad (>100 larvae/m^3 in 1999).

The influence of spring water temperatures on walleye recruitment is well-documented across their distribution (Busch et al., 1975; Serns, 1982; Hansen et al., 1998), including Kansas (Quist, 2002). Although many of these studies suggest that temperature during the incubation period influences recruitment (Busch et al., 1975), others suggest that temperature during the spring is most important for larvae (Serns, 1982). The relationship between variable spring temperatures in Glen Elder Reservoir and poor recruitment in 1999 is consistent with studies that have shown the potential for increased larval mortality with sudden temperature changes (Koenst and Smith, 1976; Hokanson, 1977; Colby et al., 1979). In addition, growth of larval walleyes is directly related to temperature (Colby et al., 1979), suggesting that cool, variable temperatures resulted in reduced growth rates and mediated interactions with larval gizzard shad.

The results of this study illustrate the importance of spring temperatures and prey availability on larval walleyes and have important implications regarding walleye recruitment. Contrary to our predictions, zooplankton densities did not appear to influence survival of larval walleyes, because even though zooplankton densities were similar among years, recruitment of walleyes was variable. Spring temperatures and interactions with larval gizzard shad appeared to have the greatest influence on larval walleye survival. Low temperatures during 1999 resulted in reduced growth of walleyes and an inability to consume larval gizzard shad during their peak abundance. In addition, high densities of larval gizzard shad in 1999 probably resulted in competitive interactions for zooplankton resources, potentially causing even further reductions in growth and survival of larval walleyes.

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