Recruitment dynamics of walleyes (*Stizostedion vitreum*) in Kansas reservoirs: generalities with natural systems and effects of a centrarchid predator

Michael C. Quist, Christopher S. Guy, and James L. Stephen

Abstract: Knowledge of factors influencing recruitment dynamics of walleyes (*Stizostedion vitreum*) in different systems and regions is important for developing a better understanding of walleye ecology. Therefore, we investigated associations among walleye recruitment and climatic, water-level, and biotic characteristics in four Kansas reservoirs during 1985–1999. Walleye recruitment was positively related to spring storage ratios and temperatures and negatively associated with spring water levels and abundance of 130- to 199-mm white crappies (*Pomoxis annularis*). The influence of juvenile white crappie predation on larval walleyes was examined by conducting a manipulative experiment. Regardless of zooplankton density or water clarity, mortality of larval walleyes resulting from white crappie predation was over 90%. Based on our empirical and experimental results, we propose a biotic–abiotic confining hypothesis (BACH) to explain abiotic and biotic effects on walleye recruitment dynamics. Specifically, high variability in walleye recruitment was observed during years with low densities of 130- to 199-mm white crappies and likely resulted from the effects of abiotic factors. When white crappie abundance was high, walleye recruitment was low and exhibited little variability, suggesting that white crappies can have an overriding influence on walleye recruitment regardless of abiotic conditions.

Résumé : Une connaissance des facteurs qui influencent la dynamique du recrutement des dorés jaunes (*Stizostedion vitreum*) dans divers systèmes et régions est nécessaire pour mieux comprendre l'écologie de ce poisson. Nous avons donc étudié les associations entre le recrutement du doré et les caractéristiques du climat et du niveau de l'eau, ainsi que les caractéristiques biotiques, dans quatre réservoirs du Kansas de 1985 à 1999. Le recrutement du doré est en relation positive avec les coefficients de stockage au printemps et les températures et en relation négative avec les niveaux d'eau au printemps et l'abondance des mariganes blanches (*Pomoxis annularis*) de 130–199 mm. Une expérience de manipulation a permis de déterminer l'influence de la prédation des jeunes mariganes sur les larves de dorés. Quelle que soit la densité du zooplancton ou la clarté de l'eau, la mortalité des larves de dorés due aux mariganes est supérieure à 90 %. D'après nos résultats empiriques et expérimentaux, nous proposons une hypothèse BACH (hypothèse contraignante biotique–abiotique) pour expliquer les effets abiotiques et biotiques sur la dynamique de recrutement des dorés. Plus spécifiquement, il y a une forte variabilité dans le recrutement des dorés durant les années de faible abondance de mariganes de 130–199 mm qui résulte sans doute des effets des facteurs abiotiques. Lorsque l'abondance des mariganes est élevée, le recrutement des dorés est faible et peu variable, ce qui fait croire que les mariganes ont une influence prépondérante sur le recrutement des dorés, quelles que soient les conditions abiotiques.

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Introduction

The mechanisms whereby similar species coexist remain under debate (Huisman and Weissing 2000). Many researchers suggest that if species are too similar in resource use, they cannot coexist indefinitely and species that do coexist in nature do so by partitioning resources (Vermeij 1994). One of the important theories regarding the coexistence of species is

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that enemy-related (i.e., competitors and predators) adaptations have brought about long-term evolutionary trends in organisms such that competition and predation are reduced (Vermeij 1994; Huisman and Weissing 2000). These adaptations may include differing morphologies and habitat use or changes in the timing of major life history events (e.g., spawning, diet shifts) that allow for resource partitioning (Werner and Gilliam 1984). If species are able to coexist because of their long evolutionary histories, then an obvious question arises in systems where species have been introduced into unique habitats and communities — how do competitors and predators interact when they have little or no history of co-occurrence?

In natural lake and river ecosystems, a dynamic equilibrium has developed over thousands of years among the physical, chemical, and biological characteristics of the system (Noble 1986). Consequently, fish communities are well structured in natural systems provided that there has been a long evolutionary history of predator and prey assemblages (MacLean and Magnuson 1977). Conversely, reservoirs are typically less than 70 years old (Thornton et al. 1990) and represent novel habitats for fishes. Most reservoirs in the U.S. are concentrated in southern latitudes, whereas most natural lakes are located in the northern glaciated regions; therefore, reservoirs tend to be warmer and shallower than natural lakes and have longer growing seasons (Thornton et al. 1990). Reservoirs also tend to display high nutrient and sediment inputs and experience frequent water-level fluctuations. In addition to unique abiotic conditions, reservoir fish communities usually consist of species with little or no evolutionary history of co-occurrence.

Walleyes (*Stizostedion vitreum*), white crappies (*Pomoxis annularis*), white bass (*Morone chrysops*), and gizzard shad (*Dorosoma cepedianum*) are important consumers in aquatic systems throughout much of North America. The native distribution of walleyes is generally limited to the natural lakes and rivers of Canada and the northern U.S. (Colby et al. 1979; Carlander 1997), whereas that of white crappies, white bass, and gizzard shad encompasses the midwestern and southern U.S. (Lee et al. 1980). After the completion of large-scale reservoir construction during the 1940s to 1970s, introductions expanded the distribution of walleyes to include most of North America (Carlander 1997). Because the ontogeny of walleyes has been shaped by their long evolutionary history with the chemical, physical, and biological characteristics of natural lakes and rivers (MacLean and Magnuson 1977), understanding how walleye populations respond to the unique abiotic conditions and biotic interactions in reservoirs is important for predicting population and community dynamics.

Recruitment is often cited as the governing and most variable component of fish population dynamics (Gulland 1982). Thus, understanding mechanisms responsible for variations in recruitment of walleyes has been the focus of many applied and basic ecological studies (Colby et al. 1979; Carlander 1997; Hansen et al. 1998). Although previous studies have been conducted in a variety of ecosystems (e.g., natural lakes, rivers, reservoirs), several generalizations have emerged regarding the factors affecting walleye recruitment dynamics. The most common factors associated with walleye recruitment variability are water temperature, wind, and water-level characteristics (Colby et al. 1979; Carlander 1997). For example, spring temperatures may influence walleye recruitment dynamics by altering the time of spawning, duration of egg incubation, or the growth of larvae (Busch et al. 1975; Colby et al. 1979). Prolonged incubation periods may expose eggs to high winds, causing dislodgement or stranding of eggs (Busch et al. 1975). Wind-generated water currents may also concentrate larvae in habitats that are unsuitable for growth and survival (Noble 1972). In addition to abiotic constraints, biotic interactions, such as competition, cannibalism (Forney 1980), and interspecific predation (Schiavone 1985), may have a negative effect on walleye recruitment.

Although recruitment dynamics of walleyes have been extensively studied, most of our knowledge has emerged from research on native populations in natural systems (Colby et al. 1979; Carlander 1997). Comparatively few studies on walleye recruitment have been conducted in systems outside their native distribution, despite the importance of understanding how introduced walleye populations respond to abiotic conditions and biotic interactions characteristic of reservoirs. Therefore, the objectives of this study were to examine the importance of abiotic factors and biotic interactions on walleye recruitment in several southern Great Plains reservoirs. Specifically, we investigated the influence of climatic factors and water-level characteristics on walleye recruitment dynamics to determine if the same factors (e.g., thermal and water-level characteristics) that are important for walleye recruitment in native populations can be generalized to Kansas reservoirs. Intraspecific and interspecific interactions (i.e., white crappie, white bass, gizzard shad) were examined to determine the role of biotic factors on walleye recruitment dynamics. In addition, a manipulative experiment was conducted to identify mechanisms that influence larval walleye survival in the presence of white crappies.

Materials and methods

Study area

We selected four Kansas reservoirs (Table 1) as our study system based on their similarity to reservoirs throughout Kansas and availability of long-term information. Walleyes were introduced to Kansas reservoirs in the 1940s and are currently one of the most popular sport fish in Kansas. Kansas reservoirs are unique systems with respect to the ecology of walleyes, not only because they are artificial, but also because the highly variable climate of the southern Great Plains results in frequent water-level fluctuations and high summer water temperatures (i.e., >30°C; Quist et al. 2002). Nearly all of the reservoirs are U.S. Bureau of Reclamation projects and are used for flood control and irrigation. Similar to other Great Plains reservoirs (Thornton et al. 1990), the study reservoirs are shallow and turbid and rarely thermally stratify because of persistent, high winds. Sport fish populations are dominated by white bass, walleyes, white crappies, and channel catfish (*Ictalurus punctatus*). Gizzard shad are the primary prey species in all reservoirs (Quist et al. 2002).

Biotic interactions and abiotic conditions

Fish populations were sampled yearly in each reservoir from 1985 to 1999 using standardized fall (i.e., October and November) samples. Catch rates of walleyes (age 0, <300 mm; age 1 and older, >300 mm; Quist et al. 2003),

Table 1. Surface area (SA; ha), mean depth (m), watershed area (WA; km^2), and shoreline development index (SDI) for Kansas reservoirs used in analysis of walleye recruitment variation during 1985–1999.

Reservoir	SA	Depth	WA	SDI
Glen Elder	5093	5.8	17 702	3.9
Kirwin	2055	5.9	3 540	3.7
Webster	1513	6.6	2 978	5.8
Wilson	3642	8.8	4 965	7.5

Note: SDI = shoreline length/$(2(\mathrm{SA} \times \pi)^{1/2}$.

white bass (age 0, <250 mm; age 1 and older, >250 mm; Guy et al. 2002), and adult gizzard shad (age 1 and older, >125 mm; Quist et al. 2001) were calculated from gill net complements (catch-per-unit-effort (CPUE) = number per gill net complement night (NCN); Table 2). One gill net complement consisted of four separate gill nets (30.5 m long × 2.4 m deep sinking gill nets), each with a different mesh size (2.5-, 3.8-, 6.4-, and 10.2-cm bar-measure mesh). All gill net complements were set during the evening and allowed to fish until the following morning. Recruitment of walleyes was assessed using CPUE of age-0 walleyes. Preliminary analysis determined that CPUE of age-0 walleyes provides an excellent index for recruitment to later ages (CPUE of age-1 walleyes in year $t + 1 = \beta_0 + \beta_1 \times$ CPUE age-0 walleyes in year t; $r^2 = 0.74$ to 0.96, $P = 0.05$ to 0.007 by reservoir). Similar results were reported by Willis and Stephen (1987) for Kansas reservoirs.

Abundance of white crappies and juvenile gizzard shad (age 0, <125 mm; Quist et al. 2001) was assessed using data from fall trap net samples (CPUE = number per trap net night (TNN); Table 2). Trap nets (1.2 m × 1.5 m frame; 15.2 m long × 1.8 m deep lead) were fished overnight during October and November. Trap nets with 2.5-cm mesh were the standard gear for sampling white crappies in all reservoirs until 1985 and are currently used intermittently in a few reservoirs; however, we limited our analysis to white crappies sampled in trap nets with 1.3-cm mesh (i.e., 1985–1999). CPUE of white crappies was refined by calculating CPUE by length category (Table 2). These length categories correspond to age-0 (<130 mm), age-1 (130–199 mm), and age-2 and older (>200 mm) white crappies (M.C. Quist, unpublished data).

Precipitation ($\mathrm{mm \cdot day^{-1}}$), air temperature (°C), and wind speed ($\mathrm{m \cdot s^{-1}}$) data were obtained from National Oceanic and Atmospheric Administration weather stations in Russell, Kansas. Distance from the study reservoirs to the weather station varied from 40 to 140 km (mean ± standard error (SE); 90.1 ± 21.4 km). Climatic data were summarized by time period: month, season (winter = December through February, spring = March through May, summer = June through August, fall = September through November), and year (Table 2). Reservoir elevation (metres above mean sea level (m msl)) and outflow ($\mathrm{m^3 \cdot s^{-1}}$) data were obtained from the U.S. Army Corps of Engineers and U.S. Bureau of Reclamation. Reservoir elevations and storage ratios (SR = volume at conservation pool/reservoir discharge volume) were also summarized by month, season, and year.

Multiple regression analysis was used to explore factors related to walleye recruitment dynamics. CPUE of age-0 walleyes (i.e., $\log_{10}$(CPUE +1)) was plotted against abiotic and biotic (i.e., $\log_{10}$(CPUE +1)) data to determine which variables exhibited trends with walleye recruitment in each reservoir. After potentially important variables were identified, stepwise multiple-regression analysis was conducted for each reservoir using a backward selection procedure (Ott 1993). Although the selection procedure was used to identify the best model for each reservoir (i.e., highest R^2), other variables not included in the selection procedure were iteratively added to each model to examine their contribution. The contribution of individual variables was then tested using F tests, and regression equations were limited to variables that contributed significantly ($P < 0.05$) to the model. Each model was also compared with a reduced model (e.g., four-variable model versus three-variable model) using an F test based on reductions in the residual sums of squares (Milliken and Johnson 1992):

$$F = [(\mathrm{RSS}_{\mathrm{red}} - \mathrm{RSS}_{\mathrm{full}})/(\mathrm{df}_{\mathrm{red}} - \mathrm{df}_{\mathrm{full}})](\mathrm{RSS}_{\mathrm{full}}/\mathrm{df}_{\mathrm{full}})^{-1}$$

where RSS represents residual sums of squares for the reduced ($\mathrm{RSS}_{\mathrm{red}}$) and full ($\mathrm{RSS}_{\mathrm{full}}$) models and df is degrees of freedom (df = sample size – number of parameters – 1) of the reduced ($\mathrm{df}_{\mathrm{red}}$) and full ($\mathrm{df}_{\mathrm{full}}$) models. The F value is compared with $F_{[0.05,1,\mathrm{df}_{\mathrm{full}}]}$ to test the null hypothesis that the reduced model is significantly better than the full model. Multicollinearity was assessed by examining tolerance values and variance inflation factors as recommended by Sokal and Rohlf (1995). Multicollinearity was not observed among variables in any of the final models. In addition to developing regression models separately for each reservoir, an overall model using data from all reservoirs was developed using standardized values (i.e., z scores) of each variable (Ott 1993). In the final regression models, squared partial correlation coefficients (r^2_{partial}) were estimated as sums of squares for the variable (SS) divided by the error sums of squares (SSE) plus the sums of squares for the variable (i.e., $r^2_{\mathrm{partial}} = \mathrm{SS}(\mathrm{SSE} + \mathrm{SS})^{-1}$; Freund and Littell 1991).

Mesocosm experiment

The influence of juvenile white crappie predation on walleye survival was examined by conducting a manipulative experiment. Experiments were conducted at Milford Fish Hatchery (MFH; Junction City, Kansas) in cylindrical, polyethylene mesocosms (2.2 m diameter × 1.1 m deep; 4190-L capacity). Although the primary purpose of the experiment was to determine if juvenile white crappie consume larval walleyes, we were secondarily interested in the effect of reduced water clarity and alternative prey (i.e., zooplankton) densities as a buffer against predation. Larval walleyes were obtained directly from MFH, whereas water, zooplankton, and white crappies were obtained from the MFH supply lake. The MFH supply lake is a 41-ha reservoir used primarily as a water source for fish hatchery operations, but it also provides a recreational fishery because of abundant white crappie, channel catfish, and white bass populations.

Three zooplankton treatments (low, intermediate, and high) were examined. The low zooplankton density treatment reflected ambient zooplankton densities of the MFH supply

Table 2. Abiotic and biotic variables used to examine relationships in walleye recruitment in four Kansas reservoirs during 1985–1999.

Variable	Temporal scale	Statistics
Abiotic		
Temperature	Month, season, year	Mean, CV, warming rate
Reservoir elevation	Month, season, year	Mean, CV
Precipitation	Month, season, year	Mean, CV
Wind speed	Month, season	Mean, CV
Biotic		
Walleye ≥300 mm	Fall sampling	Gill net CPUE
White crappie <130 mm	Fall sampling	Trap net CPUE
White crappie 130–199 mm	Fall sampling	Trap net CPUE
White crappie ≥200 mm	Fall sampling	Trap net CPUE
White bass <250 mm	Fall sampling	Gill net CPUE
White bass >250 mm	Fall sampling	Gill net CPUE
Gizzard shad <125 mm	Fall sampling	Trap net CPUE
Gizzard shad >125 mm	Fall sampling	Gill net CPUE

Note: Abiotic variables were summarized by estimating the mean and coefficient of variation (CV = $100\cdot\text{std.dev.}\cdot\text{mean}^{-1}$) by month, season (winter = December through February, spring = March through May, summer = June through August, and fall = September through November), and year. Abiotic variables included air temperature (°C), reservoir elevation (metres above mean sea level), precipitation (mm), and wind speed ($\text{m}\cdot\text{s}^{-1}$). Warming rate was estimated as the temperature change per day ($°\text{C}\cdot\text{day}^{-1}$) between 1 April and 15 May. Biotic data represent catch-per-unit-effort in gill nets (CPUE = fish per gill net complement night) or trap nets (CPUE = fish per trap net night).

lake, whereas elevated densities (i.e., intermediate and high treatments) were obtained by adding zooplankton collected with a conical net (0.5 m diameter × 1.5 m long, 500-μm mesh) towed for either 5 min (intermediate treatment) or 10 min (high treatment). Zooplankton treatments were randomly assigned to each of the mesocosms, and two juvenile white crappies (157.9 ± 5.4 mm) were stocked into each mesocosm. White crappies were allowed to acclimate for at least 24 h before the addition of larval walleyes. After 24 h, 10 larval walleyes (7.1 ± 0.6 mm) were added to each mesocosm. The experiment ran for 8 h and then white crappies were removed and euthanatized. The stomach from each white crappie was removed and preserved in 10% formalin to confirm predation on larval walleyes. Mesocosms were drained through 500-μm mesh to retrieve remaining walleyes. Zooplankton samples were collected before stocking walleyes using a conical plankton net (0.1 m diameter × 0.3 m long, 80-μm mesh) and preserved in 70% ethanol. Zooplankton were enumerated by counting all organisms in a 5-mL subsample. Water temperature (°C) and dissolved oxygen ($\text{mg}\cdot\text{L}^{-1}$) were measured twice during the experiment using a multiprobe (model 85; Yellow Springs, Inc., Yellow Springs, Ohio) and turbidity (nephelometric turbidity units (NTU)) was measured before stocking walleyes in each mesocosm using a turbidimeter (model 2100P; Hach Company, Loveland, Colo.). Control experiments were conducted using the same methods except that white crappies were not added to mesocosms. Each treatment was replicated seven times.

Multivariate analysis of variance (MANOVA; Johnson 1998) was first used to determine if the dependent variables (mean zooplankton densities (number per litre of total zooplankton and *Daphnia* spp.), turbidity) differed among treatments (i.e., low, intermediate, and high zooplankton density). One-way analysis of variance (ANOVA) was performed on each variable because the MANOVA indicated that treatments were different for one or more of the variables (Wilks' $\lambda = 0.01$, $F_{[8,30]} = 30.4$, $P = 0.0001$; Milliken and Johnson 1992; Johnson 1998). When one-way ANOVA models were significant, multiple comparisons were conducted using least-squares means. Differences in mean walleye mortality, expressed as a proportion (%), were assessed using a Kruskal–Wallis test.

Results

Empirical associations

Walleye recruitment was related to a variety of abiotic and biotic variables among reservoirs (Table 3). A significant four-variable model was developed for all reservoirs except Wilson Reservoir; however, the four-variable model did not provide a significantly better fit than the three-variable model for each reservoir ($F_{[1,7 \text{ to } 9]} = 0.99–4.40$, $P < 0.05$). Similarly, three-variable models provided a significantly better fit than two-variable models in each reservoir ($F_{[1,8 \text{ to } 10]} = 4.33–11.08$, $P < 0.05$). In Glen Elder and Webster reservoirs, walleye recruitment was positively associated with spring storage ratio and negatively related to spring elevation and catch rates of 130- to 199-mm white crappies (Table 3). Based on the squared partial correlation coefficients, spring storage ratio appeared to have the largest influence on the model for Glen Elder, followed by spring elevation and juvenile white crappie abundance. In Kirwin and Wilson reservoirs, high catch rates of age-0 walleyes occurred during years with warm spring temperatures, high storage ratio, and low catch rates of 130- to 199-mm white crappies (Table 3). White crappie abundance and spring storage ratios had the highest squared partial correlation values, followed by mean spring temperatures in both reservoirs. When data from all reservoirs were combined, high walleye recruitment was related to high spring storage ratios and low abundance of

Table 3. Multiple regression models developed to assess factors influencing catch-per-unit-effort (CPUE = fish per gill net complement night) of age-0 walleyes (WAE = $\log_{10}$(CPUE + 1)) in four Kansas reservoirs during 1985–1999.

	r^2_{partial}					Model statistics		
Model	Temp.	Wind	WHC	SR	Elev.	RSS	R^2	P
Glen Elder Reservoir (N = 12)								
WAE = –118.378 + 0.047(Temp.) – 0.216(WHC) + 1.338 (SR) – 0.260(Elev.)	0.15		0.22	0.55	0.43	0.121	0.68	0.045
WAE = –101.459 – 0.211(WHC) + 1.228(SR) – 0.221(Elev.)[a]			0.32	0.56	0.42	0.191	0.66	0.026
WAE = –56.8761 + 0.611(SR) – 0.129(Elev.)				0.15	0.06	0.370	0.15	0.27
WAE = 0.714 + 0.387(SR)						0.489	0.10	0.20
Kirwin Reservoir (N = 13)								
WAE = 8.132 + 0.115(Temp.) – 0.289(Wind) – 0.378(WHC) + 0.003(SR)	0.29	0.21	0.72	0.42		0.675	0.74	0.007
WAE = 9.926 + 0.148(Temp.) – 0.477(WHC) + 0.004(SR)[a]	0.27		0.65	0.48		0.759	0.71	0.008
WAE = 8.211 – 0.467(WHC) + 0.003(SR)			0.32	0.47		1.297	0.52	0.01
WAE = 7.049 – 0.346(WHC)						2.680	0.15	0.19
Webster Reservoir (N = 14)								
WAE = –118.138 + 0.274(Temp.) – 1.221(WHC) + 0.007(SR) – 0.203(Elev.)	0.48		0.67	0.72	0.54	0.830	0.70	0.01
WAE = –87.340 – 0.835(WHC) + 0.008(SR) – 0.154(Elev.)[a]			0.48	0.48	0.27	1.061	0.65	0.01
WAE = 1.163 – 0.744(WHC) + 0.003(SR)			0.36	0.45		2.237	0.44	0.02
WAE = 0.706 + 0.002(SR)						3.196	0.21	0.02
Wilson Reservoir (N = 14)								
WAE = –0.593 + 0.116(Temp.) – 0.693(WHC) + 0.649(SR)	0.27		0.53	0.55		0.450	0.66	0.038
WAE = 0.515 – 0.434(WHC) + 0.731(SR)[a]			0.37	0.60		0.645	0.59	0.007
WAE = 0.582 + 0.419(SR)						1.080	0.16	0.053
All reservoirs								
WAE = 10.220 + 1.884(Temp.) – 0.135(WHC) + 0.134(SR)	0.04		0.10	0.22		12.541	0.31	0.003
WAE = 18.799 – 0.154(WHC) + 0.082(SR)[a]			0.09	0.23		12.616	0.29	0.002
WAE = 13.873 + 0.125(SR)						15.431	0.13	0.004

Note: Independent variables include mean spring (March through May) temperature (Temp., °C), mean spring wind speed (Wind, m·s^{-1}), catch-per-unit-effort (CPUE = fish per trap net night) of 130- to 199-mm white crappies (WHC = $\log_{10}$(CPUE + 1)), spring storage ratio (SR = volume at conservation pool/reservoir discharge volume), and mean spring elevation (Elev., m). The best four-, three-, two-, and one-variable models (i.e., lowest residual sums of squares and highest R^2) are provided for each reservoir. Squared partial correlation coefficients (r^2_{partial}) and model statistics (RSS = residual sums of squares, R^2 = adjusted coefficient of determination) are provided for each model.

[a] The best model based on comparisons of residual sums of squares.

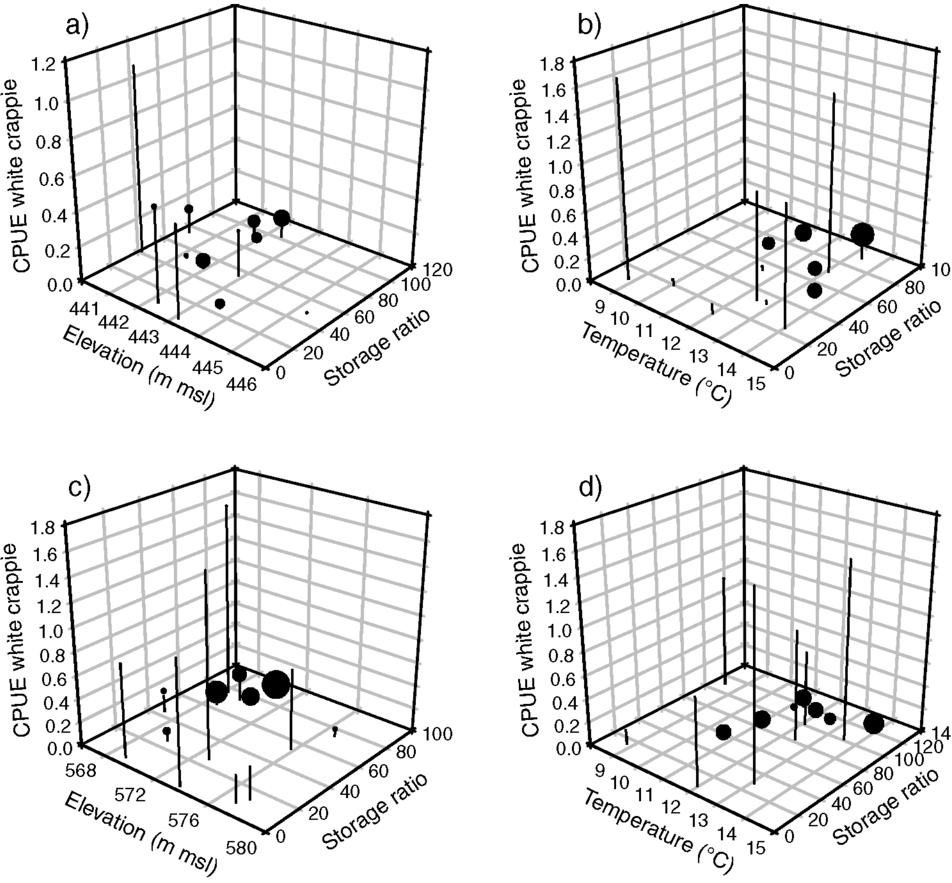
130- to 199-mm white crappies (Table 3). Regardless of abiotic conditions, walleye recruitment was low when juvenile white crappies were abundant (Fig. 1). For example, in Kirwin and Wilson reservoirs, years with high spring storage ratios and warm spring temperatures should have produced high catch rates of age-0 walleyes, but this was not observed when juvenile white crappie densities were high (Fig. 1). A similar relationship was observed using information from all reservoirs (Fig. 2). Therefore, white crappies appeared to have an overriding influence on walleye recruitment when juvenile white crappie densities were high.

Mesocosm experiment

Results from the mesocosm experiment corroborated the empirical observations. Water temperatures in the mesocosms averaged 15.5°C (SE = 0.1°C) and dissolved oxygen was above 8 mg·L^{-1} (9.6 ± 0.1 mg·L^{-1}) during the experiment. Zooplankton communities in the low zooplankton treatment were dominated by copepod nauplii (mean frequency by number ± SE; 64.8 ± 0.5%), whereas *Daphnia* spp. (primarily *D. pulicaria* and *D. galeata*) dominated communities in the intermediate (53.0 ± 3.6%) and high (80.5 ± 0.9%) treatments. *Bosmina* spp. were common in all treatments and averaged 8.6% by number (SE = 2.4). Total zooplankton ($F_{[2,18]}$ = 36.5, P = 0.001; low = 43.4 ± 3.6 zooplankton·L^{-1}, intermediate = 91.9 ± 6.2 zooplankton·L^{-1}, high = 187.5 ± 19.7 zooplankton·L^{-1}) and *Daphnia* spp. densities ($F_{[2,18]}$ = 60.5, P = 0.0001; low = 3.4 ± 0.9 *Daphnia*·L^{-1}, intermediate = 53.2 ± 4.0 *Daphnia*·L^{-1}, high = 148.2 ± 15.8 *Daphnia*·L^{-1}) were significantly different among treatments and were almost 50 times higher in the high zooplankton treatment than in the low zooplankton treatment. Similar to zooplankton densities, turbidity differed among treatments ($F_{[2,18]}$ = 603.8, P = 0.0001; low = 20.1 ± 1.8 NTU, intermediate = 36.0 ± 0.5 NTU, high = 60.4 ± 1.2 NTU), indicating that our method of supplementing zooplankton not only elevated zooplankton densities, but also significantly reduced water clarity.

Control experiments without white crappies indicated that retrieval of larval walleyes averaged 90% (SE = 5.8%; Fig. 3). Therefore, missing walleyes were assumed to have been consumed by white crappies. Walleye mortality averaged 93.6% (SE = 0.9) and did not differ among treatments (Kruskal–Wallis statistic, H = 2.8, df = 2, P = 0.29). White crappie diets were dominated by *Daphnia* spp. (frequency of occurrence = 96%), but the presence of walleyes in white

Fig. 1. Relationships between catch-per-unit-effort (CPUE = fish per trap net night) of 130- to 199-mm white crappies (*Pomoxis annularis*; CPUE white crappie = $\log_{10}(\mathrm{CPUE} + 1)$), mean spring (March through May) elevation (metres above mean sea level (msl)), spring storage ratio (SR = volume at conservation pool/reservoir discharge volume), mean spring temperature (°C), and catch-per-unit-effort (CPUE = fish per gill net complement night) of age-0 walleyes (*Stizostedion vitreum*; CPUE = $\log_{10}(\mathrm{CPUE} + 1)$) in (*a*) Glen Elder, (*b*) Kirwin, (*c*) Webster, and (*d*) Wilson reservoirs, Kansas, during 1985–1999. Symbol size is directly proportional to $\log_{10}(\mathrm{CPUE} + 1)$ of age-0 walleyes, with large symbols representing high catch rates and small symbols representing low catch rates of age-0 walleyes.



crappie stomachs (frequency of occurrence = 53%) confirmed consumption of walleyes.

Discussion

Knowledge of factors associated with recruitment variability across a variety of systems and regions is important for a complete understanding of walleye ecology and for predicting the response of walleye population dynamics to changes in abiotic conditions (e.g., water-level alterations, elevated thermal regimes) and biotic interactions (e.g., species introductions or losses). Understanding these factors is especially important in reservoirs where species have no evolutionary history with the abiotic conditions and little or no history of co-occurrence with members of reservoir fish assemblages, especially in the southern Great Plains where the highly variable climate results in marginal walleye habitat (e.g., high summer temperatures). Despite differences among aquatic systems (i.e., lotic, lentic, and reservoir) and regions, several generalizations have emerged from the results of previous research and our study.

The most important abiotic factors associated with recruitment of walleyes across their distribution appear to be temperature, wind, and water-level characteristics during the spring. Busch et al. (1975) and Madenjian et al. (1996) found that temperature warming rate during spring was related to walleye recruitment in Lake Erie. Hansen et al. (1998) found that variation in temperature during May partially explained walleye recruitment dynamics in Escanaba Lake, Wisconsin. Although we expected that spring warming rate or variation in temperature would be related to walleye recruitment, only mean temperature was related to catch rates of age-0 walleyes in Kansas reservoirs. Water temperatures are influenced by a variety of factors in addition to air temperature, such as precipitation or reservoir inflow. Thus, our measure of temperature (i.e., air temperature) was probably insensitive to small differences in the rate of warming or variation in water temperatures. For instance, water temperatures in Glen Elder Reservoir during the spring of 1999 were highly variable and exhibited a slow rate of warming compared with 2000 and 2001 (Quist 2002). Although mean air and water temperatures have been known to be highly correlated for Kansas reservoirs (Quist et al. 2002), air temperature failed to display large differences in warming rates or temperature variability. However, air temperatures were about 4°C lower in 1999 relative to 2000 and

Fig. 2. Relationship between catch-per-unit-effort (CPUE = fish per trap net night) of 130- to 199-mm white crappies (*Pomoxis annularis*; CPUE white crappie = $\log_{10}$(CPUE + 1)), spring storage ratio (SR = volume at conservation pool/reservoir discharge volume), and catch-per-unit-effort (CPUE = fish per gill net complement night) of age-0 walleyes (*Stizostedion vitreum*; CPUE = $\log_{10}$(CPUE + 1)) in all four Kansas reservoirs during 1985–1999.

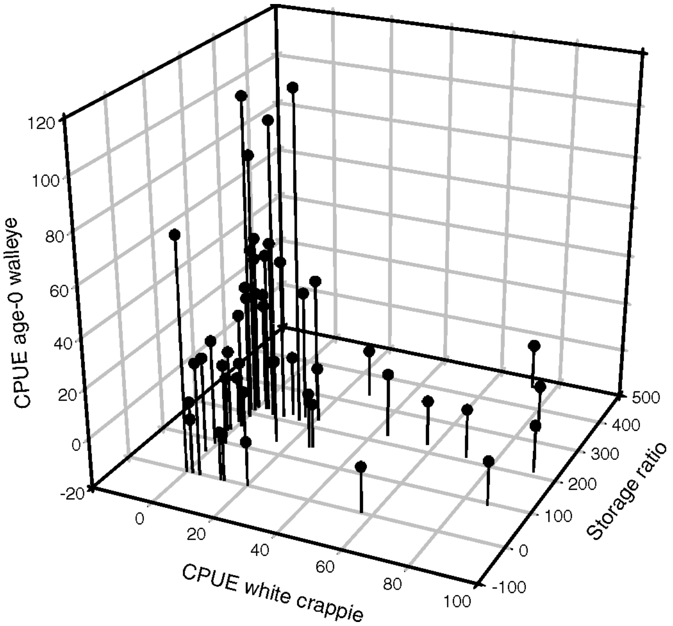
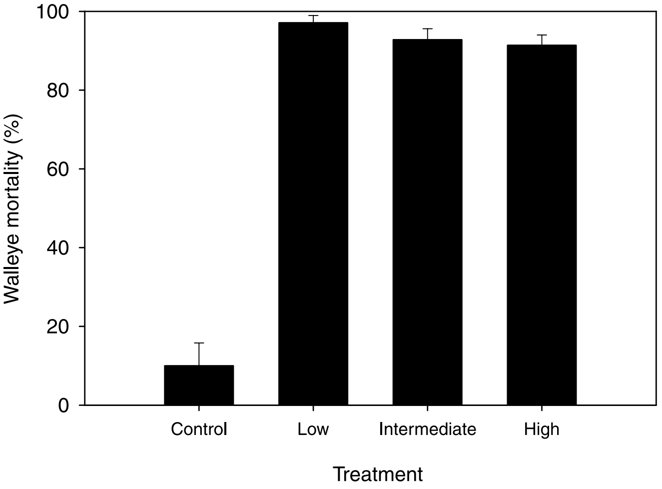


Fig. 3. Mean walleye mortality (%) owing to predation of juvenile white crappies (*Pomoxis annularis*) at three zooplankton treatments. Error bars represent 1 SE. Walleye mortality in the low, intermediate, and high zooplankton treatments was not significantly different ($P = 0.29$).



2001, suggesting that our surrogate measure of water temperature may not only reflect lower mean water temperatures, but also slower warming rates or higher variability. Regardless, weak walleye year classes were produced during years with low mean air temperatures during the spring, which may have caused extended incubation times resulting in prolonged risk of egg predation, increased exposure to the effects of wind (Houde 1969; Busch et al. 1975), or reduced growth and survival of larvae (Colby et al. 1979).

In addition to climatic factors, we found that walleye recruitment was related to low spring elevations and high spring storage ratios. Willis and Stephen (1987) found a similar relationship between walleye recruitment and storage ratio in several Kansas reservoirs and suggested that loss of walleyes during high discharge events (i.e., low storage ratio) was the dominant mechanism. Although direct loss of walleyes may be an important factor during extremely high discharge events, our study suggests that strong walleye year classes were only produced during years with both high storage ratios and low elevations. During years with low elevations and high storage ratios, we observed relatively small (i.e., ≤1.5 m) increases in water levels. Chevalier (1977) reported similar results, where small increases in water level (i.e., 1–2 m) were important for recruitment of walleyes in Rainy Lake, Minnesota and Ontario. Water-level increases less than 1 m were related to high recruitment of walleyes in lakes from Voyageurs National Park, Minnesota (Kallemeyn 1987). Similar results have been reported for Missouri River reservoirs, where small, gradual increases in reservoir elevation were important for walleye recruitment (Nelson and Walburg 1977). The specific mechanisms responsible for the trends observed in our study are unknown, but previous research suggests that walleye recruitment may be enhanced by small increases in water levels by either increased quantity and quality of spawning habitat or indirectly by increased production of prey species (Chevalier 1977; Nelson and Walburg 1977).

Walleye recruitment is undoubtedly influenced by abiotic constraints across their distribution; however, interactions with other members of the fish community may have an overriding influence on walleye recruitment dynamics. Competition and cannibalism have been shown to influence walleye recruitment in a variety of systems (Colby et al. 1979). Interspecific predation by endemic species such as smallmouth bass (*Micropterus dolomieu*; Johnson and Hale 1977), yellow perch (*Perca flavescens*; Mion et al. 1998), and sauger (*Stizostedion canadense*; Swenson and Smith 1976) may also influence walleye recruitment in natural systems. If predation by endemic species can influence recruitment of walleyes in natural systems, we would expect biotic interactions to be as important in systems with introduced species. In our study, the abundance of adult walleyes, white bass, and gizzard shad were unrelated to walleye recruitment. Contrary to many other systems (e.g., Forney 1980), cannibalism does not appear to influence recruitment dynamics of walleyes. Quist et al. (2002) examined the stomach contents of 247 walleyes from Glen Elder Reservoir and no evidence of cannibalism was observed. Although gizzard shad may negatively influence recruitment of piscivores (Stein et al. 1995), gizzard shad abundance was not a significant variable in any of our models. However, recent investigations suggest that low water temperatures in Glen Elder Reservoir mediate interactions between larval gizzard shad and walleyes, where low water temperatures resulted in poor growth of larval walleyes, an inability to switch to piscivory, and poor recruitment (Quist 2002). Abundance of white crappies was the only biotic variable that was related to walleye recruitment in our study.

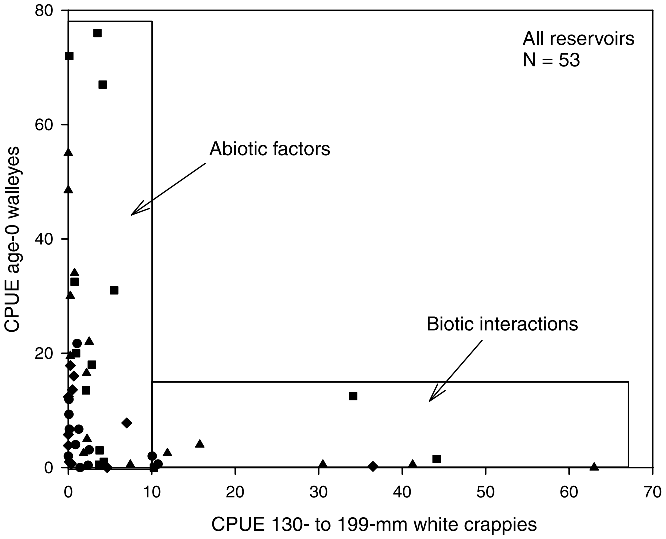
An important theory regarding the native distribution of percids in North America states that interactions with centrarchids restricted their success in southern latitudes (Collette et al. 1977). Several studies support this hypothesis of introductions of centrarchids to systems with native walleye populations (Schiavone 1985) or introductions of walleyes to centrarchid-dominated systems (Santucci and Wahl 1993) resulting in poor walleye recruitment. The results of our empirical analysis and mesocosm experiment also support this hypothesis.

Adult white crappies potentially limit recruitment of larval fishes in some systems (Kim and DeVries 2001), but the influence of juvenile white crappies on larval fish mortality has not been previously investigated. Juvenile white crappies prey almost exclusively on zooplankton until they reach a length of about 170 mm (O'Brien et al. 1986), but smaller white crappies will consume larger prey items when available. For example, Wright and O'Brien (1982) found that the reactive distance of white crappies increased linearly with prey size (i.e., larval *Chaoborus*) and that movement of prey doubled the distance that prey could be detected. White crappies also have a saltatory search strategy (i.e., alternating swim–search behavior) that can be modified when prey are located to increase consumption rates (e.g., reduce time between searches; O'Brien et al. 1986). If larval fishes have a patchy distribution owing to factors such as wind-generated water currents or the indirect effect of prey distributions, predation rates may be high given the behavior and size of larval fishes and the feeding ecology of juvenile white crappies (Wright and O'Brien 1982; O'Brien et al. 1986).

Although the mesocosms used in this study were large enough to avoid small-container effects (de Lafontaine and Leggett 1987), experiments were conducted using larval densities (2.3 walleyes·m^{-3}) much higher than those observed in the field (i.e., <1.0 walleyes·m^{-3}; Quist 2002). Despite differences in density, the ratio of *Daphnia* spp. to larval walleyes in the high zooplankton treatment was equal to or higher than that observed in the field. Thus, even though white crappies had to locate walleyes among the same (or higher) number of zooplankton, mortality still exceeded 90% over a short time period.

Abiotic and biotic factors were associated with walleye recruitment in Kansas reservoirs, but the results of our empirical and experimental analyses suggest that biotic interactions can have an overriding influence on walleye recruitment dynamics. For example, strong walleye year classes should have been produced when abiotic characteristics were suitable in each reservoir, but walleye recruitment was limited when juvenile white crappies were abundant. Therefore, we propose a biotic–abiotic confining hypothesis (BACH) to explain the role of abiotic and biotic mechanisms on walleye recruitment in Kansas reservoirs. During years with low white crappie abundance, walleye recruitment is highly variable and is likely confined by abiotic factors (Fig. 4). However, when juvenile white crappie abundance reaches some threshold value, which will vary by reservoir, walleye recruitment is low. The influence of white crappies on walleye recruitment is probably direct, as suggested by our experimental results. Furthermore, if white crappies did not have an influence on walleyes, we would expect to observe high variability in walleye recruitment at all levels of white crappie abundance, but this has not occurred in any reservoir over the past 15 years.

Fig. 4. Relationship between catch-per-unit-effort (CPUE = fish per gill net complement night) of age-0 walleyes (*Stizostedion vitreum*) and CPUE (CPUE = fish per trap net night) of 130- to 199-mm white crappies (*Pomoxis annularis*) in four Kansas reservoirs (Glen Elder, ●; Kirwin, ■; Webster, ▲; and Wilson, ◆) during 1985–1999. Based on this relationship, we propose a biotic–abiotic confining hypothesis (BACH) to explain the role of biotic interactions and abiotic conditions on walleye recruitment dynamics in Kansas reservoirs.



In conclusion, the results of this study provide important information on factors influencing recruitment dynamics of walleyes in reservoir ecosystems and suggest that spring temperatures and water levels are important for walleyes regardless of the ecosystem or region. The specific mechanisms for the abiotic relationships are unknown for Kansas reservoirs but are probably similar to systems in northern latitudes. This study also illustrates the potential influence of biotic interactions on walleye recruitment in reservoirs, and the BACH provides a model for conceptualizing factors influencing walleye recruitment. Although our analysis was limited to Kansas reservoirs, similar factors probably influence walleye recruitment in other Great Plains reservoirs because of similarities in reservoir fish communities and abiotic conditions (e.g., water-level fluctuations, thermal regimes) throughout the southern Great Plains region.

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