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Environmental factors regulating the recruitment of walleye *Sander vitreus* and white bass *Morone chrysops* in irrigation reservoirs

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Abstract – Understanding the environmental factors that regulate fish recruitment is essential for effective management of fisheries. Generally, first-year survival, and therefore recruitment, is inherently less consistent in systems with high intra- and interannual variability. Irrigation reservoirs display sporadic patterns of annual drawdown, which can pose a substantial challenge to recruitment of fishes. We developed species-specific models using an 18-year data set compiled from state and federal agencies to investigate variables that regulate the recruitment of walleye *Sander vitreus* and white bass *Morone chrysops* in irrigation reservoirs in south-west Nebraska, USA. The candidate model set for walleye included only abiotic variables (water-level elevation, minimum daily air temperature during winter prior to hatching, annual precipitation, spring warming rate and May reservoir discharge), and the candidate model set for white bass included primarily biotic variables (catch per unit effort (CPUE) of black crappie *Pomoxis nigromaculatus*, CPUE of age-0 walleye, CPUE of bluegill *Lepomis macrochirus* and CPUE of age-3 and older white bass), each of which had a greater relative importance than the single abiotic variable (minimum daily air temperature during winter after hatching). Our findings improve the understanding of the recruitment of fishes in irrigation reservoirs and the relative roles of abiotic and biotic factors.

Key words: environmental factors; irrigation reservoir; recruitment; walleye; white bass

Introduction

Game management is often predicated on the desire to maintain predictable populations that can sustain consistent harvest over multiple years (Rosenberg et al. 1993; Heino 1998). Unfortunately, in many systems, population variability is the norm rather than the exception (Gaston & McArdle 1994). For example, recruitment – often considered to be the most influential factor governing fish populations (May 1974; Gulland 1982; Donald 1997; Houde 2002) – is inherently less consistent in systems with high intra- and interannual variability. Fish are especially vulnerable during early life stages, particularly in reservoirs where unpredictable water fluctuations are common (June 1977; Beam 1983; Maceina & Stimpert 1998), as habitat constancy is inherently linked to constancy

in weather patterns (Houde 1987; Mion et al. 1998; Hoxmeier et al. 2004). Challenges for fish to recruit are exacerbated by water-level variability (Carline 1986), especially in irrigation reservoirs that experience unpredictable and often amplified summer drawdowns in response to sporadic extremes in abiotic conditions (Quist et al. 2003b; Olds et al. 2011).

Abiotic and biotic factors are known to regulate the recruitment of fishes, but specific factors regulating individual species are more difficult to ascertain. Abiotic conditions such as temperature, light, salinity and oxygen clearly regulate growth (Brett 1979) and in some cases survival (Oliver et al. 1979; Post & Evans 1989; Fox & Keast 1991; Johnson & Evans 1991). However, biotic conditions are often equally important, although generally more complex. For example, survival and growth generally covary with food avail-

ability (Persson & Greenberg 1990; Leggett & DeBlois 1994), which is influenced by prey abundance (Ritchie & Colby 1988; Peterson et al. 2006), temporal and spatial overlap of predator hatching with prey availability (i.e., match/mismatch; Cushing 1990; Chick & VanDenAvyle 1999; Kaemingk et al. 2011), intraspecific competition (Partridge & DeVries 1999; Knoll 2007) and interspecific competition (Michaletz et al. 1987; Roseman et al. 1996; Garvey & Stein 1998; Kaemingk et al. 2012). Similarly, predation also regulates recruitment (Leggett & DeBlois 1994; Köster & Möllmann 2000) and is influenced by cannibalistic conspecifics (Chevalier 1973; Fox 1975; Polis 1981) and interspecific interactions (Pope et al. 1996; Quist et al. 2003b). Ultimately, understanding fish population dynamics, particularly in environments with strong periodic cycles in fish abundance, requires understanding the extent to which biotic and abiotic factors interact to limit fish recruitment.

Walleye *Sander vitreus* and white bass *Morone chrysops* are among the most popular sportfish in the reservoirs of the Great Plains, USA (Stone 1996; Bauer 2002; Hurley & Duppong-Hurley 2005). Despite the considerable effort by the Nebraska Game and Parks Commission (NGPC) stocking walleye and managing reservoirs for walleye and white bass, populations of walleye and white bass in south-west Nebraska (USA) reservoirs are dynamic (Huber 2010a–d; Newcomb 2010), as erratic recruitment has led to 'boom and bust' fisheries for these two species. Although analyses from regionally similar systems provide some insight (Quist et al. 2002, 2003b), differences exist among systems, and specific reasons for the dynamic nature of these populations are largely unknown. Thus, further knowledge of the factors regulating walleye and white bass recruitment in irrigation reservoirs is required to understand the ecology of these fishes in the semi-arid Great Plains region.

Methods

Study area and reservoirs

The Republican River is an impounded tributary to the Kansas River; the Republican River basin is contained within three states (Fig. 1) in the Great Plains region of the United States of America. Forty per cent of the basin is in Nebraska, where it drains nearly 25,000 km^2 of primarily rangeland and cropland into 1,826 km of streams and rivers (Bliss & Schainost 1973). Catastrophic flooding in 1935 prompted the construction of five large multipurpose reservoirs (Table 1, Fig. 1) in the Republican River basin in Nebraska: Enders Reservoir, Harlan County Lake, Medicine Creek Reservoir (Harry D. Strunk Lake), Red Willow Reservoir (Hugh Butler Lake)

and Swanson Reservoir. Harlan County and Swanson reservoirs are on the mainstem of the Republican River, whereas Enders, Medicine Creek and Red Willow reservoirs are on separate tributaries to the Republican River. Species commonly present in these reservoirs include black crappie *Pomoxis nigromaculatus*, bluegill *Lepomis macrochirus*, channel catfish *Ictalurus punctatus*, common carp *Cyprinus carpio*, freshwater drum *Aplodinotus grunniens*, flathead catfish *Pylodictis olivaris*, gizzard shad *Dorosoma cepedianum*, hybrid striped bass *M. chrysops* × *Morone saxatilis*, largemouth bass *Micropterus salmoides*, northern pike *Esox lucius*, smallmouth bass *Micropterus dolomieu*, walleye, white bass and white crappie *Pomoxis annularis*. Most of the species present in the reservoirs are indigenous to the drainage; nonindigenous species include black crappie, common carp, hybrid striped bass, largemouth bass and smallmouth bass (USGS 2009).

As a result of agricultural overdevelopment (i.e., overappropriation of groundwater wells for cropland irrigation) in the region, flows are substantially reduced compared to circa 1970 levels throughout the Republican River basin (Szilagyi 1999, 2001). This reduction in flow has been attributed to cropland irrigation, changes in vegetative cover, water conservation practices and construction of reservoirs and artificial ponds in the basin, all of which increase the amount of water lost to evaporation over the basin (Szilagyi 1999, 2001). Thus, only Medicine Creek Reservoir delivers water for irrigation on a regular basis; the other reservoirs deliver water for irrigation only sporadically when there is sufficient inflow.

Data collection

Data for walleye, white bass, bluegill, black crappie, white crappie, freshwater drum and gizzard shad were obtained from standardised experimental gillnet surveys conducted by NGPC during autumn 1993–2010. A standard survey consisted of 4–8 gillnets that were set overnight once in each reservoir during autumn of each year. Gillnets were 45.6 m long and 1.8 m deep, with six 7.6-m panels consisting of 1.9, 2.5, 3.2, 3.8, 5.1 and 7.6 cm bar mesh. We used catch per unit effort (CPUE; number per gillnet night) as an index of abundance. Although trapnets are the standard gear for assessing bluegill and crappie populations, use of the experimental gillnet data set provided us with both longer-term data and more complete data than the use of the trapnet data set. Ages of captured walleye and white bass were determined by a single reader from NGPC, using scales pressed into acetate slides and a microfiche reader (Smith 1954). Age was not assigned to other fishes. Autumn age-0 fish are often considered an acceptable stage to measure recruitment (Willis
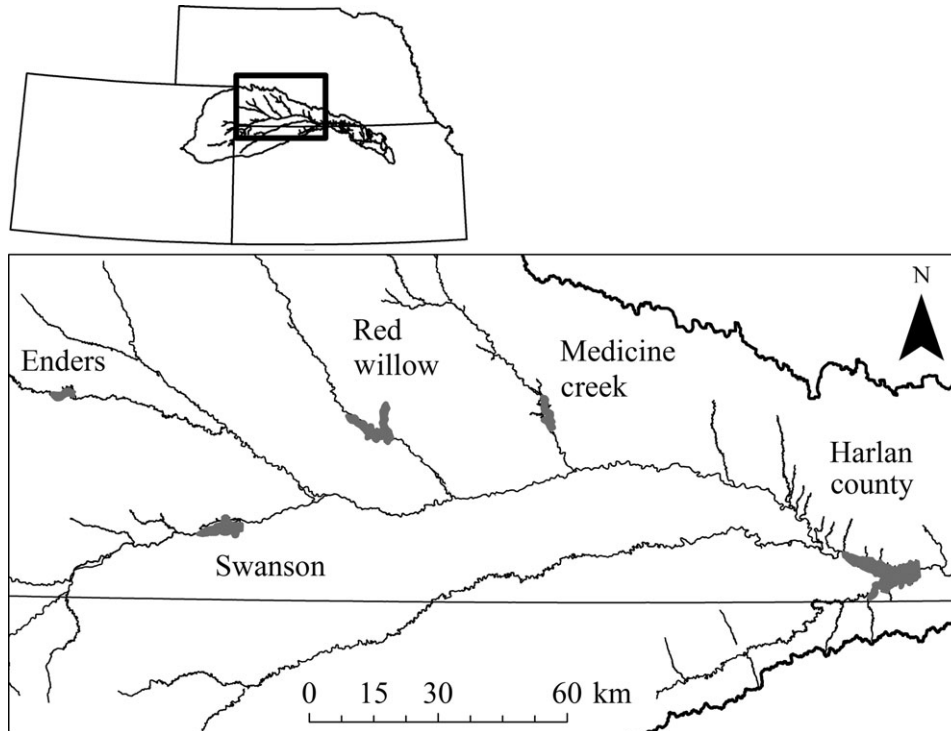
Fig. 1. Map of the Republican River basin in Colorado, Kansas and Nebraska, USA, and the five irrigation reservoirs in Nebraska.

Table 1. Hydrological characteristics of the Republican River reservoirs in Nebraska, USA. Surface area and maximum depth are based on active conservation pool elevation. Annual fluctuation is the mean ± SE during 1993–2009.

Reservoir	Surface area (ha)	Maximum depth (m)	Basin (ha)	Annual fluctuation (m)
Enders	485	18.3	284,100	2.6 ± 1.5
Harlan County	5362	15.2	1,855,500	2.9 ± 1.8
Medicine Creek	737	13.7	227,900	4.3 ± 1.8
Red Willow	659	15.8	189,000	2.3 ± 1.2
Swanson	2023	14.6	2,232,600	2.4 ± 1.6

1987); however, here we considered age-1 walleye and age-1 white bass from autumn gillnets to be recruited to the population as this is a more conservative estimate that considers overwinter mortality (*sensu* Pratt & Fox 2002). Furthermore, experimental gillnets do not accurately sample young-of-year walleye or white bass. We obtained hydrological data for reservoirs (e.g., water elevation, irrigation fluctuation and precipitation; see Table 2) for 1993–2009 (1-calendar-year advance of age-1 walleye and age-1 white bass data) from the U.S. Bureau of Reclamation (USBR 2010). We obtained air temperature data (Table 2) unique to each reservoir for 1993–2009 (1-calendar-year advance of age-1 walleye and age-1 white bass data) from the National Oceanic and Atmospheric Administration's National Climatic Data Center (NCDC 2010).

Statistical analysis

We used one-way ANOVA to test for differences in minimum monthly air temperature between the months of April and May during 1994–2009 to verify that minimum air temperature did in fact increase during spring. Likewise, we used one-way ANOVA to test for differences in extent of range of monthly air temperature (maximum monthly temperature minus minimum monthly temperature during a given year) between the months of April and May during 1993–2009 to verify that temperature fluctuations decreased as spring progressed. We used independent Durbin–Watson tests to test for temporal autocorrelation on residuals in the candidate model sets. We $\log_e$-transformed ($\ln[x + 1]$) CPUE of each species and transformed independent variables when appropriate. Of 79 available year-by-reservoir combinations, there were 12 instances of zero catch of age-1 walleye and seven instances of zero catch of age-1 white bass (Fig. 2). All independent variables were assigned a 1-calendar-year advance, so as to model their effect on age-0 walleye and age-0 white bass. From the 51 independent variables (43 for each species, Table 2), we developed multiple linear regression models that best described ln(CPUE) during 1994–2010 for age-1 walleye and age-1 white bass independently (Fig. 2), using reservoir as a fixed factor. We developed a model set using stepwise multiple linear regression, with variables added based on their adjusted R^2. Each

Table 2. Input variables for models and explanation of variable abbreviations. We obtained hydrological data for reservoirs (e.g., water elevation, irrigation fluctuation, precipitation) for 1993–2009 from the U.S. Bureau of Reclamation. We obtained air temperature data unique to each reservoir for 1993–2009 from the National Oceanic and Atmospheric Administration's National Climatic Data Center. We obtained fish data from standardised gillnet surveys conducted by the Nebraska Game and Parks Commission during autumn 1993–2010. 'Annual' refers to January through December, unless otherwise stated. Age groups of fish are pooled, unless otherwise stated.

Model variable	Explanation
PRECIP_MR	March precipitation (cm)
PRECIP_AP	April precipitation (cm)
PRECIP_MAY	May precipitation (cm)
PRECIP_JU	June precipitation (cm)
SPR_PRECIP	Spring precipitation[†] (cm)
PRECIP_YR	Annual precipitation (cm)
Q_AP	April reservoir discharge (millions of m^3)
Q_MAY	May reservoir discharge (millions of m^3)
Q_JUNE	June reservoir discharge (millions of m^3)
SPR_Q	Spring reservoir discharge[†] (millions of m^3)
Q_YR	Annual reservoir discharge (millions of m^3)
IN_APRIL	April reservoir inflow (m^3)
IN_MAY	May reservoir inflow (m^3)
ACP_APRIL	April reservoir elevation (m, relative to active conservation pool)
ACP_MAY	May reservoir elevation (m, relative to active conservation pool)
ACP_MAX	Maximum reservoir elevation (m, relative to active conservation pool)
ACP_MIN	Minimum reservoir elevation (m, relative to active conservation pool)
MAY_SEPT	Change in reservoir elevation, May–September (m)
MAX_MIN	Change in reservoir elevation, Maximum to Minimum (m)
ELV_YR_PRIOR	Annual change in reservoir elevation (April–April) (m)
APR_TMIN	Minimum daily air temperature during April (°C)
APR_TMEAN	Mean daily air temperature during April (°C)
APR_TMAX	Maximum daily air temperature during April (°C)
MAY_TMIN	Minimum daily air temperature during May (°C)
MAY_TMEAN	Mean daily air temperature during May (°C)
WIN_TMEAN_ED	Mean daily air temperature during winter prior to hatching[‡] (°C)
MAY_TMAX	Maximum daily air temperature during May (°C)
JUN_TMIN	Minimum daily air temperature during June (°C)
JUN_TMEAN	Mean daily air temperature during June (°C)
JUN_TMAX	Maximum daily air temperature during June (°C)
SPR_TMIN	Minimum daily air temperature during spring[†] (°C)
SPR_TMEAN	Mean daily air temperature during spring[†] (°C)
SPR_TMAX	Maximum daily air temperature during spring[†] (°C)
WIN_TMIN_ED	Minimum daily air temperature during winter prior to hatching[‡] (°C)
WIN_TMAX_ED	Maximum daily air temperature during winter prior to hatching[‡] (°C)
WIN_TMIN_OWM	Minimum daily air temperature during winter after hatching[‡] (°C)
WIN_TMEAN_OWM	Mean daily air temperature during winter after hatching[‡] (°C)
WIN_TMAX_OWM	Maximum daily air temperature during winter after hatching[‡] (°C)
APR_GDD	Number of growing-degree days (maximum temperature > 10 °C) during April
JUN_GDD	Number of growing-degree days (maximum temperature > 10 °C) during June
SPRING_GDD	Number of growing-degree days (maximum temperature > 10 °C) during April–June
GSD	Catch per unit effort (CPUE) of gizzard shad (catch per gill net night)
BLG	CPUE of bluegill (BLG, catch per gill net night)
FWD	CPUE of freshwater drum (FWD, catch per gill net night)
BLC	CPUE of black crappie (BLC, catch per gill net night)
WHC	CPUE of white crappie (WHC, catch per gill net night)
CRP	CPUE of black and white crappie (catch per gill net night)
PREDS	CPUE of BLG + FWD + BLC + WHC (catch per gill net night)
WAE_3_PLUS	CPUE of walleye $\geq$ age 3[§] (catch per gill net night)
WHB_3_PLUS	CPUE of white bass $\geq$ age 3[§] (catch per gill net night)
WAE	CPUE of age-1 walleye[¶] (catch per gill net night)
WHB	CPUE of age-1 white bass[**] (catch per gill net night)

[†]Spring includes the months of March, April and May.
[‡]Winter includes the months of December, January and February.
[§]Fish $\geq$ age 3 used as a surrogate for spawner abundance; no internal evaluation of fish was performed.
[¶]Used as dependent variable for walleye model and independent variable for white bass model.
[**]Used as dependent variable for white bass model and independent variable for walleye model.
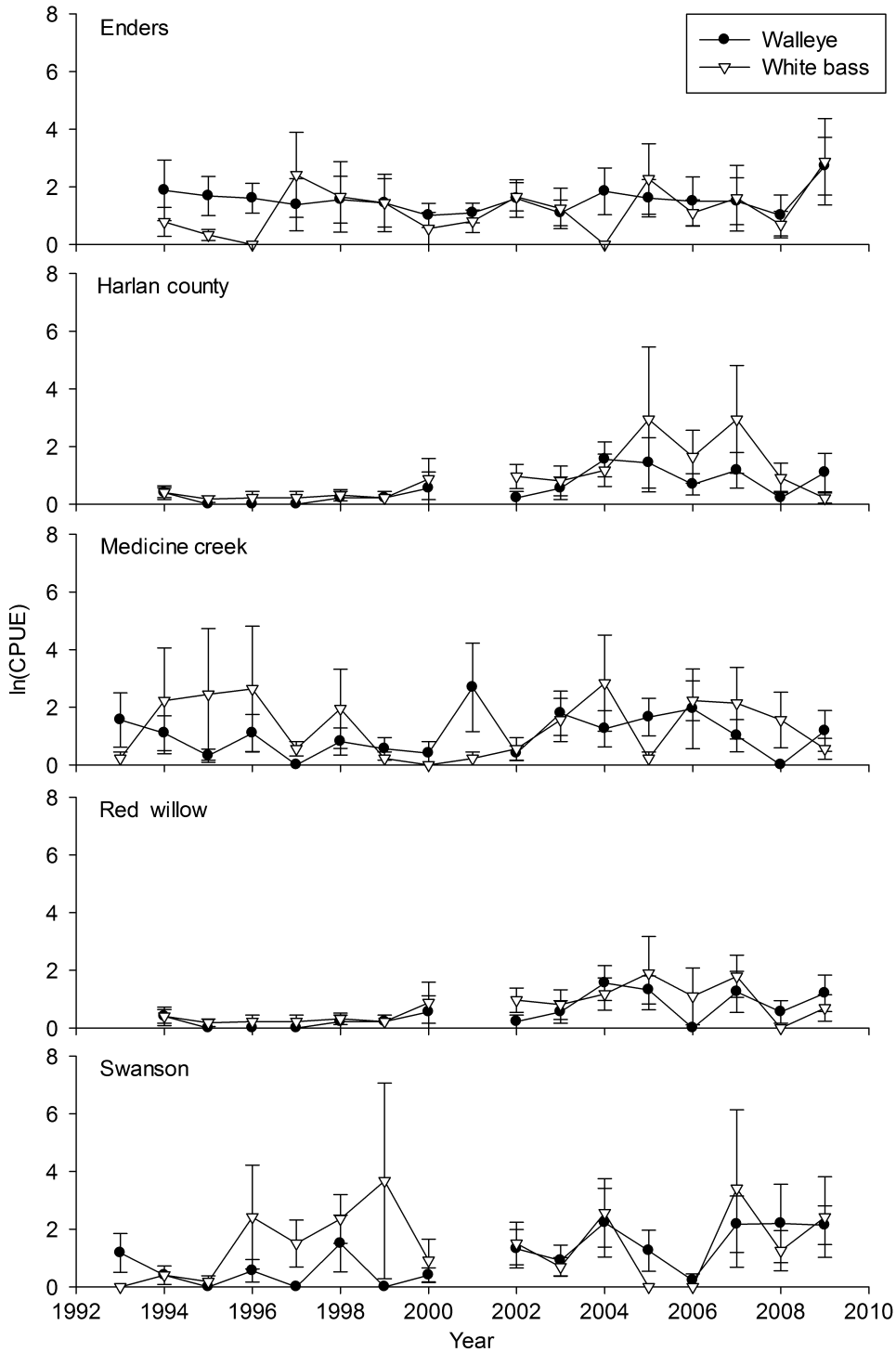
Fig. 2. Log$_e$-transformed (ln[x + 1]) catch per unit effort (ln(CPUE); number per gillnet night) of age-1 walleye and age-1 white bass during 1994–2010 from the five reservoirs of the Republican River basin in Nebraska, USA.

model produced by an iteration of the stepwise selection process was included in the model set until a maximum of adjusted R^2 for each model set was determined. We then selected a subset of candidate models from among the set of developed models using Akaike's Information Criterion (Akaike 1987) corrected for small sample size (AIC$_c$, Hurvich & Tsai 1989). We excluded models with a ΔAIC$_c$ > 2 from the subset of candidate models (Royall 1997). We assessed relative variable importance (RVI) by summing the AIC$_c$ weights over all models including the explanatory variable. We conducted statistical

analyses using SAS (version 9.2; SAS Institute Inc., Cary, NC, USA) and R (version 2.14.0; The R Foundation for Statistical Computing, Vienna, Austria).

Results

Durbin–Watson tests for temporal autocorrelation on model residuals were not significant. The minimum temperature in this region during April (-7.5 ± 2.8 °C, mean ± SD) was significantly less (one-way ANOVA, $F = 337.3$, d.f. = 156, $P < 0.0001$) than during May (0.1 ± 2.4 °C). Furthermore, the mean monthly extent of temperature range during April (37.6 ± 4.4 °C) was significantly greater (one-way ANOVA, $F = 28.56$, d.f. = 156, $P < 0.0001$) than during May (33.9 ± 4.5 °C).

The candidate model set for walleye (Table 3) included two models with a $\Delta AIC_c \leq 2$. There were five abiotic and no biotic variables present in the candidate model set; reservoir was also present in the walleye candidate model set. The mean (±SE) adjusted R^2 for the walleye candidate model set was 0.67 ± 0.01. Four variables in the candidate model set had an RVI > 0.9; three variables had an RVI > 0.99 (Table 4).

The candidate model set for white bass (Table 5) included three models with a $\Delta AIC_c \leq 2$. There were four biotic variables and one abiotic variable present in the candidate model set; reservoir was not present in the white bass candidate model set. The mean adjusted R^2 for the white bass candidate model set was 0.33 ± 0.02. Two variables in the candidate model set had an RVI > 0.9 (Table 4).

Discussion

Walleye recruitment

The most important variable in the candidate model set for walleye was maximum reservoir water level, which was negatively related to year-class strength of walleye. Quist et al. (2003b) also found year-class strength of walleye to be negatively correlated with reservoir elevation, although they were unable to explain the mechanism behind these trends; they hypothesised it may have to do with small (i.e., 1–2 m) increases in reservoir water level during low-water years, providing increased spawning habitat or increased production of prey species. In our study reservoirs, high reservoir water levels generally indicated sufficient volume in the reservoir for irrigation discharge. Another variable in the candidate model set was May reservoir discharge, which was also negatively related to year-class strength of walleye. However, annual precipitation was also included in the candidate model set, but it was positively related to year-class strength of walleye. Sufficient volume for irrigation discharge was generally only present in years with abundant annual precipitation, although irrigators need to apply less water in wet years. Thus, discharge was at a lower volume and typically started later in the year, after some of the age-0 walleye had moved away from the dam. Nonetheless, high discharge can entrain age-0 walleye through the dam leading to a direct reduction in the number of potential recruits in the reservoir (Walburg 1971). High discharge levels during May could also lead to low zooplankton abundance (*sensu* Watson et al. 1996; Kalff 2003), which could reduce food availability for larval walleye at a critical stage. Furthermore, previous studies indicate that harvest (Aggus & Bivin 1982), standing crop, natural reproduction and spawning success of walleye (Willis & Stephen 1987) are greater in reservoirs with low discharge (i.e., retention time > 1 year); as such, larval walleye may not be suitable for stocking into reservoirs with high discharge (Willis & Stephen 1987; Johnson et al. 1988).

The second-most important variable in the candidate model set for walleye was maximum winter temperature (experienced by sexually mature adult walleye prior to spawning), which was negatively

Table 3. Parameter estimates for variables (Table 2) in candidate model sets for the recruitment of walleye to age 1. Models with a $\Delta AIC_c > 2$ were excluded from consideration. Data are from the Republican River basin, Nebraska, USA, 1993–2009.

Model	Intercept	ACP_MAX	WIN_TMAX_ED	RES	PRECIP_YR	SPRING_GDD	Q_MAY	Adj. R^2	ΔAIC_c	AIC_c w
1	0.58	−0.15	−0.09	Enders: 0.57 Harlan County: 0.02 Medicine Creek: 0.55 Red Willow: −0.22 Swanson: 0.00	0.01	0.02	−0.04	0.69	0	0.64
2	0.29	−0.17	−0.08	Enders: 0.56 Harlan County: −0.05 Medicine Creek: 0.56 Red Willow: −0.20 Swanson: 0.00	0.01	0.03	−*	0.66	1.13	0.36

*Variable not included in model.

Table 4. Relative variable importance (RVI) for variables (Table 2) present in the candidate models sets for the recruitment of walleye (Table 3) and white bass (Table 5) to age 1. Data are from the Republican River basin, Nebraska, USA, 1993–2009.

Variable	RVI
Walleye	
ACP_MAX	0.999
WIN_TMAX_ED	0.997
RES	0.991
PRECIP_YR	0.939
SPRING_GDD	0.872
Q_MAY	0.642
White bass	
BLC	0.950
WAE	0.948
BLG	0.824
WHB_3PLUS	0.731
WIN_TMIN_OWM	0.604

related to year-class strength of walleye; recruitment is weak the following year when winter temperatures are warm (Colby & Nepszy 1981). Annual maturation of adult walleye gonads requires water temperatures below 10 °C; thus, if water temperatures are not sufficiently cold enough for a long enough duration, walleye may skip spawning and resorb their gametes over the next season (Colby & Nepszy 1981). Ova resorption interferes with the development of next generation of oocytes, leading to skipping of the next spawning period (Colby et al. 1979). Thus, failure to spawn in one season because of increased winter water temperature may lead to failure to spawn in the following season, leading to the loss of back-to-back year classes (this was unaccounted for in our models).

The number of spring growing-degree days was positively related to year-class strength of walleye. Warm spring water temperatures may accelerate spawning and shorten egg incubation time (Busch et al. 1975; Colby et al. 1979) and result in greater growth rates for larval walleye (Busch et al. 1975; Colby et al. 1979). These factors allow larval walleye to accelerate their development, switching to piscivory earlier and therefore increasing their resource intake and ultimately increasing recruitment (*sensu* Quist et al. 2003a). In previous studies, both spring warming rate (Busch et al. 1975; Madenjian et al.

1996) and mean spring temperature (Quist et al. 2003b) were positively related to the recruitment of walleye.

Reservoir, included in the models as a fixed factor, was present in the candidate model set for walleye. Thus, there may be differences among these reservoirs in walleye recruitment. Though age-0 walleye abundance was present in the candidate model set for white bass, age-0 white bass abundance was not present in the candidate model set for walleye. This is most likely because the abiotic factors mentioned above had a greater influence on walleye recruitment. Moreover, we believe the stocking of walleye potentially confounds the relationship between walleye recruitment and abundance of age-3 and older walleye, which is why it was not present in our candidate model set.

Ultimately, these abiotic conditions not only influence walleye, but also influence the entire reservoir community, which in turn affects the walleye population. Thus, it is likely that these abiotic factors act both directly and indirectly on walleye recruitment. If early-season storms or abrupt changes in temperature (an abiotic factor) influence larval walleye production, they likely also influence the production of zooplankton (a biotic factor), in particular the phenology and abundance. Changes in zooplankton composition and abundance could also affect many other age-0 and adult fishes, thus complicating the nature of the relationship between abiotic and biotic factors influencing walleye recruitment.

White bass recruitment

The most important variable in the candidate model set for white bass was black crappie abundance, which was positively related to year-class strength of white bass. The second-most important variable in the candidate model set for white bass was age-0 walleye abundance, which was also positively related to year-class strength of white bass. Given that larval white bass compete for resources with other age-0 fishes, including walleye (Michaletz et al. 1987; Beck et al. 1998) and black crappie (Pope et al. 1996; Galinat et al. 2002), it is likely that resource conditions (e.g., abundant zooplankton and reservoir

Table 5. Parameter estimates for variables (Table 2) in candidate model sets for the recruitment of white bass to age 1. Models with a $\Delta AIC_c > 2$ were excluded from consideration. Data are from the Republican River basin, Nebraska, USA, 1993–2009.

Model	Intercept	BLC	WAE	BLG	WHB_3PLUS	WIN_TMIN_OWM	Adj. R^2	ΔAIC_c	$AIC_c\ w$
1	1.56	0.47	0.51	−0.62	0.29	0.06	0.36	0	0.51
2	0.35	0.47	0.44	−0.63	0.28	–*	0.32	1.05	0.30
3	1.78	0.46	0.57	−0.68	–*	0.05	0.31	1.96	0.19

*Variable not included in model.

inflow) that favour the recruitment of one of these species will also benefit the other two. It is also possible that adult crappie and age-0 walleye predation on abundant age-0 gizzard shad (Michaletz 1997; Quist et al. 2003a) reduces competition between age-0 white bass and age-0 gizzard shad for zooplankton (Michaletz et al. 1987). Alternatively, it is possible that large abundances of age-0 walleye may provide a 'shading effect' (as alternative prey, *sensu* Forney 1976) for age-0 white bass. White bass, black crappie and saugeye *S. vitreus* × *S. canadensis* also respond similarly to reservoir hydrology, producing weak year classes in dry years and strong year classes in wet years (Sammons & Bettoli 2000). As we discussed with walleye, the distinction between abiotic or biotic factors as regulators of recruitment of white bass is complicated.

The third-most important variable in the white bass candidate model set was bluegill abundance, which was negatively related to year-class strength of white bass. Age-0 white bass consume both zooplankton and invertebrates before becoming piscivores (Matthews et al. 1992; Quist et al. 2002). Age-0 bluegill consume primarily zooplankton (Kaemingk et al. 2012), and age-1 and older bluegill consume primarily macroinvertebrates (Olson et al. 2003). This could create scenarios where bluegill and age-0 white bass compete for food resources, which could explain the negative correlation in our model. However, given that year-class strength of white bass was positively correlated with both black crappie abundance and age-0 walleye abundance and negatively correlated with bluegill abundance, further investigation of species–specific interactions in these systems is needed.

Another variable in the white bass candidate model set was abundance of age-3 and older white bass, which was positively related to year-class strength of white bass. Abundance of age-3 and older white bass was used as a surrogate metric for abundance of spawning adults, as no evaluation of the condition of white bass gonads was performed in the field during sampling. The coefficient ($\approx$0.3) for this stock-recruit regression (log[WHB]−log[WHB_3_PLUS]) is <1; thus, there is likely a density-dependent mechanism that is influencing white bass recruitment. Spawning activity of white bass is positively related to reservoir inflows during spring (Quist et al. 2002); however, there was no evidence in these reservoirs of a white bass spawning migration during the spring (Martin et al. 2009) likely because of limited inflows in most of the years studied. Spawning adult abundance is generally considered to be positively related to year-class strength of most fishes (Myers & Barrowman 1996). However, unlike walleye populations, which are regularly augmented by stocking, white bass populations in these systems are self-sustaining, thus leading to the presence of a relationship between white bass recruitment and abundance of age-3 and older white bass.

Minimum winter air temperature (winter after hatching) was the only abiotic variable included in the white bass candidate model set; the relationship was positive, indicating white bass recruitment is positively influenced by milder (i.e., warmer minimum temperatures) winters. Predation and starvation are important overwintering factors for age-0 white perch *Morone americana* (Fitzgerald et al. 2006). In another study, 71% of age-0 white perch died at 2.5 °C versus only 11% at 4.0 °C, a finding linked to the white perch remaining active but not feeding at 2.5 °C, maintaining their basal metabolic rate while reducing their energy intake leading to a net energy deficit (Johnson & Evans 1991). Size-dependent overwinter mortality was also a factor; smaller white perch (Johnson & Evans 1991) and smaller striped bass *Morone saxatilis* (Hurst & Conover 1998; Sutton & Ney 2001) died before larger conspecifics of the same cohort. Other abiotic factors have been related to white bass recruitment, including spring precipitation and air temperature in eastern South Dakota glacial lakes (Pope et al. 1997), spring air temperature in a north-western South Dakota reservoir (Phelps et al. 2011) and spring inflow in Kansas reservoirs (Quist et al. 2002; Schultz et al. 2002).

Interspecific differences in spawning period

There is a need to refine existing knowledge about factors that regulate the recruitment of fishes, particularly in changing environments (Baccante et al. 2011). Earlier-spawning species are likely more subjected to adverse abiotic conditions because weather in this region is typically more volatile during early spring (i.e., greater likelihood of cold fronts and greater temperature variability during early spring than during late spring; Coupland 1958). In contrast, later-spawning species are likely less subjected to adverse abiotic conditions and likely more subjected to adverse biotic conditions because many species, including numerically dominant common carp and gizzard shad, spawn during this period, and zooplankton abundance declines during this period (Sullivan et al. 2012) and could become limited.

The candidate model set for walleye (Table 3) included only abiotic variables, and the candidate model set for white bass (Table 5) included mostly biotic variables, each of which had a greater relative importance than the single abiotic variable in the candidate model set. Essentially, we believe earlier-spawning species like walleye spawn during a period typified by predictable biotic conditions and unpre-

dictable abiotic conditions, whereas later-spawning species like white bass spawn during a period typified by unpredictable biotic conditions and predictable abiotic conditions. In most of the reservoirs we studied, walleye were one of the first, if not the first, species to spawn each year; only northern pike spawn earlier among the suite of common species. Thus, in a given year, larval walleye are typically the first to emerge and feed in an environment that is biotically predictable. However, walleye in these systems spawn during a period where early spring storms and cold fronts produce strong winds that can dislodge or damage walleye eggs, increase water turbidity or present a lingering decrease in air temperature, all of which can negatively affect walleye recruitment. Furthermore, changing temperatures could also lead to reduced hatching success, or alter adult behaviour and thus the duration or periodicity of spawning activity.

Alternatively, white bass spawn approximately a month after walleye (Carlander 1997), and the larvae emerge into a dramatically different environment. There are several species that spawn approximately the same time as white bass, including smallmouth bass, black crappie, white crappie and freshwater drum (Carlander 1977; Bur 1984). Furthermore, common carp and gizzard shad, which also spawn approximately the same time as white bass (Quist et al. 2004), can numerically dominate the age-0 fish community in these systems (Sullivan et al. 2011). Larval white bass must compete for zooplankton with other fishes, in particular hyperabundant common carp and gizzard shad larvae. Furthermore, zooplankton abundance declines during this period (Sullivan et al. 2011) and could become limited. Therefore, the emergence of these fishes within a short period creates an environment that is biotically unpredictable as compared to when walleye larvae emerged. However, the abiotic environment during this later period is more predictable than when walleye spawn, with milder temperatures and more consistent temperature fluctuations.

We believe that these scenarios offer the most plausible interpretation of the observed patterns. Alternatively, it is possible that adhesive eggs are more vulnerable to abiotic conditions than semi-buoyant eggs or that demersal spawning activities may be regulated by abiotic factors and pelagic spawning activities may be regulated by biotic factors. However, it is also plausible that abiotic factors regulate the recruitment of both walleye and white bass, with white bass recruitment being regulated indirectly by the abundance of other species that are regulated by abiotic conditions. Additional research from other regions and species is needed to provide further evidence and to fully explore inherent complexities.

Conclusion

Our study provides essential information regarding factors regulating the recruitment of walleye and white bass in irrigation reservoir ecosystems, and indicates that variability in the fish's environment within and among years may be influential in determining the nature of those factors. Our models could be used by biologists and managers to better understand the recruitment of walleye and white bass in irrigation reservoirs throughout the southern Great Plains. Understanding the recruitment of fishes is a critical step in improving our knowledge of their ecology, not only in this region, but also throughout semi-arid regions of the world.

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