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ECOLOGY OF
FRESHWATER FISH

# Factors influencing recruitment of walleye and white bass to three distinct early ontogenetic stages

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Abstract – Determining the factors that influence recruitment to sequential ontogenetic stages is critical for understanding recruitment dynamics of fish and for effective management of sportfish, particularly in dynamic and unpredictable environments. We sampled walleye (*Sander vitreus*) and white bass (*Morone chrysops*) at 3 ontogenetic stages (age 0 during spring: 'age-0 larval'; age 0 during autumn: 'age-0 juvenile'; and age 1 during autumn: 'age-1 juvenile') from 3 reservoirs. We developed multiple linear regression models to describe factors influencing age-0 larval, age-0 juvenile and age-1 juvenile walleye and white bass abundance indices. Our models explained 40–80% (68 ± 9%; mean ± SE) and 71%–97% (81 ± 6%) of the variability in catch for walleye and white bass respectively. For walleye, gizzard shad were present in the candidate model sets for all three ontogenetic stages we assessed. For white bass, there was no unifying variable in all three stage-specific candidate model sets, although walleye abundance was present in two of the three white bass candidate model sets. We were able to determine several factors affecting walleye and white bass year-class strength at multiple ontogenetic stages; comprehensive analyses of factors influencing recruitment to multiple early ontogenetic stages are seemingly rare in the literature. Our models demonstrate the interdependency among early ontogenetic stages and the complexities involved with sportfish recruitment.

## Introduction

Fish recruitment refers to the size, age or developmental stage at which a fish surpasses a certain benchmark (Everhart et al. 1975). Autumn age-0 fish are often considered an acceptable stage to measure recruitment (Willis 1987), however, age-1 abundance is a more conservative estimate that considers overwinter mortality (*sensu* Pratt & Fox 2002), among other factors. Successful recruitment is often considered to be a function of a series of successfully navigated sequential events or stages (Neill et al. 1994). Determining the factors that influence recruitment to sequential ontogenetic stages or benchmarks (i.e. age 0 during spring: 'age-0 larval'; age 0 during autumn: 'age-0 juvenile'; and age 1 during autumn: 'age-1 juvenile') is critical for understanding recruitment dynamics of fish and for effective management of sportfish (Ludsin & DeVries 1997; Hoxmeier et al. 2006; Kaemingk et al. 2014a). These factors are more identifiable if fish abundances are monitored during each of the early ontogenetic stages from hatch to recruitment (Forney 1976), as survival gradually increases with progression through early ontogenetic stages; mortality rates for freshwater fish larvae average 15% per day, although mortality rates for juveniles are often an order of magnitude less (Houde 2002).

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First-year survival, and therefore year-class strength (i.e. the relative number of individuals in a cohort), of fish is often less consistent in dynamic and unpredictable environments because abiotic and biotic environmental factors can interact to affect year-class strength of fish (Boehlert & Mundy 1988; Hansen et al. 1998; Daskalov 1999; DeBoer et al. 2013; Uphoff et al. 2013; Kaemingk et al. 2014b). For a particular cohort, environmental regulation of year-class strength likely begins before that cohort even hatches; environmental factors can affect parental fish condition and thus reproductive investment by adult fish (Baltz & Moyle 1982; Johnston & Leggett 2002; DeBoer et al. 2015). Dynamic abiotic conditions – including temperature and water levels – can decrease survival of deposited eggs (Walburg 1972; Groen & Schroeder 1978; Colby et al. 1979; Schaeffer & Margraf 1987). After hatching, age-0 fish survival and growth are often positively correlated to habitat temporal stability and food availability (Houde 1987; Mion et al. 1998; Hoxmeier et al. 2004); fish in reservoirs are especially vulnerable during the age-0 larval and age-0 juvenile stages, often due to unpredictable water-level fluctuations for which reservoirs – particularly irrigation reservoirs and their patterns of annual drawdown – are known (June 1977; Quist et al. 2003; Olds et al. 2011). A high reservoir flushing rate can lead to low zooplankton abundance (sensu Watson et al. 1996; Kalff 2003), which could reduce food availability for age-0 fish at a critical stage. Compounding the difficulty of locating prey in dynamic abiotic conditions, age-0 fish may also contend with hyperabundant competitors such as gizzard shad (*Dorosoma cepedianum*) (Michaletz et al. 1987; Dettmers & Stein 1992). Failure to consume enough prey restricts growth and may thus prevent age-0 fish from making ontogenetic shifts, which are often necessary to consume higher energy prey that increase growth rates. Age-0 fish in temperate climates must survive this myriad of environmental challenges prior to the onset of winter, as undersized – and thus often undernourished – individuals in a cohort often perish during the overwinter period, a key stage in determining year-class strength (e.g. Johnson & Evans 1991; Hurst & Conover 1998; Sutton & Ney 2001). Therefore, we believe it is important to evaluate the influence of key environmental factors at multiple stages prior to recruitment to gain a better understanding of not only what factors are influential, but also the stage or period at which those influences are manifested.

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). Populations of walleye and white bass in south-west Nebraska irrigation reservoirs are dynamic (DeBoer et al. 2013), despite considerable effort by the Nebraska Game and Parks Commission (NGPC) stocking walleye and managing reservoirs for walleye and white bass. Age-0 walleye feed on zooplankton and macroinvertebrates (Hoxmeier et al. 2004), but shift to piscivory as soon as they are able (Galarowicz et al. 2006). Age-0 white bass feed primarily on zooplankton, although they will utilise more insects and fish as the summer progresses, including age-0 gizzard shad (Michaletz et al. 1987; Schultz et al. 2002; Willis et al. 2002). Diet overlap between walleye and white bass can be highly variable at both the larval and juvenile stages (J. DeBoer unpublished data), although diet overlap in and of itself does not result in competition, as abundant prey can preclude food limitation. Nonetheless, in years when preferred zooplankton abundance is low and suitable alternative prey is scarce, larval walleye and white bass may compete with each other (Michaletz et al. 1987; Beck et al. 1998), as well as with age-0 gizzard shad (Michaletz et al. 1987; Quist et al. 2004; Sullivan et al. 2011), and other fishes (e.g. yellow perch (*Perca flavascens*), Michaletz et al. 1987; freshwater drum (*Aplodinotus grunniens*), Sullivan et al. 2012; black crappie (*Pomoxis nigromaculatus*), Pope et al. 1996; Galinat et al. 2002) and juvenile walleye and white bass prey on age-0 gizzard shad (Hartman & Margraf 1992; Einfalt & Wahl 1997; Michaletz 1997; Schultz et al. 2002; Willis et al. 2002; Quist et al. 2003; Olson et al. 2007). However, diet overlap between age-0 walleye and white bass may be limited depending on selective feeding traits (Bulkley et al. 1976) or diet divergence (Willis et al. 2002), which could result from differences in spawning seasons for adult walleye and white bass (DeBoer et al. 2013).

There is a need for more large-scale, multilake studies (Hinch et al. 1991); abiotic variance is problematically reduced with smaller spatial and temporal scales. Irrigation reservoirs are inherently perturbed systems, which compounds the difficulty of our study because even fish populations in unperturbed systems tend to fluctuate in abundance (Kelso & Bagenal 1977). Management of water levels in reservoirs is typically guided by hydrological and economic factors (e.g. flood control, hydropower generation and crop irrigation), with little consideration given to fish populations (Sammons et al. 1999; Sammons & Bettoli 2000). Our objective was to understand the factors affecting year-class strength of walleye and white bass, and whether and how those factors might change during a progression through early ontogenetic stages in irrigation reservoirs. This study will help managers design proper courses of action for managing walleye and white bass populations in these dynamic ecosystems and provide information

about factors regulating year-class strength of fish in semi-arid regions such as the Great Plains USA. We focused on walleye and white bass to make inferences about sportfish in unpredictably dynamic ecosystems. These two species are top-level predators that often flourish in Midwestern reservoirs, have similar life expectancy and also have similar feeding strategies across multiple ontogenetic stages.

## Methods

There are several major multipurpose reservoirs located in the Republican River basin in Nebraska (see DeBoer et al. (2013) for descriptions). As a result of over appropriation of groundwater wells in the region, most of these reservoirs did not refill annually over the last decade and thus did not regularly discharge water for irrigation (USBR 2013). We sampled age-0 larval, age-0 juvenile and age-1 juvenile walleye and white bass from Enders, Red Willow and Medicine Creek reservoirs.

### Field and laboratory data collection

We obtained reservoir data (e.g. water level) from the U. S. Bureau of Reclamation (USBR 2013). We sampled age-0 larval fish once weekly beginning in accordance with an estimation of the start of hatching of age-0 larval walleye (approximately mid-April) and continuing until age-0 larval walleye and white bass were no longer captured, typically in early summer (approximately late June), from 2008 to 2011. We used nine paired nearshore and offshore transects, with starting points for nearshore transects randomly selected using GIS software (ArcMap 9.3.1; ESRI, Inc., Redlands, CA, USA). Where possible, starting points for nearshore transects were located ≤25 m from shore and starting points for offshore transects were located ~100 m offshore from nearshore starting points. We selected transects using a stratified random sampling design (Johnson & Nielsen 1983) along the longitudinal reservoir gradient. Transects were parallel to shore, fixed (i.e. sampled repeatedly) within a year and rerandomised in each subsequent year. We sampled transects after dark using two 0.5-m diameter, 750-µm mesh, bow-mounted icthyoplankton push nets. The nets were pushed at ~0.7 m/s for 5 min (approximately 200 m) per transect, or until nets became clogged. We estimated age-0 larval fish densities by recording the volume of water filtered through each net, using a calibrated flow meter (Model 2030 flow meter; General Oceanics, Miami, FL, USA) attached to the mouth of each net. After completing each sampling transect, we collected water-temperature and zooplankton-assemblage data to better understand factors influencing early life his-

tory of fishes in these reservoirs. We measured water temperature (°C) within 0.5 m of the water's surface using a YSI multimeter (model 556; YSI Environmental, Yellow Springs, OH, USA). We sampled the zooplankton assemblage from the top 2 m of the water column using a 2.1-m (7.5-cm diameter, 8.8-l volume) plastic tube sampler placed vertically in the water column (DeVries & Stein 1991). We filtered the sample through an 80-µm mesh net, preserved the sample with 4% sucrose–formalin solution (Haney & Hall 1973) and transported the sample back to the laboratory. We identified, enumerated and measured (TL, nearest 0.1 mm; up to 10 individuals per taxon) a 25% subsample of zooplankton from each sample. If <250 total zooplankters were counted in a subsample, we processed additional 25% subsamples until ≥250 total zooplankters were counted. We identified calanoid and cyclopoid copepods to order, copepod nauplii to subclass and *Bosmina* and *Daphnia* to genus. We examined stomach contents of all captured age-0 larval walleye and white bass. We removed individual prey items from the stomach by dissection and identified them to the lowest possible taxonomic group using a dissecting microscope to determine which zooplankton were important to larval walleye and white bass diets (using the linear index of food selection (Strauss 1979); J. DeBoer unpublished data).

We sampled age-0 juvenile walleye and white bass every other week beginning in late August and continuing until mid-October from 2008 to 2011; autumn assessments of age-0 fish targeted water temperatures between 10 and 20 °C to maximise catch per unit effort (CPUE) (Borkholder & Parsons 2001). We sampled at night using a boat electrofisher with pulsed DC, along 100-m transects in ≤2 m water depth. We sampled 9 randomly selected shoreline transects every other week during 2008 and 2009 and 12 randomly selected shoreline transects every other week during 2010 and 2011. We randomly selected starting points for transects using GIS software and rerandomised transects for each sampling trip. We netted, enumerated and measured (total length (TL), mm) only walleye and white bass. We collected water-temperature data at the end of each transect, as detailed above. For age-verification purposes (i.e. confirming that fish were age 0), we removed sagittal otoliths from up to 25 walleye and 25 white bass (that we believed to be age 0, based on size) per sampling week and transported otoliths to the laboratory for further processing. We air-dried sagittal otoliths from juvenile walleye and white bass and placed them in a water-filled black plastic cap; a single reader viewed otoliths through a dissecting microscope to confirm that these fish were age-0 individuals (and not ≥ age 1).

We sampled gizzard shad using small-mesh gillnets in cooperation with NGPC staff during autumn from 2008 to 2011. A standard small-mesh gillnet survey consisted of 2 monofilament gillnets that were set overnight once in each reservoir during September of each year. Gillnets were 60.9 m long and 1.8 m deep, with two 30.45-m panels consisting of 1.3- and 1.9-cm bar mesh. We identified (to species), enumerated and measured (TL, 10-mm length groups) all fish captured.

We sampled age-1 juvenile walleye and white bass and adult walleye and white bass using experimental gillnets in cooperation with NGPC staff during autumn from 2008 to 2012. A standard experimental gillnet survey consisted of four monofilament gillnets that were set overnight once in each reservoir during October 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 measured (TL, mm) and weighed (g) the first 10 white bass and 10 walleye from each cm length group. Subsequent walleye and white bass from each cm length group were only enumerated. A single reader from NGPC determined ages of captured walleye and white bass (from experimental gillnet surveys) using scales pressed into acetate slides and a microfiche reader (Smith 1954).

## Data analyses

We modelled factors affecting age-0 larval walleye and white bass abundances, age-0 juvenile walleye and white bass abundances and age-1 juvenile walleye and white bass abundances using data from Enders, Red Willow and Medicine Creek reservoirs. For all models, we only included data from Red Willow reservoir for 2008 and 2009 because an extreme drawdown occurred at the reservoir during winter 2009 (Chizinski et al. 2014; DeBoer et al. in press). We indexed age-0 larval walleye, white bass and gizzard shad abundances (from the larval trawls) as the maximum mean daily densities for each reservoir and year. We indexed diet zooplankton taxa abundances for age-0 larval walleye and age-0 larval white bass as the mean densities of diet taxa (collected from larval trawl locations) pooled across days for each reservoir and year. We indexed age-0 juvenile walleye and age-0 white bass abundances as the maximum mean daily CPUE (number per hour of electrofishing) for each reservoir and year. We indexed mean size and maximum size of age-0 juvenile walleye and white bass as the mean and maximum for each species for each reservoir and year for fish captured after September 15 (i.e. during the last two sampling events) of each year. We chose to truncate the data to the period when fish had likely completed growth for the year (because of cooling water temperatures), which is a critical benchmark for many temperate freshwater fishes (e.g. Johnson & Evans 1991; Hurst & Conover 1998; Sutton & Ney 2001). We indexed age-1 juvenile walleye and age-1 juvenile white bass abundances as the CPUE (number per gillnet night) for each reservoir and year.

We indexed spring warming rate (during larval fish sampling period) as the slope of the regression line from modelling the mean daily water temperature as a function of day of year for each reservoir and year. We indexed autumn cooling rate (during juvenile fish sampling period) as the slope of the regression line from modelling the mean daily water temperature as a function of day of year for each reservoir and year. We indexed the rate of spring water-level change as the slope of the regression line of water level versus day of year (i.e. February 1–April 30 for walleye, February 1–May 31 for white bass; typical open water period prior to predicted end of spawning). We indexed the rate of water-level change during irrigation season as the slope of the regression line of water level versus day of year (i.e. June 1–September 31; typical irrigation season). We indexed autumn gizzard shad abundance as the CPUE (number per gillnet night) from small-mesh gillnet surveys for each reservoir and year. We included gizzard shad because they numerically dominate the age-0 fish assemblage and are important prey for piscivores in these systems. We indexed body condition of adult (those with maturing gametes) walleye and white bass using relative weight ($W_r$; Wege & Anderson 1978). The equation for $W_r$ is as follows:

$$W_r = 100 \cdot W/W_s$$

where $W$ is total weight of the fish (g) and $W_s$ is the standard weight of the fish derived from equations (walleye: Murphy et al. 1990; white bass: Brown & Murphy 1991). We included adult condition because we believe a well-conditioned adult population could positively affect larval abundance (i.e. year-class strength, *sensu* Donelson et al. 2008; Venturelli et al. 2010). We intended to include walleye stocking as an independent variable, but larval walleye were stocked in all study reservoirs at similar densities during all years of study; thus, we did not include walleye stocking. We also included reservoir as a categorical variable.

We developed multiple linear regression model sets that best described ln(CPUE) for age-0 larval (during 2008–2011), age-0 juvenile (during 2008–2011) and age-1 juvenile (during 2009–2012) walleye and white bass independently. All independent variables were treated as random effects except for reservoir,

which was a fixed effect; we did not include nesting or interactions of variables. We log$_e$-transformed (ln [$x + 1$]) CPUE of each fish species and transformed independent variables when appropriate. We used independent Durbin–Watson tests for temporal auto-correlation on residuals in the candidate model sets. We assigned a 1-calendar-year advance to all independent variables used to model age-1 juvenile walleye and white bass abundances, so as to understand their effect on age-0 walleye and white bass. For example, we included autumn water temperature cooling rate from 2008 to model abundance of age-1 juvenile walleye from 2009, so as to understand the effect of autumn cooling rate on age-0 walleye. We screened independent variables for autocorrelation (using $r = 0.7$) and removed the less influential variable. We added independent variables to ontogenetic-stage-specific models as they became relevant (i.e. the age-0 juvenile model contains all variables in the age-0 larval model, plus additional variables; Tables 1 and 2). We developed a complete model set using an all-subsets approach. This resulted in 128 possible models in the complete age-0 larval model

sets, 1,024 possible models in the complete age-0 juvenile model sets and 65,536 possible models in the complete age-1 juvenile model sets. These large complete model sets are not problematic because we did not use a significance approach, but rather we selected a candidate model set from the complete model set using Akaike's Information Criterion (Akaike 1987) corrected for small sample size (AIC$_c$, Hurvich & Tsai 1989). We excluded models with a $\Delta$AIC$_c > 2$ from the candidate model set (*sensu* Royall 1997). We calculated $R^2$ for each model in the candidate set to evaluate goodness of fit. We assessed relative variable importance (hereafter, 'importance'; $1 =$ very important, $0 =$ not important) by summing the AIC$_c$ weights over all models including the explanatory variable (Murray & Conner 2009). The relative variable importance is the probability that, of the variables considered, a certain variable is in the best approximating model (Yu et al. 2014). We used SAS (Version 9.2, SAS Institute Inc., Cary, NC) and R (Version 3.0.1, The R Foundation for Statistical Computing; Vienna, Austria) for statistical analyses.

Table 1. Input variables for models and explanation of variable abbreviations. We obtained annual water-level fluctuation data from the U.S. Bureau of Reclamation. We obtained fish data from our own surveys and from standardised gillnet surveys conducted by the Nebraska Game and Parks Commission during 2008–2012.

| Model variable | Explanation | Age-0 larval models | | Age-0 juvenile models | | Age-1 juvenile models | |
|---|---|---|---|---|---|---|---|
| | | Walleye | White bass | Walleye | White bass | Walleye | White bass |
| RES | Reservoir | X | X | X | X | X | X |
| LARV_WAE | Larval walleye abundance (N·m$^{-3}$) | X† | X | X | X | X | X |
| LARV_WHB | Larval white bass abundance (N·m$^{-3}$) | X | X† | X | X | X | X |
| LARV_GSD | Larval gizzard shad abundance (N·m$^{-3}$) | X | X | X | X | X | X |
| SPR_RATE | Spring water temperature warming rate (°C per day of year) | X | X | X | X | X | X |
| WAE_Wr | Relative weight ($W_r$) of adult walleye | X | | X | | X | |
| WAE_SPRING | Rate of spring water-level change from Feb 1 – April 30 | X | | X | | X | |
| WAE_ZOOPS | Abundance of zooplankton selected for by larval walleye (N·l$^{-1}$) | X | | X | | X | |
| WHB_Wr | $W_r$ of adult white bass | | X | | X | | X |
| WHB_SPRING | Rate of spring water-level change from Feb 1–May 31 | | X | | X | | X |
| WHB_ZOOPS | Abundance of zooplankton selected for by larval white bass (N·l$^{-1}$) | | X | | X | | X |
| JUV_WAE | Catch per unit effort (CPUE) of juvenile walleye (catch per minute of electrofishing) | | | X† | X | X | X |
| JUV_WHB | CPUE of juvenile white bass (catch per minute of electrofishing) | | | X | X† | X | X |
| IRRIG | Rate of water-level change during typical irrigation season from June 1–Sept 31 | | | X | X | X | X |
| AGE1_WAE | CPUE of age-1 walleye (catch per gillnet night) | | | | | X† | X |
| AGE1_WHB | CPUE of age-1 white bass (catch per gillnet night) | | | | | X | X† |
| AUT_RATE | Autumn water temperature cooling rate (°C per day of year) | | | | | X | X |
| JWAE_MAX | Maximum total length (TL) of juvenile walleye | | | | | X | |
| JWAE_MEAN | Mean TL of juvenile walleye | | | | | X | |
| JWHB_MAX | Maximum TL of juvenile white bass | | | | | | X |
| JWHB_MEAN | Mean TL of juvenile white bass | | | | | | X |
| GSD_SM | CPUE of gizzard shad (catch per gillnet night) | | | | | X | X |

†Used as dependent variable.

## Results

### Age-0 larval walleye and white bass models

Durbin–Watson tests for temporal autocorrelation on all age-0 larval model residuals were not significant. The candidate model set for age-0 larval walleye (Table 3) included one model with a $\Delta AIC_c \leq 2$, the global model. Larval gizzard shad abundance, larval white bass abundance and $W_r$ of adult walleye had a negative effect on age-0 larval walleye abundance, whereas spring warming rate, rate of spring water-level change and walleye diet zooplankton taxa abundance had a positive effect. There was a consistent pattern in these variables among the reservoirs, with greatest age-0 larval walleye abundance at Red Willow reservoir and least age-0 larval walleye abundance at Medicine Creek reservoir. The model had an $R^2$ of 0.80, and each independent variable had an importance of 1.

The candidate model set for age-0 larval white bass (Table 3) included one model with a $\Delta AIC_c \leq 2$, the global model. Larval gizzard shad abundance, larval walleye abundance, spring warming rate and white bass diet zooplankton taxa abundance had a negative effect on age-0 larval white bass abundance, whereas $W_r$ of adult white bass and rate of spring water-level change had a positive effect. There was a consistent pattern in these variables among the reservoirs, with greatest age-0 larval white bass abundance at Enders reservoir, and least age-0 larval white bass abundance at Red Willow and Medicine Creek reservoirs. The model had an $R^2$ of 0.97, and each independent variable had an importance of 1.

### Age-0 juvenile walleye and white bass models

Durbin–Watson tests for temporal autocorrelation on all age-0 juvenile model residuals were not significant. The candidate model set for age-0 juvenile walleye (Table 3) included two models with a $\Delta AIC_c \leq 2$. Larval gizzard shad abundance had a positive effect on age-0 juvenile walleye abundance, and rate of water-level change during irrigation season had a negative effect. The top model had an $AIC_c$ weight more than double that of the second model. The mean $\pm$ SE $R^2$ for the age-0 juvenile walleye candidate model set was $0.57 \pm 0.17$. Larval gizzard shad abundance had an importance of 0.63, and rate of water-level change during irrigation season had an importance of 0.43.

The candidate model set for age-0 juvenile white bass (Table 3) included one model with a $\Delta AIC_c \leq 2$. Larval white bass abundance had a positive effect on age-0 juvenile white bass. The model had an $R^2$ of 0.71, and larval white bass abundance had an importance of 0.96.

### Age-1 juvenile walleye and white bass models

Durbin–Watson tests for temporal autocorrelation on all age-1 juvenile model residuals were not significant. The candidate model set for age-1 juvenile walleye (Table 3) included one model with a $\Delta AIC_c \leq 2$. Autumn cooling rate and gizzard shad CPUE both had a negative effect on age-1 juvenile walleye abundance. The model had an $R^2$ of 0.77. Autumn cooling rate had an importance of 0.72, and gizzard shad CPUE had an importance of 0.49.

Table 2. Mean $\pm$ SE of variables (refer to Table 1 for units) used to model recruitment of walleye and white bass. Data are from Enders, Red Willow and Medicine Creek reservoirs in the Republican River basin, Nebraska, USA 2008–2011 (Red Willow 2008–2009 only).

| Variable | Enders | Red Willow | Medicine Creek | Overall |
|---|---|---|---|---|
| LARV_WAE | 0.1 ± 0.04 | 0.2 ± 0.09 | 0.07 ± 0.02 | 0.1 ± 0.02 |
| LARV_WHB | 0.09 ± 0.04 | 0.07 ± 0.03 | 0.02 ± 0.003 | 0.06 ± 0.02 |
| LARV_GSD | 8.9 ± 4.2 | 5.6 ± 0.9 | 6.0 ± 1.4 | 7.1 ± 1.7 |
| SPR_RATE | 0.2 ± 0.01 | 0.2 ± 0.003 | 0.2 ± 0.01 | 0.2 ± 0.005 |
| WAE_Wr | 86.4 ± 1.4 | 88.0 ± 3.3 | 89.9 ± 1.9 | 88.1 ± 1.1 |
| WAE_SPRING | 0.01 ± 0.003 | 0.001 ± 0.002 | 0.01 ± 0 | 0.01 ± 0.002 |
| WAE_ZOOPS | 49.2 ± 6.2 | 55.1 ± 17.5 | 52.2 ± 8.1 | 51.6 ± 4.6 |
| WHB_Wr | 92.3 ± 2.8 | 92.8 ± 5.4 | 95.4 ± 2.7 | 93.6 ± 1.7 |
| WHB_SPRING | 0.01 ± 0.003 | 0.02 ± 0.01 | 0.01 ± 0.002 | 0.01 ± 0.002 |
| WHB_ZOOPS | 62.6 ± 5.3 | 70.6 ± 19.8 | 110.7 ± 14.0 | 83.4 ± 9.7 |
| JUV_WAE | 0.2 ± 0.1 | 0.1 ± 0.09 | 0.3 ± 0.09 | 0.2 ± 0.06 |
| JUV_WHB | 2.2 ± 0.4 | 1.9 ± 0.7 | 1.3 ± 0.2 | 1.8 ± 0.2 |
| IRRIG | −0.01 ± 0.002 | −0.03 ± 0.01 | −0.05 ± 0.01 | −0.03 ± 0.01 |
| AGE1_WAE | 4.6 ± 3.2 | 1.5 ± 0.8 | 1.3 ± 0.5 | 2.7 ± 1.3 |
| AGE1_WHB | 4.9 ± 3.9 | 0.5 ± 0.5 | 6.1 ± 2.4 | 4.5 ± 1.8 |
| AUT_RATE | −0.2 ± 0.03 | −0.2 ± 0.06 | −0.2 ± 0.03 | −0.2 ± 0.02 |
| JWAE_MAX | 221.0 ± 17.4 | 217.0 ± 29.0 | 206.5 ± 16.2 | 214.4 ± 10.0 |
| JWAE_MEAN | 179.9 ± 15.0 | 183.4 ± 24.6 | 167.6 ± 12.3 | 175.7 ± 8.3 |
| JWHB_MAX | 190.8 ± 14.6 | 199.5 ± 28.5 | 223.8 ± 5.9 | 205.7 ± 8.7 |
| JWHB_MEAN | 117.3 ± 12.4 | 137.9 ± 5.4 | 140.0 ± 2.8 | 130.5 ± 5.9 |
| GSD_SM | 63.8 ± 29.9 | 108.5 ± 104.0 | 162.5 ± 85.9 | 112.2 ± 39.5 |

Table 3. Parameter estimates for variables (Table 1) in candidate model set for age-0 larval, age-0 juvenile and age-1 juvenile walleye and white bass. Models with a ΔAIC_c > 2 were excluded from consideration. Data are from Enders (EN), Medicine Creek (MC) and Red Willow (RW) reservoirs in the Republican River basin, Nebraska, USA 2008–2011 (RW 2008–2009 only).

| Stage | Species | Model | Intercept | Variable | Parameter estimate | | $R^2$ | $\Delta AIC_c$ | $AIC_c$ $w$ |
|---|---|---|---|---|---|---|---|---|---|
| Age-0 larval | Walleye | 1 | 0.3 | RES | EN | 0 | 0.80 | 0 | 1 |
| | | | | | MC | −0.2 | | | |
| | | | | | RW | 0.05 | | | |
| | | | | LARV_GSD | | −0.08 | | | |
| | | | | LARV_WHB | | −1.2 | | | |
| | | | | SPR_RATE | | 5.9 | | | |
| | | | | WAE_K | | −1.6 | | | |
| | | | | WAE_SPRING | | 30.8 | | | |
| | | | | WAE_ZOOPS | | 0.002 | | | |
| | White bass | 1 | −0.8 | RES | EN | 0 | 0.97 | 0 | 1 |
| | | | | | MC | −0.1 | | | |
| | | | | | RW | −0.1 | | | |
| | | | | LARV_GSD | | −0.1 | | | |
| | | | | LARV_WAE | | −0.2 | | | |
| | | | | SPR_RATE | | −1.2 | | | |
| | | | | WHB_K | | 1.1 | | | |
| | | | | WHB_SPRING | | 9.1 | | | |
| | | | | WHB_ZOOPS | | −0.001 | | | |
| Age-0 juvenile | Walleye | 1 | −0.3 | LARV_GSD | | 0.2 | 0.73 | 0 | 0.72 |
| | | | | IRRIG | | −3.7 | | | |
| | | 2 | −0.1 | LARV_GSD | | 0.2 | 0.40 | 1.9 | 0.28 |
| | White bass | 1 | −0.8 | LARV_WHB | | 4.1 | 0.71 | 0 | 1 |
| Age-1 juvenile | Walleye | 1 | −0.5 | AUT_RATE | | −13.2 | 0.77 | 0 | 1 |
| | | | | GSD_SM | | −0.3 | | | |
| | White bass | 1 | 0.1 | JUV_WAE | | 5.7 | 0.71 | 0 | 0.58 |
| | | 2 | 1.2 | JUV_WAE | | 7.4 | 0.83 | 0.64 | 0.42 |
| | | | | AUT_RATE | | 7.5 | | | |

The candidate model set for age-1 juvenile white bass (Table 3) included two models with a ΔAIC_c ≤ 2. Age-0 juvenile walleye abundance and autumn cooling rate had a positive effect on age-1 juvenile white bass abundance. Both models had an AIC_c weight of >0.4. The mean ± SE $R^2$ for the age-0 juvenile white bass candidate model set was 0.77 ± 0.06. Age-0 juvenile walleye abundance had an importance of 0.83, and autumn cooling rate had an importance of 0.22.

## Discussion

It is imperative to accurately describe factors influencing year-class strength of sportfish. However, description of year-class strength has been difficult; many fishes require different prey and habitat while progressing through their first year of life, and other biotic and abiotic factors that may affect year-class strength are difficult to identify. Overall, our models demonstrate the interdependency among early ontogenetic stages and the complexities involved with sportfish recruitment processes. Our models explained 40%–80% (68 ± 9%; mean ± SE) and 71%–97% (81 ± 6%) of the variability in catch for walleye and white bass respectively; this compares favourably with other models describing year-class strength of walleye (31%, Quist et al. 2003; 57%–

97%, Hoxmeier et al. 2004; 66%–69%, DeBoer et al. 2013) and white bass (31%–36%, DeBoer et al. 2013) in multiple water bodies. Environmental factors often explain much of the variation in year-class strength observed in fish populations (Boehlert & Mundy 1988; Hansen et al. 1998; Daskalov 1999; DeBoer et al. 2013; Uphoff et al. 2013; Kaemingk et al. 2014a); these factors are more identifiable if fish abundances are monitored during each of the early ontogenetic stages from hatch to recruitment (Forney 1976; Hoxmeier et al. 2006), as survival gradually increases through early ontogenetic stages (Houde 2002).

### Age-0 larval walleye and white bass

Age-0 larval walleye abundance was negatively related with both larval gizzard shad abundance and age-0 larval white bass abundance; age-0 larval white bass abundance was negatively related with both larval gizzard shad abundance and age-0 larval walleye abundance. This is likely because larval walleye (or saugeye *Sander vitreus* × *S. canadensis*) and white bass may compete for resources with each other (Michaletz et al. 1987; Beck et al. 1998), as well as larvae of other species, including gizzard shad (Michaletz et al. 1987; Dettmers & Stein 1992; Quist et al. 2004), yellow perch, (Michaletz et al. 1987)

and black crappie (Pope et al. 1996; Galinat et al. 2002). Thus, it is likely that age-0 larval walleye and white bass abundances are greater in years or reservoirs with fewer competitors.

Age-0 larval walleye abundance was positively related with walleye diet zooplankton taxa abundance, although age-0 larval white bass abundance was negatively related with white bass diet zooplankton taxa abundance. It is likely that age-0 larval walleye abundance is greater in years or reservoirs with greater preferred zooplankton abundance. Conversely, although white bass-preferred zooplankton prey may be abundant, they could be larger or smaller than the size range preferred by age-0 larval white bass (Michaletz et al. 1987; Beck et al. 1998), which could partially explain the negative relationship seen in our model.

Age-0 larval walleye abundance was positively related with spring warming rate, a similar effect to walleye recruitment in Lake Erie (Madenjian et al. 1996). Unlike age-0 larval walleye abundance, age-0 larval white bass abundance was negatively related with spring warming rate. Rapidly warming water temperature during incubation leads to better survival of fish eggs (Colby et al. 1979), as colder temperature can delay hatching (Becker 1983; Pflieger 1997) and subject fish eggs to increased risk of predation and sedimentation (Schaeffer & Margraf 1987; Lisle 1989; Steinhart et al. 2004; Kock et al. 2006). Greater survival during the egg stage could result in greater age-0 larval walleye abundances. Additionally, fish grow faster when enzymatic and metabolic activity increases with temperature (Higley et al. 1986; Clarke & Johnston 1999), and there is a high correlation between growth and survival for age-0 fish (reviewed by Sogard 1997). Age-0 walleye growth (and presumably survival) was positively affected by the number of growing-degree days in a nearby reservoir (Uphoff et al. 2013). The negative relationship between spring warming rate and age-0 larval white bass abundance was unexpected, given that growth of white bass has been positively correlated to water temperature (Ruelle 1971) or air temperature (Pope et al. 1997; Phelps et al. 2011). In our systems, it is possible that warmer temperatures allow potential competitors (i.e. earlier hatching larval fish such as walleye) a greater advantage than larval white bass, thus resulting in the negative relationship seen in our age-0 larval white bass model.

Age-0 larval walleye and white bass abundances were positively related with rate of spring water-level change. Constant postspawn water levels in reservoirs are important for survival of walleye and sauger eggs (Walburg 1972; Groen & Schroeder 1978), and year-class strength of walleye has been positively correlated with increases in reservoir spring water level (Cohen & Radomski 1993). Although walleye year-class strength was negatively related to spring water level in Kansas, low spring elevations were observed in years with high storage ratios (i.e. stable water levels) and relatively small increases in water level (Quist et al. 2003). Additionally, walleye, saugeye and white bass often produce strong year classes in wet years (Martin et al. 1981; Sammons & Bettoli 2000). As a consequence of increasing spring water levels in reservoirs, there is a greater availability of spawning habitat, which can have a direct benefit on white bass year-class strength (Beck et al. 1997; Pope et al. 1997; DiCenzo & Duval 2002). In addition, incoming water flows have been directly linked to white bass spawning success (Martin et al. 1981; DiCenzo & Duval 2002), as have spring air temperature and precipitation (Pope et al. 1997; Sammons & Bettoli 2000; Quist et al. 2002; Schultz et al. 2002), which may influence incoming water flow.

Age-0 larval walleye abundance was negatively related with adult walleye $W_r$, whereas age-0 larval white bass abundance was positively related with adult white bass $W_r$. Walleye populations in these reservoirs are augmented by stocking; white bass populations in these reservoirs are not augmented by stocking and are thus reliant on natural production. Parents in better condition can commence spawning earlier and increase their reproductive output, relative to parents in worse condition (Donelson et al. 2008). Earlier spawning generally results in offspring having a longer first growing season, which affords them the potential for increased size; larger size often provides benefits to offspring by reducing their susceptibility to size-selective mortality (Eckmayer & Margraf 2004; Donelson et al. 2008). Offspring from parents with a higher condition survive better than offspring from parents with a lower condition (Donelson et al. 2008; Venturelli et al. 2010); thus, larval fish could be more abundant in systems that have parental fish with a higher condition and could thus suffer negative density-dependent effects if food is limited and competitors (either inter- or intraspecific) are abundant. Alternatively, the negative effect of adult walleye condition could be manifesting itself indirectly, perhaps via predator–prey interaction. Populations of adult walleye with a high $W_r$ could be indicative of abundant adult walleye prey such as gizzard shad (Madenjian et al. 1996; VanDeHey et al. 2014), which can produce abundant gizzard shad larvae (Miller 1960; Pierce 1977) that could compete with larval walleye if preferred larval walleye prey is limiting (Michaletz et al. 1987; Quist et al. 2004), thus indirectly manifesting the negative effect of adult walleye condition on age-0 larval walleye abundance.

For age-0 larval walleye and white bass, the disparities in abundance indices among reservoirs (Table 3) are likely resultant from differences in the variables described above, as well as other regulating factors that we did not include in our models. It was not possible to differentiate among the variables in the age-0 larval walleye and white bass models using importance because the global model was the only model selected for both species; thus, all variables in the candidate models had an importance of 1. Nonetheless, it is important to understand the nature of the effect that each variable had on age-0 larval walleye and white bass abundances.

### Age-0 juvenile walleye and white bass

The most important variable in the age-0 juvenile walleye candidate model set was larval gizzard shad abundance during spring. The relationship was positive, indicating years (or reservoirs) with greater larval gizzard shad abundance had greater relative abundances of age-0 juvenile walleye. This is interesting, given the negative relationship seen above between age-0 larval walleye and larval gizzard shad. As we stated, larval walleye can compete for resources with larval gizzard shad; conversely, age-0 juvenile walleye are known to prey preferentially on age-0 shad (Hartman & Margraf 1992; Einfalt & Wahl 1997). Thus, the presence of an abundant competitor at one ontogenetic stage can have a different effect than the presence of an abundant prey at a later stage.

The second most important variable in the age-0 juvenile walleye candidate model set was rate of water-level change during irrigation season. In these reservoirs, summer water levels are typically regulated by the nuances of agricultural irrigation demands; thus, the rate of water-level change during irrigation season is generally negative. The relationship between age-0 juvenile walleye abundance and rate of water-level change was negative, indicating years (or reservoirs) with a faster rate of water-level change during irrigation season (i.e. greater water-level decrease) had higher relative age-0 juvenile walleye abundances. It is possible that quickly decreasing water levels concentrate age-0 walleye and their prey, resulting in greater foraging efficiency, and increased growth and survival of age-0 juvenile walleye. Furthermore, concentrated age-0 walleye should have greater catchability with our gear, and it is also possible their increased abundance is an artefact of increased catchability (*sensu* Schoenebeck & Hansen 2005).

The only variable in the age-0 juvenile white bass candidate model set was age-0 larval white bass abundance; the relationship was positive, indicating that greater age-0 juvenile white bass abundances are related to greater age-0 larval white bass abundances. We believe this indicates that there is no recruitment bottleneck for white bass in these systems between the age-0 larval and age-0 juvenile stages. However, neither age-0 larval abundance nor age-0 juvenile abundance was included in the age-1 juvenile white bass model (described below); thus, it seems unfeasible to use either age-0 stage as an early index of year-class strength for white bass (*sensu* Sammons & Bettoli 1998). It also seems possible that the overwinter period may be strongly regulating the year-class strength of white bass in these reservoirs.

### Age-1 juvenile walleye and white bass

The most important variable in the age-1 juvenile walleye candidate model set was autumn cooling rate; the relationship was negative, indicating that age-1 juvenile walleye abundance was positively related with a faster cooling rate (i.e. colder temperatures). The second most important variable in the age-1 juvenile white bass candidate model set was autumn cooling rate; counter to age-1 juvenile walleye, this relationship was positive, indicating that age-1 juvenile white bass abundance was negatively related with a faster cooling rate. Although the specific mechanism for this relationship is unknown, we suspect it may be a function of fish metabolism and thus growth and survival. A slower cooling rate during autumn would result in a higher basal metabolic rate (Kelso 1972; Madon & Culver 1993; *sensu* Jonas & Wahl 1998), which would require higher energy intake. Even if shad densities were high enough to sustain walleye growth, a high metabolic rate could deplete walleye energy reserves going into winter, reducing overwinter survival. However, fish grow faster when enzymatic and metabolic activity increase with temperature (Higley et al. 1986; Clarke & Johnston 1999); thus, a slower autumn cooling rate affords age-0 juvenile white bass a longer growing season (Wilde & Muoneke 2001). It is also possible that the decrease in overwinter survival is a function of predation; smaller age-0 walleye (Chevalier 1973; Pratt & Fox 2002) and white bass (Eckmayer & Margraf 2004) are more subject to over-winter predation by other fishes, perhaps a consequence of behavioural changes resulting from depleted energy reserves (Jonas & Wahl 1998). Indeed, for many temperate freshwater fishes, survival during the overwinter period is a key factor in determining year-class strength (e.g. Johnson & Evans 1991; Hurst & Conover 1998; Sutton & Ney 2001).

The second most important variable in the age-1 juvenile walleye candidate model set was gizzard shad CPUE; the relationship was negative, indicating reservoirs (or years) with fewer age-1 juvenile walleye

were related with greater gizzard shad abundances. We believe there is no direct mechanism by which gizzard shad affect age-1 juvenile walleye abundance, but that abundant gizzard shad larvae and juveniles can directly affect age-0 walleye abundance (described above) and thereby indirectly affect age-1 juvenile walleye abundance by affecting the number of walleye in a cohort at an early stage.

The most important variable in the age-1 juvenile white bass candidate model set was age-1 juvenile walleye abundance. The relationship was positive, indicating that age-1 juvenile white bass abundance is likely linked to age-1 juvenile walleye abundance; perhaps both fishes are responding to other factors in a similar manner. Thus, it is likely that resource conditions (e.g. stable hydrology: Sammons & Bettoli 2000; abundant prey: Michaletz et al. 1987; Beck et al. 1998) that favour year-class strength of white bass or walleye may also benefit the other.

## Conclusions

In reviewing the candidate model sets among stages for each species, it was interesting to note how the variables in each candidate model set changed, or did not change, as ontogenesis progressed. For walleye, gizzard shad were present in the candidate model sets for all three ontogenetic stages we assessed. However, the relationship between gizzard shad and walleye was both negative and positive, which highlights the complex interaction between these two species; potential competitors at one stage, predator and prey at another. For white bass, there was no unifying variable in all three stage-specific candidate model sets, although walleye abundance was present in two of the three white bass candidate model sets. We believe life-history similarities between these two species may link their ontogeny in these dynamic ecosystems; resource conditions that benefit one species likely also benefit the other. For both species, the variables included in the stage-specific candidate model sets were most often the variables added to the models as they became relevant at that ontogenetic stage; rarely were variables from preceding stages included in candidate model sets unless they were a relevant prey item (i.e. larval gizzard shad in the age-0 juvenile walleye candidate model set) or the abundance of a preceding ontogenetic stage (e.g. age-0 larval white bass abundance in the age-0 juvenile white bass candidate model set). These results demonstrate the interdependency among early ontogenetic stages and the complexities involved with sportfish recruitment.

It is important that we improve our knowledge about factors that regulate year-class strength of fish, particularly in unpredictable environments (Baccante et al. 2011). Comprehensive analyses of factors influencing recruitment to multiple early ontogenetic stages are seemingly rare in the literature (but see Ludsin & DeVries 1997; Hoxmeier et al. 2006; Kaemingk et al. 2014a), yet we were able to determine several factors affecting walleye and white bass year-class strength at multiple ontogenetic stages. This knowledge will improve our understanding of recruitment dynamics and overall ecology for these fishes, not only in Great Plains irrigation reservoirs, but also in other regions, habitat types and for other species as well. For example, there are numerous studies dealing with how environmental factors affect recruitment of stream-living salmonids (e.g. Lobón-Cerviá & Rincón 2004; Lobón-Cerviá 2007) in Europe, but far fewer for the same species in the North American parts of their expanded range. Similarly, future studies on environmental factors affecting striped bass (*Morone saxatilis*) or zander (*Sander lucioperca*) recruitment (e.g. Shideler & Houde 2014; Heikinheimo et al. 2014) might consider a research approach like ours from related species.

Additional studies on walleye and white bass recruitment should seek to assess if the factors we determined important translate to populations in natural lakes, flood-control reservoirs and irrigation reservoirs throughout a wet–dry cycle (incorporating floods and droughts). These types of studies are needed to better understand differences in recruitment dynamics among systems. Understanding the factors affecting year-class formation at different ontogenetic stages is important from a variety of perspectives (Maceina 1997), including improving the knowledge of fish ecology and effectively managing sportfish in irrigation reservoirs and other dynamic ecosystems.

Nebraska-Lincoln Institutional Animal Care and Use Committee (protocol # 07-03-013E).

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