

A population model for walleye in Nebraska irrigation reservoirs

By

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A population model for walleye in Nebraska irrigation reservoirs

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Understanding how and why fish population size changes between years is a central theme in fisheries ecology. Fishery agencies have limited time and financial resources, thus there is a need for a quantitative way to direct the limited time and financial resources so agencies can manage fisheries more efficiently. I developed a tool for fishery managers that synthesizes common population indices and evaluated the relative importance of those indices given varying uncertainty in age-0 walleye *Sander vitreus* survival. Under most circumstances, I determined that resources are best utilized in reducing age-0 survival uncertainty when understanding walleye population growth. I applied our model to walleye populations in irrigation reservoirs in southwest Nebraska to understand how often a strong year class must be produced to sustain walleye populations, and found that a strong year class must be produced at least once every four years at Harlan County Lake, Medicine Creek Reservoir, and Red Willow Reservoir, and once every 7 years at Swanson Reservoir. Additionally, I hypothesized the effects of increased water temperature resulting from climate change in the region, and determined that a strong year class must be produced at least once every 3 years at Harlan County Lake and Medicine Creek Reservoir, once every 2 years at Red Willow Reservoir, and once every 4 years at Swanson Reservoir to sustain walleye populations (i.e., populations had a higher risk of quasi-extinction during the climate change scenarios).

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Dedication

To my parents, for encouraging my curiosity in the natural world.

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CHAPTER 1. INCORPORATING COMMON POPULATION INDICES FOR WALLEYE INTO A COHESIVE TOOL TO BETTER UNDERSTAND CHANGES IN POPULATION GROWTH

Introduction

Understanding how and why fish population size changes between years is a central theme in fisheries ecology (e.g., Schaefer 1957, Nelson and Walburg 1977, Kaemingk et al. 2012). The development of tools that forecast fish population size dates back to at least 1918 (Baranov 1918). Since then, a wealth of knowledge has been developed to help understand fish population size changes including, but not limited to, stock-recruitment models (e.g., Beverton and Holt 1957, Ricker 1958, Shepherd 1982), growth models (e.g., von Bertalanffy 1938, Richards 1959, Ricker 1975), and condition indices (e.g., Le Cren 1951, Murphy et al. 1990, Wootton 1990).

A great amount of fisheries research is focused on survival during the first year of life (Miller et al. 1988, Thompson et al. 1991, Miranda and Hubbard 1994), because it is often regarded as the most important aspect regulating fish population dynamics (Gulland 1982). Direct measurements for survival during the first year of life are difficult to obtain (DeAngelis et al. 1993), thus recruitment indices are often developed to give managers and researchers insight into variability in survival during the first year (Maceina and Pereira 2007). Commonly, researchers link variability in survival during the first year of life to environmental influences such as water temperature, precipitation, predator abundance, and water level (e.g., Busch et al. 1975, Humphries et al. 1999, Cardinale and Arrhenius 2000).

Although survival during the first year of life is often considered the most important aspect regulating fish population dynamics, several other population indices

including individual growth, condition, and catch per unit effort are assessed through standardized sampling (Bonar and Hubert 2002). The aforementioned indices are especially abundant for sportfish because many agencies practice some form of standardized sampling for fish populations within a state (e.g., Gabelhouse et al. 1992, Bonar et al. 2000, Hayes et al. 2003). Even though sportfish population indices are ample and are utilized to inform management actions, they are rarely synthesized into standard tools, and are even less often scrutinized for the relative amount of useful information they provide (Bonar and Hubert 2002).

Fishery agencies, like most other entities, have limited time and financial resources. Fishing participation is on a decline in North America (Duda et al. 2009, Martin et al. 2012, Kuehn et al. 2013); thus, there is a need for a quantitative way to direct the limited time and financial resources so agencies can manage fisheries more efficiently. Given the underlying question of how and why fish population size changes between years, and the ample amount of data and population indices currently available for sportfish, it would be incredibly useful to synthesize the current information into a cohesive tool. Then, areas where more thorough information is needed can be identified and distinguished from areas where current information is sufficient.

The walleye *Sander vitreus* is widespread and among the most popular of sport fishes in North America (Craig 2000). Given walleye's popularity among anglers (Hurley and Duppong Hurley 2002) there has been an intense amount of research into understanding how and why populations change between years (e.g., Steen et al. 2010, Berger et al. 2012, Schueller et al. 2012). Additionally, several reviews are available for population indices across the range of walleye, including latitudinal differences in growth

(Quist et al. 2003), relative weight indices (Murphy et al. 1990), mortality estimates (Carlander 1997), and fecundity-weight relationships (Carlander 1997). The extent of published literature for walleye makes the development of a cohesive tool for understanding changes in population size between years relatively straightforward.

The first objective of this study was to develop a tool for fishery managers that synthesizes common population indices and increases the understanding of changes in population growth through time. The second objective was to evaluate the relative importance of each population index. Finally, given that survival during the first year of life is often considered to be the most important aspect regulating fish population dynamics, estimates for which are difficult to attain, the third objective was to evaluate the amount of precision required to justify focusing time and financial resources toward the improvement of other population indices.

Methods

Data collection

I gathered data from the literature for North American walleye populations. I used a review by Carlander (1997) to understand the distribution of annual survival probabilities and to construct a fecundity-weight relationship, Baccante and Colby (1996) to provide a range for survival during the first year of life, Quist et al (2003) for walleye growth, and Murphy et al. (1990) to construct a length-weight relationship. The population indices were used to parameterize a Leslie matrix model so we could gain a better understanding of how and why walleye populations change between years,

evaluate which population index influenced our understanding of walleye populations the greatest, and to elucidate avenues to focus limited management time and resources for the improvement of population indices.

Model development

I used the Leslie matrix model (Leslie 1945), assuming a birth-pulse, post-birth census (Caswell 1989), following closely to the recommendations of Horst (1977). The Leslie matrix model, in its simplest form, is a deterministic, age- or size-structured matrix (I used age-structured matrix because I reasoned it was more appropriate given our data) multiplied by a population vector:

$$\begin{bmatrix} F_0 & F_1 & F_2 & F_3 & \cdots & F_{a_{max}} \\ s_0 & 0 & 0 & 0 & \cdots & 0 \\ 0 & s_1 & 0 & 0 & \cdots & 0 \\ 0 & 0 & s_2 & 0 & \cdots & 0 \\ 0 & 0 & 0 & \ddots & \cdots & 0 \\ 0 & 0 & 0 & 0 & s_{a_{max}-1} & 0 \end{bmatrix} \times \begin{bmatrix} N_0 \\ N_1 \\ N_2 \\ \vdots \\ N_{a_{max}} \end{bmatrix}_t = \begin{bmatrix} N_0 \\ N_1 \\ N_2 \\ \vdots \\ N_{a_{max}} \end{bmatrix}_{t+1} \quad [1 - 1]$$

where s is the survival probability of age a individuals, F is the fecundity at age a , and N is the number of females from each age group. The population vector at time t is multiplied by the matrix to generate a new population vector at time $t + 1$. For purposes of this study, eigenanalysis was conducted on the matrix element (Caswell 1989) to calculate the leading eigenvector, which was transformed to population growth rate λ to represent the change in the walleye population between years.

Annual survival probability after the first year of life and individual longevity

The s elements, excluding the survival during the first year of life, of the Leslie matrix (equation 1-1) were assumed to be constant and were randomly selected from a normal distribution with the mean (0.51) and standard deviation (0.14) set to reflect the data reviewed by Carlander (1997; Figure 1-1). Following the selection of an annual survival probability, the longevity of individuals composing the population was calculated using the formula used by Mollet and Cailliet (2002):

$$a_{max} = \frac{-\ln(0.01)}{1 - s} [1 - 2]$$

where a_{max} represents the longevity of individuals composing the population, and is calculated assuming that 1% of individuals remain at the maximum age for individuals in that population.

Survival probability during the first year of life

Survival probability during the first year of life is notoriously difficult to measure, thus is not well-represented in the literature. In the only account I could find, it was estimated between 0.0001 and 0.0009 in two Canadian water bodies (Baccante and Colby 1996). Given limited knowledge on this aspect of walleye life history, survival probability during the first year of life was randomly selected from a uniform distribution between 0.0001 and 0.0009 for an initial analysis, then the range was increased post-hoc to demonstrate how the relative importance of precise measurement of survival during the first year of life (compared to the importance of precise measurement for other

population indices) changes with decreasing levels of uncertainty in survival during the first year of life.

Fecundity

The F elements (equation 1-1) were selected through a process beginning with the selection of a growth rate k , expressing how quickly an individual increases in length throughout life. Growth rate is represented in the von Bertalanffy growth equation (von Bertalanffy 1938):

$$L_a = L_\infty(1 - e^{-k(a-q)}) \quad [1 - 3]$$

where L_a is the length-at-age for individuals, L_∞ is the asymptotic maximum length, and q is the theoretical age when length equals 0. Values for k were selected from a random normal distribution with the mean (0.24) and standard deviation (0.08) representing those from the walleye growth review by Quist et al. (2003), minus an outlier (Figure 1-1). Additionally, the distribution of values available for k was restricted based on annual survival probability to reflect the tendency of fast growth to accompany low survival, and vice versa, for teleosts (i.e., fast growth could not accompany high survival and vice versa; Roff 1984). To account for covariance of parameters in length-at-age for individuals, I regressed L_∞ and q separately against k (Figure 1-2). The parameter value for L_∞ was randomly selected from a random normal distribution based on the slope of the regression (-810) and the standard deviation of the residuals (105; Figure 1-1). The parameter value for q was selected based solely off of the slope of the regression line, and therefore was not randomly varied (Figure 1-2). The latter was done post-hoc, because allowing q to vary randomly occasionally yielded highly unlikely lengths-at-age

(e.g., individuals attaining 400 mm total length by age-1, and only attaining 600 mm total length by age-8).

I used L_a to describe weight-at-age W_a with the following equation:

$$W_a = pL_a^r [1 - 4]$$

where p is a scaling parameter and r represents how quickly individuals gain weight (Wootton 1990). The values for r were selected from a random normal distribution with the mean (3.14) and standard deviation (0.24) representing those from the review by Murphy et al. (1990; Figure 1-1). To account for the covariance between r and p , I regressed p against r , then p was selected from a normal distribution based on the slope of the regression (-2.64) and the standard deviation of the residuals (0.05) from the review by Murphy et al. (1990; Figure 1-2).

The last step in determining the F elements (equation 1-1) for the Leslie matrix was relating fecundity to weight. I used W_a to describe the F elements by regressing walleye fecundity by weight from data collected by Carlander (1997; Figure 1-2). The y-intercept and slope were randomly selected from a normal distribution based on the slope of the regression (94.35) and the standard deviation (48.73) of the residuals.

Sensitivity analysis

Model parameters were randomly selected so 1,000 combinations of parameters could be formed (Appendix 1), representing many combinations of population indices that reflect changes in populations between years. To simulate 1,000 possible combinations, the entire parameter-selection process was repeated 1,000 times. The resulting λ of each iteration was then paired with model parameter values of each

iteration to assess the correlation between a given parameter and λ . Spearman's rank correlation coefficient was used to determine the sensitivity of λ to changes in each parameter because I suspected the relationship between a given parameter and λ might not be linear (Zar 1972). Spearman's rank correlation coefficients closer to 1.0 or -1.0 indicate the highest sensitivity of λ to that given parameter, thus elucidating the need for precise measurements of the represented population index to best understand changes in walleye population size between years. I did not test hypotheses with the sensitivity analysis, thus I did not assess statistical significance of the Spearman's rank correlations.

Results

The Spearman's rank correlation coefficients (Figure 1-3) for the simulations restricting the range of values representing survival during the first year of life to what has been observed for walleye populations (Baccante and Colby 1996) were greatest for the maximum length of individuals ($\rho = 0.58$) composing the population and survival after the first year of life ($\rho = 0.69$). The absolute values for the Spearman's rank correlation coefficients for model parameters representing the length-weight relationship, the weight-fecundity relationship, and survival during the first year of life were all < 0.15 . No Spearman's rank correlation coefficients were negative.

When the range of the model parameter representing survival during the first year of life was increased, representing increasing levels of uncertainty in the parameter, the Spearman's rank correlation coefficients increased for survival during the first year of life and decreased for survival after the first year of life (Figure 1-4). When uncertainty in survival during the first year of life was on the order of 0.001, the Spearman's rank

correlation coefficients for survival during the first year of life and after the first year of life were approximately equal at 0.50. When uncertainty in survival during the first year of life increased past the order of 0.001, the Spearman's rank correlation coefficient quickly increased for survival during the first year, and decreased for survival after the first year of life. The Spearman's rank correlation coefficients for all other parameters (excluding survival after the first year of life) remained approximately the same (Figure 1-4) given all levels of uncertainty in survival during the first year of life. When the Spearman's Rank Correlation coefficients were summarized for all levels of uncertainty in survival of individuals during the first year of life, I saw similar values for maximum length of individuals and survival of individuals throughout life (Figure 1-5).

Discussion

Maximizing understanding of fish populations with limited resources is a common goal of fishery agencies (Hilborn 2007), and is becoming more pertinent in an era with decreasing funding due to reduced participation in recreational angling (Duda et al. 2009, Martin et al. 2012, Kuehn et al. 2013). I have demonstrated the relative utility of several population indices on understanding walleye population growth rate, and unsurprisingly found that precision in some population indices (i.e., maximum length of individuals, age-0 survival) is far more beneficial than precision in other indices (i.e., length-weight relationship, the weight-fecundity relationship, and survival during the first year of life) when using our model. I hope I provided a useful tool for understanding changes in walleye populations from year to year, which should help direct research efforts that use the increasingly scarce time and financial resources of fishery agencies.

Our study demonstrates that increasing precision for estimates of the maximum length attainable by female walleye in a population is valuable in terms of understanding population changes from year to year. This suggests that understanding the spawning stock is valuable to predicting the recruits from the spawning season. Although the importance of maternal characteristics on recruits has been detected in walleye populations (Venturelli et al. 2010), many studies report poor fits of stock-recruit models to walleye populations (Walters and Ludwig 1981, Madenjian et al. 1996, Hansen et al. 1998). This could mean that variation caused by environmental factors overrides the effect of the number of spawners, for which this study lacked the resolution to account. That is, I modeled variation in age-0 survival and its effect on population growth rate, but I did not account for influences on the variation in age-0 survival. For that reason, I am skeptical that focusing resources on understanding the spawning stock (as suggested by the high correlation of population growth rate to maximum length of individuals) will provide the most understanding of changes in population size from year to year.

This model took into account observed variation in length-weight relationships, and the variation in length-weight relationships did not correlate highly with population growth rate. Although condition indices can be very valuable in detecting issues with fish populations such as low prey availability (Kohler and Kelly 1991, Hubert et al. 1994, Porath and Peters 1997), it likely is not beneficial in understanding walleye population growth rate. I assert that including length-weight relationships is important in using the model because it permits the fecundity calculation, but I believe it is sufficient to use the walleye standard weight regression (Murphy et al. 1990) in this model to project walleye

population growth rate because of the high number of data points used in the study by Murphy et al. (1990).

I recommend the use of the data summarized by Carlander (1997) to approximate weight-fecundity relationships, because of the low correlation between population growth rate and weight-fecundity relationships for walleye. I argue this for the same reason that I argued using the standard weight equation for walleye—although it completes the conversion of population indices to a fecundity element for our model, variation in the weight-fecundity relationship changes projected walleye population growth rate by relatively small amounts. I believe additional time and financial resources could be better utilized in understanding age-1 and older survival.

It is intuitive that increasing the precision of estimates for survival of individuals from one year to the next also increases the understanding of population growth from one year to the next. However, to our knowledge, this is the first study to quantify the relative importance of survival estimates under varying precision in the age-0 survival estimate. Age-0 survival estimates likely lack the precision required to justify focusing limited time and financial resources to developing the other common population indices in our model (e.g., condition, weight-fecundity, adult annual survival). The first assessment in this study used estimates for age-0 survival reported by Baccante and Colby (1996), and thus demonstrated the potential for increased precision in age-1 and older annual survival estimates to be more valuable in understanding population growth rate than increased precision in age-0 survival. However, the range in age-0 survival reported by Baccante and Colby (1996) did not include variance in the estimate, which may have been substantial given that the estimate for age-0 survival required an estimate

of egg production and an estimate of age-1 individuals, which would likely be difficult with traditional sampling and statistical techniques. Additionally, given it was one study from one area, I reason that it may not be appropriate to assume all walleye populations behave similarly.

A likely reason for relative imprecision in age-0 survival estimates is a direct result of the logistic difficulties in assessing age-0 survival. First of all, investigators would need to gain a precise estimate of walleye egg production that is difficult simply because collecting those eggs from a water body immediately after they were deposited is full of challenges (Katt et al. 2011). Then, investigators would need to estimate age-1 individuals in the population with a great amount of precision. The ratio of the mean estimates could then be calculated, which is likely to be accompanied by relatively high variance (Walters and Ludwig 1981). Given that understanding age-0 survival became more influential on modeled walleye population growth rate when uncertainty in the estimate increased beyond 0.0001, I conclude that, consistent with the status quo, age-0 survival is the most variable and influential of the rate functions on population dynamics (Gulland 1982).

Given the logistic difficulties in assessing age-0 survival and that uncertainty in age-1 and older survival also caused great uncertainty in population growth rate, perhaps focusing more time and financial resources on assessing age-1 and older survival would be the best an agency can do with current sampling capabilities. That is, it could be that, although more precise estimates for age-0 survival would likely be most beneficial for understanding changes in walleye populations between years, they may simply not be feasible. Precision in age-1 and older annual survival is likely much easier to increase

than precision in age-0 survival because of sampling capabilities (e.g., gill nets, trap nets). Data required for catch-curve analysis (Miranda and Bettoli 2007) is often already collected by agencies, but is not always precise, and the precision could probably be increased with relatively less effort than precision in age-0 survival.

In conclusion, I have provided a tool for managers to help improve understanding of changes in walleye populations from year to year. Population indices such as length-at-age, length-weight relationships, and weight-fecundity, while useful in many situations, do not increase our understanding of walleye population growth rate. Uncertainty in age-0 survival estimates causes the greatest amount of uncertainty in projected walleye population growth rate, but may prove to be too difficult to assess with high precision.

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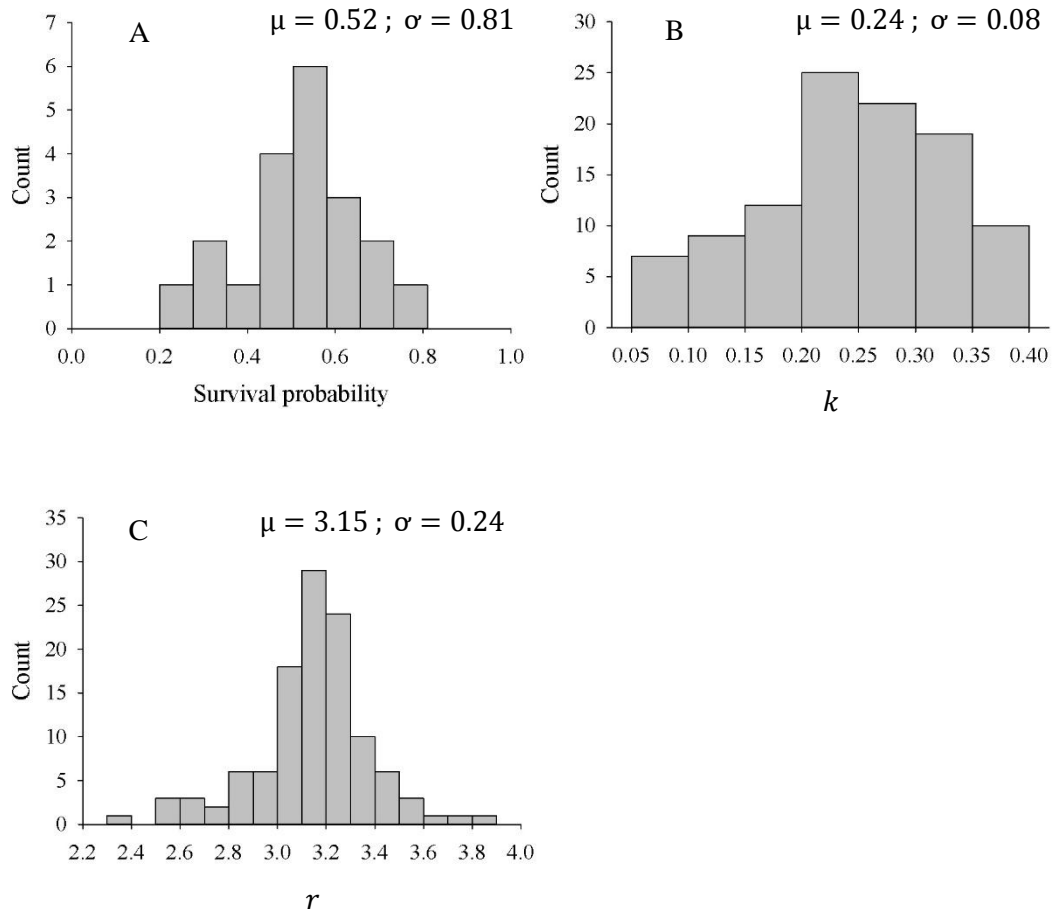


Figure 1-1. Frequency histogram of annual survival probabilities reported by Carlander (1997) for North American walleye populations (A), frequency histogram of individual growth rate k reported by Quist et al. (2003) for North American walleye populations (B), and frequency histogram of parameter r from the equation representing how quickly individuals gain weight per unit length, according to data reported by Murphy et al. (1990) for North American walleye populations (C).

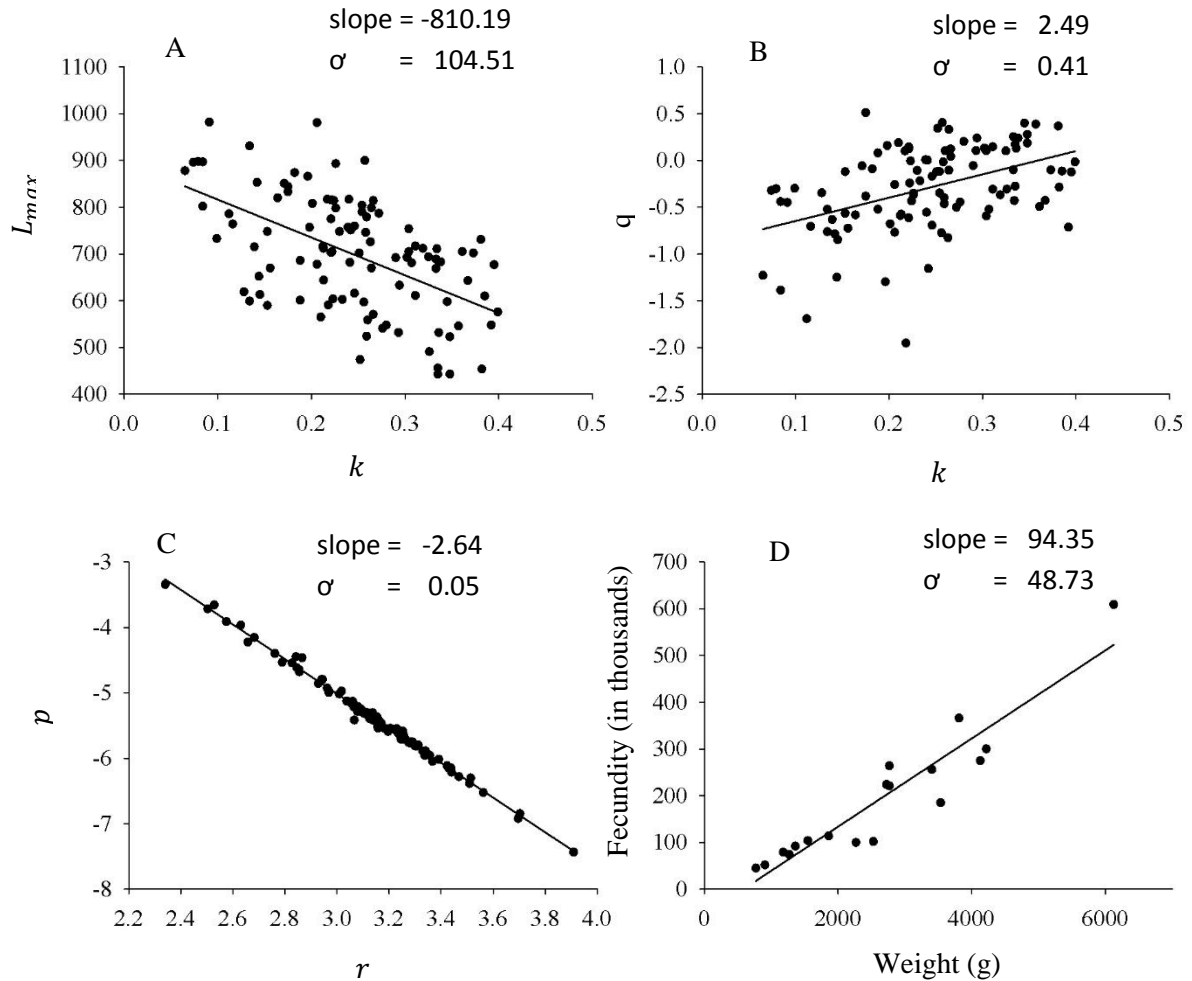


Figure 1-2. Regression of maximum length L_{max} against individual growth rate k using values reported by Quist et al. (2003) for North American walleye populations (A), regression of theoretical length when age equals zero q against individual growth rate k based off values reported by Quist et al. (2003) for North American walleye populations (B), regression of p against r , which are parameters from the equation used to represent how quickly individuals gain weight per unit length, according to values reported by Murphy et al. (1990) for North American walleye populations (C), and regression of fecundity against weight, according to values reported by Carlander (1997) for North American walleye populations (D). Slope is the slope of the regression line and σ is the standard deviation of the residuals of the regression.

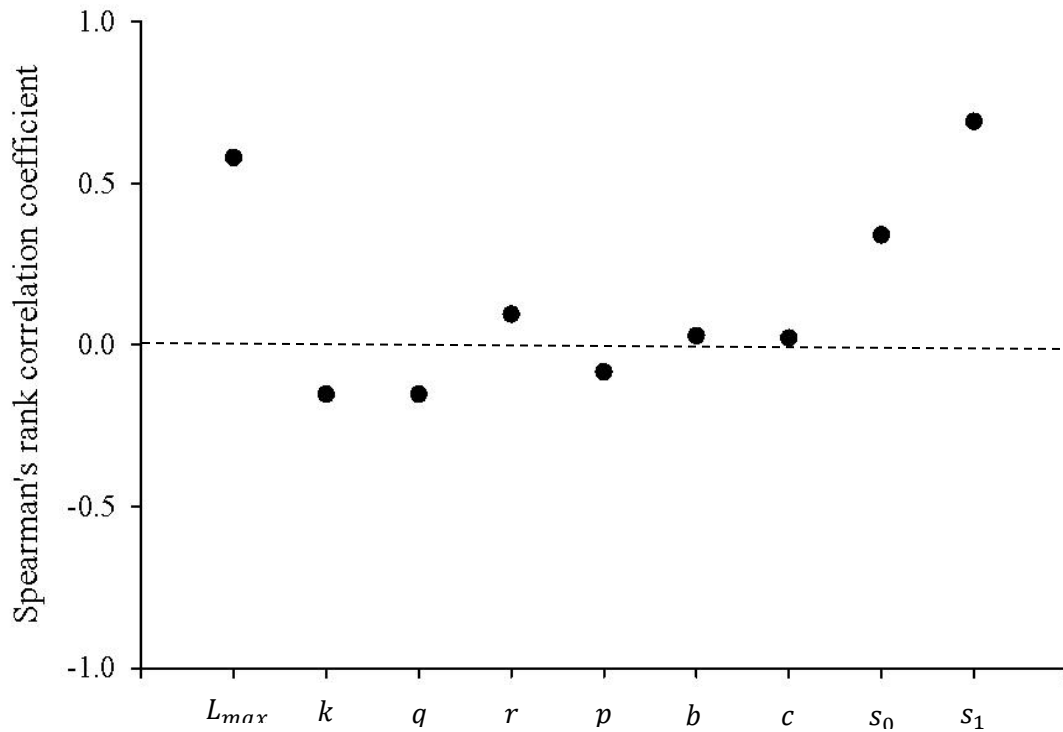


Figure 1-3. Spearman's Rank correlation coefficients of comparisons between population growth rate and model parameters for a walleye population model, assuming uncertainty in survival during the first year of life s_0 was adequately represented by Baccante and Colby (1996). Model parameters were maximum length of an individual L_{max} , individual growth rate k , theoretical age when length equals zero q , rate of weight gain per unit length r and p , the slope and intercept for the weight-fecundity relationship b and c , and survival after the first year of life s_1 . The dotted line is used as a reference line for a correlation of 0. The closer a particular model parameter is to 0, the less sensitive population growth rate is to changes in that parameter.

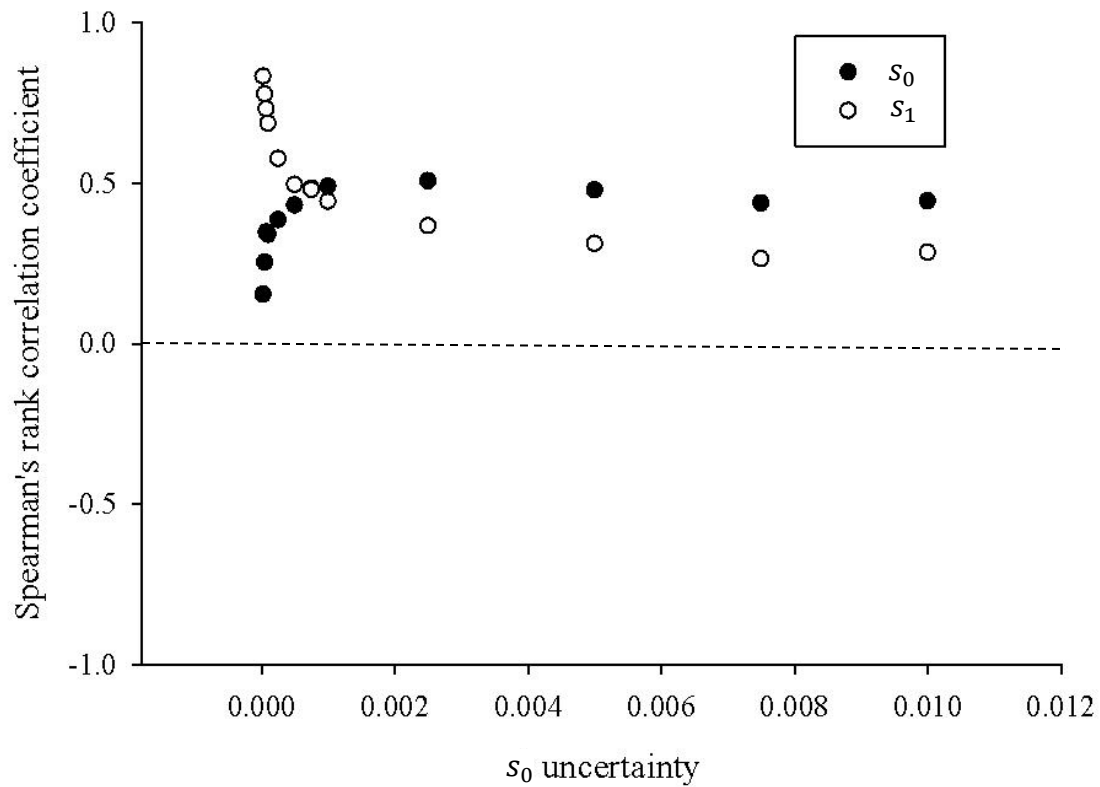


Figure 1-4. Spearman's Rank correlation coefficients of comparisons between population growth rate and model parameters for annual survival probability s_0 and s_1 for a walleye population model with increasing uncertainty in survival probability during the first year of life. The dotted line is used as a reference line for a correlation of 0. The closer a particular model parameter is to 0, the less sensitive population growth rate is to changes in that parameter.

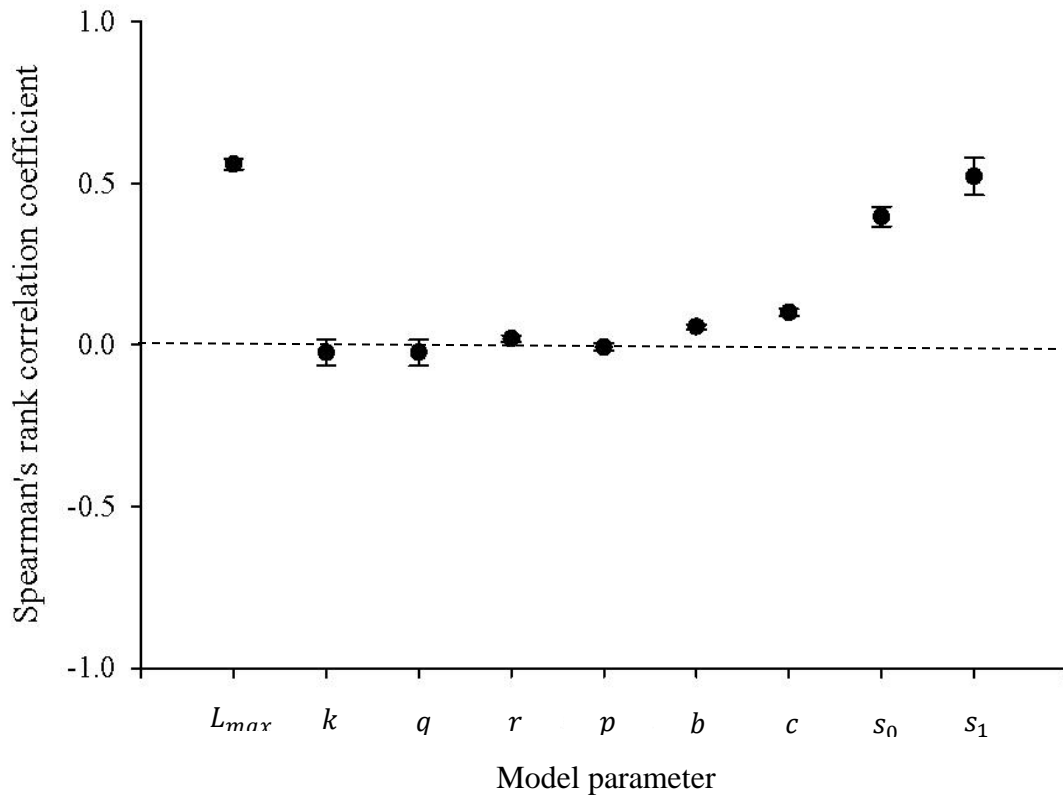


Figure 1-5. Summary of Spearman's Rank correlation coefficients of comparisons between population growth rate and model parameters for a walleye population model with increasing uncertainty in survival probability during the first year of life. Model parameters were maximum length of an individual L_{max} , individual growth rate k , theoretical age when length equals zero q , rate of weight gain per unit length r and p , the slope and intercept for the weight-fecundity relationship b and c , and survival after the first year of life s_1 . The points are the mean Spearman's Rank correlation coefficients, and the whiskers represent the standard error of the mean Spearman's Rank correlation coefficients. The dotted line is used as a reference line for a correlation of 0. The closer a particular model parameter is to 0, the less sensitive population growth rate is to changes in that parameter.

Appendix 1. R-programming code for chapter 1

```
#First load in data for survival, growth, length-weight,
weight-fecundity, and age-0 survival
wae <- read.csv("walleyelitdata.csv")
wae <- subset(wae,wae$k < 0.4) #Take out the outliers
hist(wae$k,xlab="k")
summary(wae$k)
sd(wae$k)
t0 <- wae$t0
t0 <- subset(t0, t0 > -3)

#Use linear model to account for covariation
growth.klmax <- lm(wae$Lmax~wae$k)
s.growth.klmax <- summary(growth.klmax)
growth.age <- lm(wae$Agemax~wae$Lmax)
summary(growth.age)
qk <- lm(new.t0$wae.t0~new.t0$wae.k)
summary(qk)
#Use linear model to account for covariation
limagek <- lm(wae$Agemax~wae$k)
summary(limagek)
wae2 <- read.csv("weightlength.csv")
plot(log10(wae2$W)~log10(wae2$TL),xlab="log10(TL)",ylab="log10(W)",main="r^2 = 0.94, P < 0.001")
#Use linear model to account for covariation
wl <- lm(log10(wae2$W)~log10(wae2$TL))
summary(wl)
conreg <- read.csv("condition.csv")
summary(conreg$r)
lmconreg <- lm(conreg$int~conreg$r)
summary(lmconreg)

wf <- read.csv("weight-fecundity.csv")
wfmod <- lm(wf$Fecundity~wf$Weight)
summary(wfmod)
#Age-1+ survival
survs <- read.csv("survivalcarlander.csv")
summary(survs$Survival)
#Age-0 survival using brute-force algorithm
#Find age-0 survival for lambda=1
best.surv <- seq(0.0000001,.0002,0.000001)
eigs.derv <- vector("numeric",length(best.surv))
find.eig <- vector("numeric",length(best.surv))
for(i in 1:length(best.surv)){
```

```

    leslie[2,1] <- best.surv[i]
    eigs <- eigen(leslie)
    dom.pos <- which.max(eigs[["values"]])
    L1 <- Re(eigs[["values"]][dom.pos])
    eigs.derv[i] <- L1
    find.eig[i] <- abs(L1-1)
  }
best.eig <- which.min(find.eig)
leslie[2,1] <- best.surv[best.eig]
s0l <- best.surv[best.eig]
eigs <- eigen(leslie)
dom.pos <- which.max(eigs[["values"]])
#Find population growth rate
L1 <- Re(eigs[["values"]][dom.pos])
w <- Re(eigs[["vectors"]][,dom.pos])
#Find stable-stage distribution
ssd <- w/sum(w)
#Build simulation model that randomly assigns population-
index values
t=1000 #number of iterations
N.walleye = matrix(ncol=6,nrow=t)#Not monitoring age-0
through time
N.walleye[1,]=ssd
eig.time <- matrix(ncol=1,nrow=t)
k.time <- matrix(ncol=1,nrow=t)
Lmax.time <- matrix(ncol=1,nrow=t)
ann.surv1.time<- matrix(ncol=1,nrow=t)
Q.time <- matrix(ncol=1,nrow=t)
p.time <- matrix(ncol=1,nrow=t)
r.time <- matrix(ncol=1,nrow=t)
c.time <- matrix(ncol=1,nrow=t)
b.time <- matrix(ncol=1,nrow=t)
s0.time <- matrix(ncol=1,nrow=t)
for(i in 1:t){
  #First get survival
  #Age 1+ survival
  ann.surv <- rnorm(1,0.5155,0.1427)
  ann.surv <- ifelse(ann.surv>0.99,0.99,ann.surv)
  ann.surv <- ifelse(ann.surv < 0,0.0001,ann.surv)
  ann.surv1.time[i] <- ann.surv
agemax <- floor((-log(0.01))/(1-ann.surv))+1 #+1 because of
how the LMM is set up (to include age-0)
age1 <- 1:agemax
leslie <- matrix(0,ncol=agemax,nrow=agemax)
leslie[row(leslie)==col(leslie)+1] <- ann.surv
#Growth

```

```

k <- ifelse(ann.surv >
mean(survs$Survival)+sd(survs$Survival),runif(1,mean(wae$k)
-sd(wae$k),mean(wae$k)),runif(1,mean(wae$k)-
sd(wae$k),mean(wae$k)+sd(wae$k)))
  k <- ifelse(ann.surv < mean(survs$Survival)-s
d(survs$Survival),runif(1,mean(wae$k),mean(wae$k)+sd(w
ae$k)),k)
Lmax <-
rnorm(1,coefficients(s.growth.klmax)[1,1]+k*coefficients(s.
growth.klmax)[2,1],sd(residuals(s.growth.klmax)))
Lmax <- ifelse(Lmax < 600, 600, Lmax)
Lmax.time[i,] <- Lmax
  #von B growth
  k.time[i,] <- k
  Q <-
coefficients(qk.sum)[1,1]+k*coefficients(qk.sum)[2,1]
  Q.time[i,] <- Q
  La <- Lmax*(1-exp(-k*(age1-Q)))
  #Length-weight
  r <- rnorm(1,mean(conreg$r),sd(conreg$r))
p <-
10^(rnorm(1,coefficients(sumcond)[1,1]+r*coefficients(sumco
nd)[2,1],sd(residuals(sumcond))))
  p.time[i,] <- p
  r.time[i,] <- r
  Wa <- p*La^r
  #Weight-Fecundity
  c <-
runif(1,coefficients(sum.wf)[2,1]*0.9,coefficients(sum.wf)[
2,1]*1.1)
  c.time[i,] <- c
  b <-
runif(1,coefficients(sum.wf)[1,1]*1.1,coefficients(sum.wf)[
1,1]*0.9)
  b.time[i,] <- b
  Fa <- (Wa*c + b)/2
  #Age at maturity
  Fa <- ifelse(Fa>0,Fa,0)
  Fa[is.na(Fa)] <- 0
  leslie[1,] <- Fa*1000
  Fa.time[i] <- sum(Fa*1000)
  #Age-0 survival
  #Baccante and Colby low survival -- 0.000091 high
survival -- 0.0001
  leslie[2,1] <- runif(1,0.00001,0.0025)
  s0.time[i,] <- leslie[2,1]
  eigs <- eigen(leslie)

```

```

    dom.pos <- which.max(eigs[["values"]])
    L1 <- Re(eigs[["values"]][dom.pos])
    eig.time[i,] <- L1
  }
#Build storage matrix and fill with population-index values
from simulations
stor.matrix <- matrix(nrow=t,ncol=10) #Build a storage
matrix
stor.matrix[,1] <-eig.time
stor.matrix[,2] <-Lmax.time
stor.matrix[,3] <-k.time
stor.matrix[,4] <-Q.time
stor.matrix[,5] <-r.time
stor.matrix[,6] <-p.time
stor.matrix[,7] <-b.time
stor.matrix[,8] <-c.time
stor.matrix[,9] <-s0.time
stor.matrix[,10] <-ann.surv1.time
plot(eig.time)
colnames(stor.matrix) <-
c("eig","lmax","k","q","r","p","b","c","s0","s1")
cor.sens1 <-
cor(stor.matrix,y=stor.matrix[,1],method="spearman")
#Assess sensitivity using a range of uncertainty in age-0
survival
s0.stuff <- c(0.000025-0.00001,0.00005-0.00001,0.000075-
0.00001,0.0001-0.00001,0.00025-0.00001,0.0005-
0.00001,0.00075-0.00001,0.001-0.00001,0.0025-0.00001,0.005-
0.00001,0.0075-0.00001,0.01-0.00001)
change.sens <-
cbind(cor.sens1[,1],cor.sens2[,1],cor.sens3[,1],cor.sens4[,
1],cor.sens5[,1],cor.sens6[,1],cor.sens7[,1],cor.sens8[,1],
cor.sens9[,1],cor.sens10[,1],cor.sens11[,1],cor.sens12[,1])
df.change <-
data.frame(s0.stuff,change.sens[9,],change.sens[10,])
mean.spear<- apply(change.sens,1,mean)
ster <- function(x) sd(x)/sqrt(length(x))
ster.spear <- apply(change.sens,1,ster)

```

CHAPTER 2. INFLUENCE OF STRONG YEAR CLASSES ON THE SUSTAINABILITY OF WALLEYE POPULATIONS

Introduction

Survival during the first year of life is full of obstacles for walleye *Sander vitreus* (Sissenwine 1988). A rapid spring warming event is needed to maximize survival during the egg stage (Busch et al. 1975) and is highly beneficial for newly hatched fry because it enhances growth rate (Madenjian et al. 1991), which is often correlated with first-year survival (Chevalier 1973, Forney 1976, Hoxmeier et al. 2004). Newly hatched fry depend largely on plankton as a food resource (Hoxmeier et al. 2004), which is not always ample (i.e., match-mismatch hypothesis [Cushing 1990]). Given an adequate plankton supply immediately following hatching, walleye fry quickly undergo ontogenetic shifts in diet to macroinvertebrates and eventually to piscivory (Fox et al. 1989, Mathias and Li 1982). Assuming abiotic conditions are suitable during the first few weeks of life for walleye, individuals must also contend biotic obstacles such as centrarchid predators (Santrucci and Wahl 1993, Quist et al. 2003a) or even larger walleyes as predators (Chevalier 1973, Loadman et al. 1986). The interplay of the long list of conditions required for survival during the first year of life is extremely complex and dynamic (Hansen et al. 1998, Quist et al. 2004, DeBoer et al. 2013). The overall effects of the variability are extremely important in understanding walleye population dynamics.

Walleye populations are characterized by variable year-class strength (Forney 1976, Li et al. 1996, Madenjian et al. 1996), likely arising from differences in environmental conditions during the first year of life (Sissenwine 1984). For example, a

strong year class was produced approximately every other year at Savanne Lake, Ontario (Ritchie and Colby 1988), approximately every four years at Lake Erie (Madenjian et al. 1996), and approximately every 5 years at Lake Miltone, Minnesota (Parsons and Pereira 2001). Quist et al. (2003) and DeBoer et al. (2013) both noted that strong year-class production was erratic in irrigation reservoirs in northern Kansas and southwestern Nebraska, respectively.

Relative abundance data are often used to monitor fish populations and assess year-class strength (Hubert and Fabrizio 2007), and while imperfect (Hubert and Fabrizio 2007), can provide a great amount of useful information, especially when other population metrics (e.g., total length, weight, age) are gathered along with relative abundance (Chapter 1, Hubert and Fabrizio 2007). Many limitations of relative abundance data directly stem from the gear used to collect specimens. For example, gill nets are commonly used as a sampling gear for walleye (Carlander 1953, Bulkley 1970, Willis 1987), but young-of-the-year individuals are rarely fully recruited to the gear (Hubert and Fabrizio 2007), and thus a reliable index of year-class strength is not attainable for at least one additional growing season. The problem lies in the fact that a weak walleye year class is then not immediately detected, thereby potentially delaying management actions to mitigate the weak year class. Population metrics gathered alongside relative abundance data are useful because they give managers insight into the status of the walleye population (e.g., condition, growth, size structure). The combination of information aids in identifying the future availability of the fishing resource (Hubert and Fabrizio 2007).

A useful tool for conceptualizing, comparing, and projecting populations to form an idea of the future availability of a fishing resource is the population viability analysis (Burgman 1992). Population viability analysis focuses on using models to identify the risk of a population collapse within a specified amount of time (Boyce 1992), and is especially useful when real data are used to project the modeled populations into the future (Boyce 1992) and when used to evaluate the relative risk of various management actions or population scenarios (McCarthy et al. 2003). For example, Ratner et al. (1997) predicted persistence of chinook salmon *Oncorhynchus tshawytscha* given current conditions at the time, and extinction with habitat degradation. Additionally, Jager et al. (2000) used population viability analysis to predict the persistence of several riverine fish species in response to increasing segmentation by dams.

Walleye populations are economically valuable in this region because they are highly sought after for recreational angling (Hurley and Duppong Hurley 2002). Historically, walleye year-class production has been erratic (DeBoer et al. 2013) and population collapse has remained a major concern in the region. Thus, the main objective in this study was to perform a population viability analysis for walleye populations in irrigation reservoirs in southwest Nebraska given decreases in the frequency of strong year classes. In addition to the main objective of our study, I used our model to hypothesize effects of increased water temperature, as a result of climate change, on the risk of a population collapse for our walleye populations.

Methods

Data collection

Walleye data (Catch per unit effort [CPUE], length, weight, and age) were obtained from a gillnet-survey dataset compiled by the Nebraska Game and Parks Commission during fall 1994-2009 (Nebraska Game and Parks Commission 2012). Data were combined across years at each reservoir to generalize population indices through time at each reservoir (Table 2-1). Combining data across years at each reservoir increased sample sizes (n=1896, 1461, 1461, and 1896 for CPUE, length, weight, and age, respectively) that allowed me to relax the assumption of constant catchability, as recommended by Noble et al. (2007).

Leslie matrix model

I used the Leslie matrix model (Leslie 1945), parameterized as an age-structured population and assuming a post-birth census (Caswell 1989) to project the modeled walleye population through time. The Leslie matrix model takes into account age-specific fecundity F and survival s , and is represented as:

$$\begin{bmatrix} F_0 & F_1 & F_2 & F_3 & \cdots & F_{a_{max}} \\ s_0 & 0 & 0 & 0 & \cdots & 0 \\ 0 & s_1 & 0 & 0 & \cdots & 0 \\ 0 & 0 & s_2 & 0 & \cdots & 0 \\ 0 & 0 & 0 & \ddots & \cdots & 0 \\ 0 & 0 & 0 & 0 & s_{a_{max}-1} & 0 \end{bmatrix} \times \begin{bmatrix} N_0 \\ N_1 \\ N_2 \\ \vdots \\ N_{a_{max}} \end{bmatrix}_t = \begin{bmatrix} N_0 \\ N_1 \\ N_2 \\ \vdots \\ N_{a_{max}} \end{bmatrix}_{t+1} \quad [2 - 1]$$

I used this model to project the number of female walleye N per age class a in the population at time t at each reservoir by multiplying the population vector at time t with the matrix to produce the population vector at time $t + 1$.

Fecundity

The F at each age a (equation 2-1) was derived using values obtained from a review of North American walleye populations (Carlander 1997), and is the relationship between fecundity (number of eggs) and weight (g total mass). I represented the relationship with a piecewise function:

$$F_a = \begin{cases} \frac{\max\{W_a c - b, 0\}}{2}, & a \geq 2 \\ 0, & a < 2 \end{cases} \quad [2 - 2]$$

where W is weight at age a , and b and c are the slope and intercept of the linear regression of fecundity against weight. Fecundity estimates at each age were divided by two (i.e., 1:1 sex ratio) to represent the number of females produced at each time step.

The W_a were calculated based on data from the populations,

$$W_a = pL_a^r \quad [2 - 3]$$

where L is total length (mm) at age a , and p and r are scaling parameters. The W_a were fit using the nonlinear least squares package in R (nls; R Core Team 2013). The L_a were estimated using the von Bertalanffy growth relationship (von Bertalanffy 1938) based on data from our populations,

$$L_a = L_\infty(1 - e^{-k(a-q)}) \quad [2 - 4]$$

where L_∞ is asymptotic maximum length, k is the Brody growth coefficient, and q is theoretical age when length is 0. The von Bertalanffy growth relationships were fit using the nonlinear least squares package in R (nls; R Core Team 2013).

Adult annual survival

Adult walleye annual survival probabilities (equation 2-1) were calculated by catch-curve analysis (Miranda and Bettoli 2007). Walleye CPUE was combined across

years (1994-2009) for each reservoir in attempt to achieve an adequate sample size (Miranda and Bettoli 2007). I used weighted regression during the catch-curve analysis to help mitigate the problems associated with lower catches in older age groups (Miranda and Bettoli 2007). Annual survival probability was calculated using the antilog of instantaneous mortality from the slope of the line in the catch-curve analysis (Miranda and Bettoli 2007).

Stochasticity in age-0 survival

A stochastic process is one that involves a random element. It is impossible to completely understand every aspect affecting a population, but it is possible to account for some of these aspects using stochasticity. I used stochasticity in the frequency of strong year classes (Appendix 2) similar to Daugherty and Smith (2012) by randomly assigning a strong year class on average once every three years (probability of a strong year class = 0.33 to and including once every ten years (probability of a strong year class = 0.10). When a strong year class was produced, the age-0 survival probability was randomly selected from a uniform distribution beginning with the age-0 survival probability required to maintain a population at equilibrium (Vaughan and Saila 1976) to a maximum value. The maximum value was reservoir specific and was selected using the range of values for CPUE of age-2 walleye (Figure 2-1). When a strong year class was not produced, I randomly selected an age-0 survival probability beginning at 0, and the maximum value was the age-0 survival probability required to maintain a population at equilibrium (Vaughan and Saila 1976). The populations were projected through 100 years, and the process was simulated through 1,000 iterations. I evaluated the risk of

quasi-extinction (when the population decreased lower than 10% of the initial population [Burgman et al. 1988]) by calculating the cumulative proportion of collapsed populations during each year.

Populations under each strong year class scenario were classified as critical (50% chance of quasi-extinction within two generations or 5 years, whichever was longer [Mace and Lande 1991]), endangered (20% chance of quasi-extinction within 10 generations or 20 years, whichever was longer [Mace and Lande 1991]), vulnerable (10% chance of quasi-extinction within 100 years [Mace and Lande 1991]). The appropriate classification was assigned by visually determining where the population risk trajectory crossed into the most severe classification. For example, if a population trajectory crossed into both vulnerable and endangered zones, the population was classified as endangered (the most severe classification of the two). Generation time was calculated by determining the age at which maximum contribution of recruits by mothers was attained at stable stage distribution for each population (Coale 1972; Figure 2-2).

The process was repeated incorporating a climate change scenario, in attempt to forecast potential issues associated with warming water for walleye. I used data from southern walleye populations compiled in a review by Quist et al. (2003) to parameterize our model with the idea that if the temperature in our reservoirs increased, I could expect growth and survival for walleye in our reservoirs to behave similarly to growth and survival for southern walleye populations (i.e., increased k and decreased s). The classification process remained exactly the same for the climate change scenario.

Results

Historic walleye populations

Under scenarios (Figure 2-3) where a strong year class was produced, on average, once every 3 or 4 years, the quasi-extinction risk for simulated walleye populations at Harlan County Lake was classified in the safe zone. When the frequency of strong year-class production was reduced to, on average, once every 5 or 6 years, the simulated walleye populations were classified in the vulnerable zone. Under the scenario where strong year-class production was reduced to, on average, once every 7, 8, 9, or 10 years, the simulated walleye populations were classified in the endangered zone.

For scenarios where a strong year class was produced, on average, once every 3 or 4 years, the quasi-extinction risk for simulated walleye populations at Medicine Creek Reservoir was classified in the safe zone. When the frequency of strong year-class production was reduced to, on average, once every 5, 6, or 7 years, the simulated walleye populations were classified in the vulnerable zone. Given the scenario where strong year-class production was reduced to, on average, once every 8, 9, or 10 years, the simulated walleye populations were classified in the endangered zone.

Under scenarios where a strong year class was produced, on average, once every 3 or 4 years, the quasi-extinction risk for simulated walleye populations at Red Willow Reservoir was classified in the safe zone. When the frequency of strong year-class production was reduced to, on average, once every 5 years, the simulated walleye population was classified in the vulnerable zone. Under the scenario where strong year-class production was reduced to, on average, once every 6, 7, 8, 9, or 10 years, the simulated walleye populations were classified in the endangered zone.

Under scenarios where a strong year class was produced, on average, once every 3, 4, 5, 6, or 7 years, the quasi-extinction risk for simulated walleye populations at Swanson Reservoir was classified in the safe zone. When the frequency of strong year-class production was reduced to, on average, once every 8, 9, or 10 years, the simulated walleye population was classified in the vulnerable zone. No scenarios resulted in a population in the endangered zone.

Climate change scenario

Under the scenario where a strong year class was produced, on average, once every 3 years, the quasi-extinction risk for simulated walleye populations at Harlan County Lake was classified in the safe zone for the climate change scenario (Figure 2-4). When the frequency of strong year-class production was reduced to, on average, once every 4 years, the simulated walleye population was classified in the vulnerable zone. Under the scenario where strong year-class production was reduced to, on average, once every 5, 6, 7, 8, 9, or 10 years, the simulated walleye populations were classified in the endangered zone.

Under the scenario where a strong year class was produced, on average, once every 3 years, the quasi-extinction risk for simulated walleye populations at Medicine Creek Reservoir was classified in the safe zone for the climate change scenario. No scenarios resulted in a population in the vulnerable zone. Under the scenario where strong year-class production was reduced to, on average, once every 4, 5, 6, 7, 8, 9, or 10 years, the simulated walleye populations were classified in the endangered zone.

Under the scenario where a strong year class was produced, on average, once every 3 years, the quasi-extinction risk for simulated walleye populations at Red Willow Reservoir was classified in the vulnerable zone for the climate change scenario. No scenarios resulted in a population in the vulnerable zone. When the frequency of strong year-class production was reduced to, on average, once every 4, 5, 6, 7, 8, 9, or 10 years, the simulated walleye populations were classified in the endangered zone.

Under the scenario where a strong year class was produced, on average, once every 3 or 4 years, the quasi-extinction risk for simulated walleye populations at Swanson Reservoir was classified in the safe zone for the climate change scenario. When the frequency of strong year-class production was reduced to, on average, once every 5 years, the simulated walleye population was classified in the vulnerable zone. Under the scenario where strong year-class production was reduced to, on average, once every 6, 7, 8, 9, or 10 years, the simulated walleye populations were classified in the endangered zone.

Discussion

Our study demonstrates the important role of the frequency of strong year classes on the risk of population collapse. This is an intuitive concept, and has been suggested for walleye (Busch et al. 1979, Colby and Baccante 1996, Fielder et al. 2007). However, to our knowledge this is the first study to simulate the effects of varying the frequency of strong year-class production on the sustainability of a walleye population. The risk of 10% quasi-extinction greatly increased at each reservoir as the frequency of strong year

classes decreased, emphasizing rapidly compounding negative effects of weak year classes on a walleye population through time.

The walleye population at Swanson Reservoir could be maintained with relatively infrequent strong year classes (i.e., once every 7 years), which is clearly a result of the ability for Swanson occasionally to produce very strong year classes in our model. I am unsure whether walleye populations at Swanson Reservoir, prior to 1994, produced year classes as strong as the year class produced during 2007 (observed in the gill nets during 2009), because data were not available for that period. If the strong year class observed during 2009 was a result of inflated catchability in the sampling gear during that year, I expect walleye populations at Swanson Reservoir to behave similarly to walleye populations at our other reservoirs in regard to 10% quasi-extinction. However, if the strong year class observed during 2009 accurately represented the potential for year-class strength, then it stands to reason that the walleye population at Swanson Reservoir could withstand several years of weak year classes. I would expect a similar outcome at Harlan County Lake, Medicine Creek Reservoir, and Red Willow Reservoir if populations at those reservoirs could also occasionally produce strong year classes in the future.

Walleye supplementation via stocking is a common management practice across North America, and is extensively used at our reservoirs (Bauer et al. 2011). Walleye are usually stocked annually as fry during late spring (Nebraska Game and Parks Commission 2013), and it is the general belief that natural production is limited in our reservoirs (Bauer et al. 2011). I believe our results serve as justification for the stocking of walleye at intervals no less than once every 4 years at Harlan County Lake, Medicine Creek Reservoir, and Red Willow Reservoir, and no less than once every 7 years at

Swanson Reservoir, assuming population trends of the past 14 years continue in the future. Additionally, if a strong year class is produced in a given year at a given reservoir (perhaps identified by spring seining or electrofishing for age-1 walleye), then stocking resources would probably be better-utilized elsewhere in the following year. For example, if a strong year class were observed at Medicine Creek during 2013 but not at Harlan County Lake, Red Willow Reservoir, or Swanson Reservoir, then stocking resources should be directed to Harlan County Lake, Red Willow Reservoir, and Swanson Reservoir.

The frequency of strong year classes needed to sustain the populations increased as water temperature increased. To best foresee (and therefore react) to changes in walleye populations such that I predicted with our model (i.e., increased growth rate, decreased age-1 and older annual survival probability) for the climate-change scenario, managers should closely monitor growth rates for individual walleye. If increased growth rates are apparent through time, the frequency of a strong year class needed to sustain the walleye populations will likely increase to once every two or three years. In that case, it may be necessary for populations to be stocked every year to insure at least one strong year class is produced during the time frame. A potential limitation lies in our assumption that the range of age-0 survival probabilities will remain the same given increased water temperatures.

One potential limitation of our model is that I did not specifically detail density-dependent influences on age-0 survival. Density-dependence in age-0 survival has been suggested from individual-based models for predator-prey relationships between walleye and yellow perch (Rose et al. 1999). In this study when walleye were abundant, the

yellow perch *Perca flavescens* population decreased, demonstrating the possible depletion of a food source and thus potential for food-limited survival (i.e., density-dependent survival). Conversely, age-0 walleye density was not related to survival in empirical studies conducted in rearing ponds (Fox and Flowers 1990, Kolar et al. 2003). Hoxmeier et al. (2009) observed density-dependent survival for walleye in mesocosms, but not in ponds, perhaps suggesting that age-0 walleye density must be relatively high before negative effects of density dependence occur for walleye. Our reservoirs are eutrophic and generally produce ample food for age-0 walleyes (Olds et al. 2011), thus I believe negative effects of density-dependent survival likely are not encountered in our reservoirs.

In conclusion, the frequency of strong year classes plays a major role in the sustainability of walleye populations, assuming natural reproduction. I recommend that walleye populations to be supplemented at least once every 4 years at Harlan County Lake, Medicine Creek Reservoir, and Red Willow Reservoir, and at least once every 7 years at Swanson Reservoir if a strong year class has not been produced within that time frame. I expect that strong year classes will need to be produced more frequently in the future if climate change results in an increase in water temperature in our reservoirs.

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Table 2-1. Parameter values used in this study, theoretical maximum length L_{max} , Brody growth coefficient k , theoretical age when length equals 0 q , length-weight scaling parameters p and q , and age-1 and older annual survival probability s_1 . The climate change simulation represents increased growth rate, reduced maximum length, and reduced annual survival probability (Quist et al. 2003). Parameters p and q were not changed at each reservoir for the climate change simulation.

Water body	L_{max}	k	q	p	r	s_1
Harlan County Lake	793	0.19	-2.33	2.72×10^{-6}	3.210	0.61
Medicine Creek Reservoir	689	0.21	-2.48	1.56×10^{-6}	3.298	0.47
Red Willow Reservoir	1162	0.08	-2.91	2.14×10^{-6}	3.239	0.70
Swanson Reservoir	1575	0.05	-4.37	3.31×10^{-6}	3.190	0.58
Climate change simulation	605.2	0.7282	-0.6848			0.24

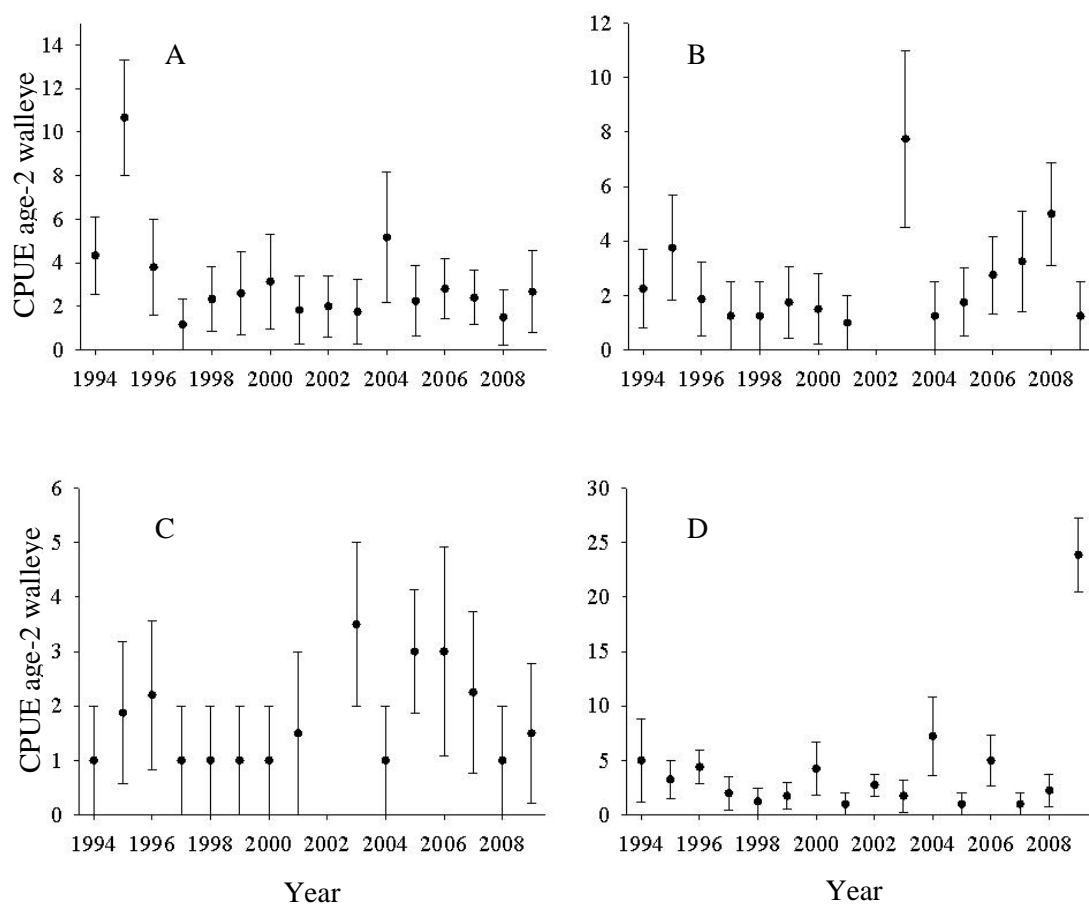


Figure 2-1. CPUE of age-2 walleye through time at Harlan County Lake (A), Medicine Creek Reservoir (B), Red Willow Reservoir (C), and Swanson Reservoir (D). Points represent the mean and whiskers represent the standard error.

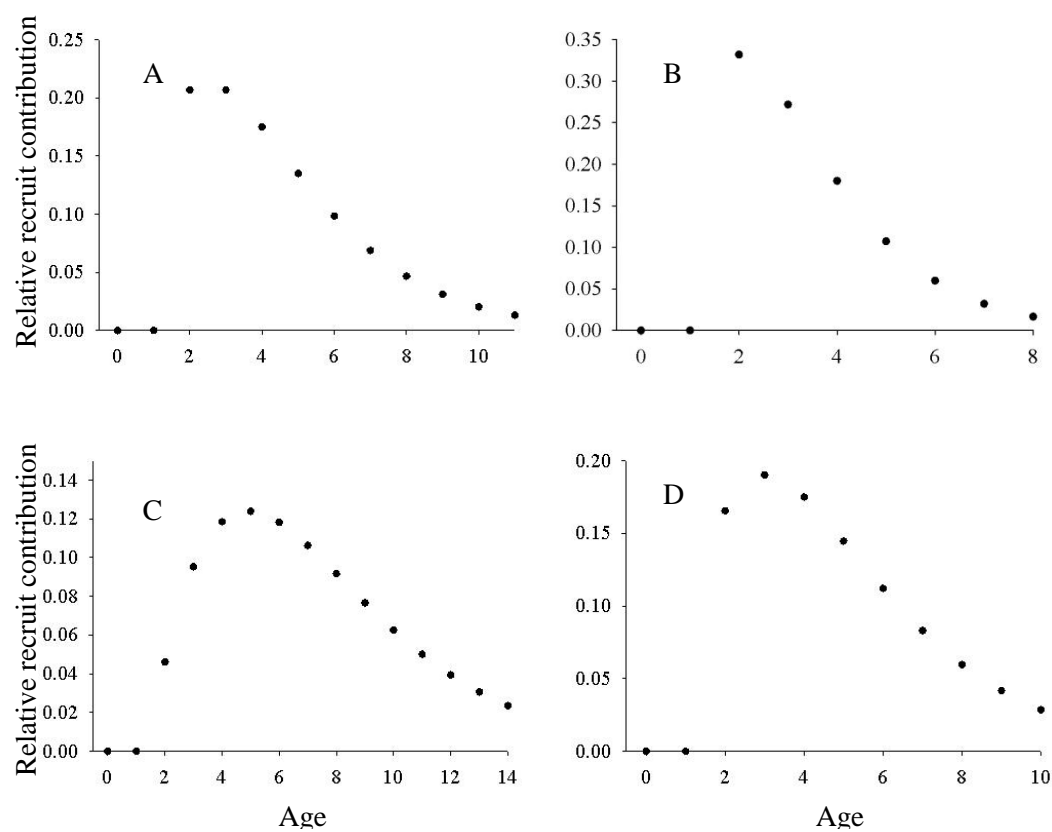


Figure 2-2. The relative contribution of recruits by mothers at each age at the stable stage distribution for walleye populations at Harlan County Lake (A), Medicine Creek Reservoir (B), Red Willow Reservoir (C), and Swanson Reservoir (D).

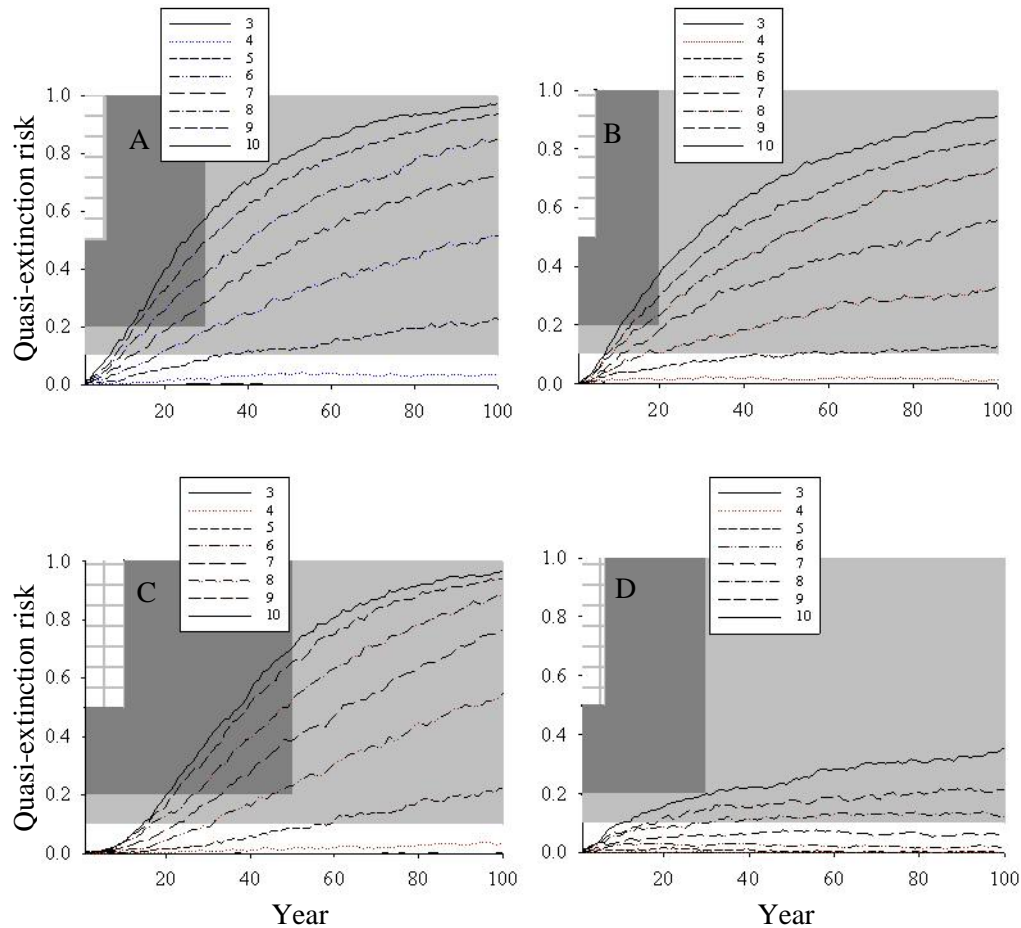


Figure 2-3. Results of simulated walleye populations at Harlan County Lake (A), Medicine Creek Reservoir (B), Red Willow Reservoir (C), and Swanson Reservoir (D) under several strong year-class production scenarios. Populations were simulated through 100 years and age-0 survival probability was stochastically varied at specified intervals (see legend). The process was iterated 1,000 times, and the cumulative frequency of quasi-extinction (population decrease below 10% of initial population) was monitored. The checkered region represents the critical zone (50% quasi-extinction risk within 2 generations or 5 years, whichever is longer), the dark gray region represents the endangered zone (20% quasi-extinction risk within 10 generations or 20 years, whichever is longer), the light gray region represents the vulnerable zone (10% quasi-extinction risk within 100 years), and the white region represents the safe zone (<10% quasi-extinction risk within 100 years).

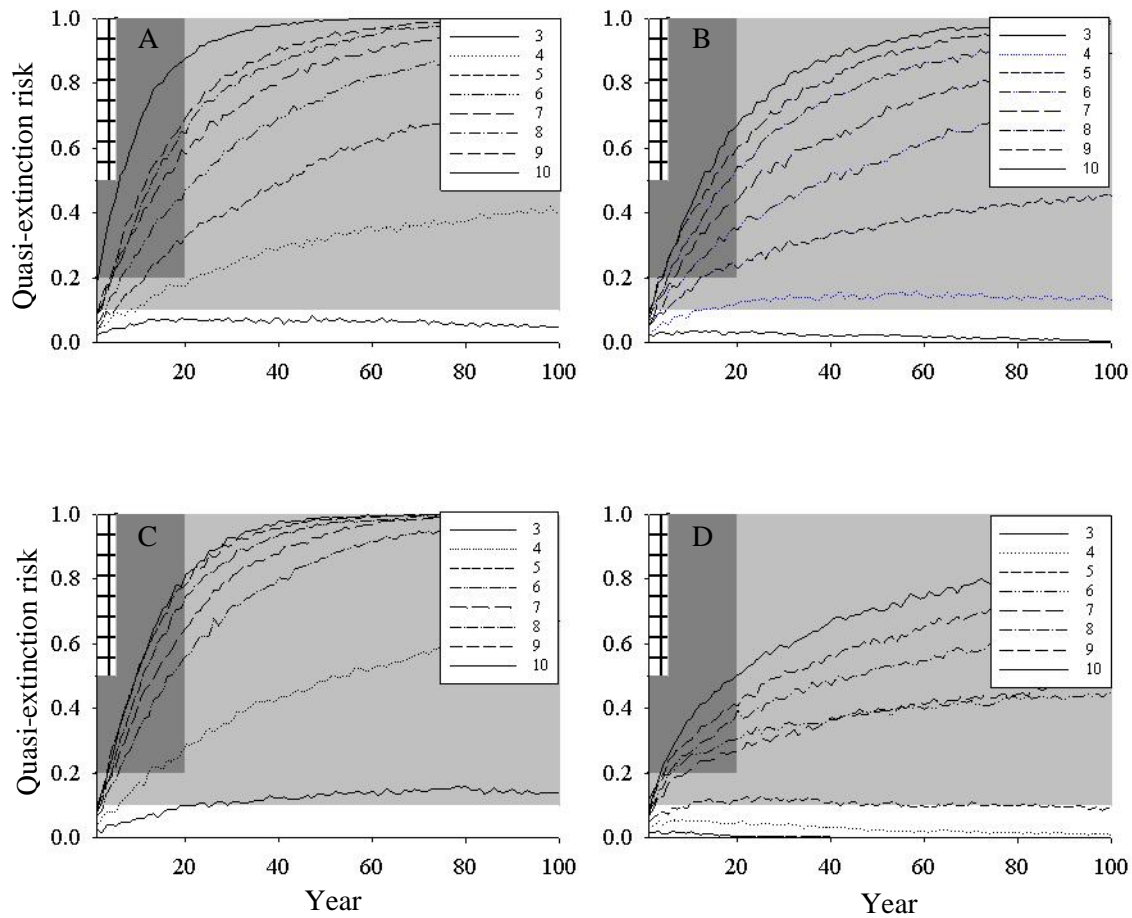


Figure 2-4. Results of simulated walleye populations at Harlan County Lake (A), Medicine Creek Reservoir (B), Red Willow Reservoir (C), and Swanson Reservoir (D) under a climate change scenario where the temperature of water in reservoirs increases and several year-class production scenarios. Populations were simulated through 100 years and age-0 survival probability was stochastically varied at specified intervals (see legend). The process was iterated 1,000 times, and the cumulative frequency of quasi-extinction (population decrease below 10% of initial population) was monitored. The checkered region represents the critical zone (50% quasi-extinction risk within 2 generations or 5 years, whichever is longer), the dark gray region represents the endangered zone (20% quasi-extinction risk within 10 generations or 20 years, whichever is longer), the light gray region represents the vulnerable zone (10% quasi-extinction risk within 100 years), and the white region represents the safe zone (<10% quasi-extinction risk within 100 years).

Appendix 2. R-programming code for chapter 2

```
#First load in data
hc.catch <- read.csv("cohortmatrixharlan.csv")
mc.catch <- read.csv("cohortmatrixmc.csv")
rw.catch <- read.csv("cohortmatrixrw.csv")
sw.catch <- read.csv("cohortmatrixsw.csv")

hc.catch <- hc.catch$Age2
mc.catch <- mc.catch$Age2
rw.catch <- rw.catch$Age2
sw.catch <- sw.catch$Age2
hc.catch <- hc.catch[1:length(hc.catch)-1]
mc.catch <- mc.catch[1:length(mc.catch)-1]
rw.catch <- rw.catch[1:length(rw.catch)-1]
sw.catch <- sw.catch[1:length(sw.catch)-1]
vonb <- read.csv("vonbcomp.csv")
en.vonb <- vonb[vonb$Reservoir=="EN" & vonb$Age!=8,]

#Fit vonB growth curve to populations
grow.fit <- nls(Length~a*(1-(exp(-b*(Age-
d)))) ,data=en.vonb,start=list(a=2000,b=0.4,d=-
1.5),trace=TRUE,control=list(maxiter=300))
#Enter survival information for reservoirs
  #Age 1+ survival
  ann.surv <- 0.58

#Calculate maximum age for individuals composing population

agemax <- floor((-log(0.01))/(1-ann.surv))+1 #+1 because of how
the LMM is set

up (to include age-0)
  agel <- 1:agemax
  leslie <- matrix(0,ncol=agemax,nrow=agemax)
  leslie[row(leslie)==col(leslie)+1] <- ann.surv
  #Population-specific growth
  k <- 0.7282
  Lmax <- 605
  Q <- -0.6848
  La <- Lmax*(1-exp(-k*(agel-Q)))
  # Population-specific length-weight
  r <- 3.21
  p <- 0.00000272
  Wa <- p*La^r
  #Weight-Fecundity
  c <-
(runif(1,coefficients(sum.wf)[2,1]*1,coefficients(sum.wf)[2,1]*1)
)
```



```

      b <-
(runif(1,coefficients(sum.wf)[1,1]*1,coefficients(sum.wf)[1,1]*1)
)
    Fa <- Wa*c+b
    #Age at maturity
    Fa <- ifelse(Fa>0,Fa,0)
    Fa[is.na(Fa)] <- 0
    leslie[1,] <- (Fa*1000)/2
    leslie[1,1:2] <- 0

#Use algorithm to solve for population at equilibrium
best.surv <- seq(0.0000001,.0002,0.0000001)
eigs.derv <- vector("numeric",length(best.surv))
find.eig <- vector("numeric",length(best.surv))

for(i in 1:length(best.surv)){
  leslie[2,1] <- best.surv[i]
  eigs <- eigen(leslie)
  dom.pos <- which.max(eigs[["values"]])
  L1 <- Re(eigs[["values"]][dom.pos])
  eigs.derv[i] <- L1
  find.eig[i] <- abs(L1-1)
}
best.eig <- which.min(find.eig)
leslie[2,1] <- best.surv[best.eig]
s01 <- best.surv[best.eig]
eigs <- eigen(leslie)
dom.pos <- which.max(eigs[["values"]])

#Determine population growth rate, assure it equals 1
L1 <- Re(eigs[["values"]][dom.pos])
w <- Re(eigs[["vectors"]][,dom.pos])

#Find the stable stage distribution
ssd <- w/sum(w)
plot(ssd*leslie[1,])
lesliel <- leslie
#Build stochasticity into simulation model for walleye
populations

iter.length <- 1000
sim.year <- 120
sim.list <- list()
sim.list2 <- matrix(0,ncol=iter.length,nrow=sim.year)
countmat <- matrix(0,ncol=iter.length,nrow=sim.year)
for(i in 1:iter.length){
  leslie <- lesliel
  n.pop <- matrix(0,nrow=ncol(leslie),ncol=sim.year)
  sum.pop <- vector("numeric",length=sim.year)
  n.pop[,1] <- ssd*100000000
  sum.pop[1] <- sum(n.pop[2:max(ncol(leslie)),1])

```

```

count.above <- vector("numeric",length=sim.year)
  for(j in 2:sim.year){
    weak.yc.hc <- runif(1,0,1)*s01

    strong.yc.hc <- runif(1, 1,18.3)*s01
    flip.coin <- runif(1,0,1)
    leslie[2,1] <- ifelse(flip.coin > (0.2),weak.yc.hc,strong.yc.hc)

    n.pop[,j] <- leslie%% n.pop[,j-1]
    sum.pop[j] <-
sum(n.pop[2:max(ncol(leslie)),j])
  }
  sim.list[[i]] <- n.pop
  sim.list2[,i] <- sum.pop
}

#Calculate the proportion of times the population collapses

crash <- function(x){ifelse(x > sum.pop[1]*0.1, 0, 1)}
crash.sim <- apply(sim.list2,1,crash)
count.crash <- ((apply(crash.sim,2,sum)))/1000#Also put it in a
csv
write.csv(count.crash,file="hcd.d.csv")

```