An integral projection model with YY-males and application to evaluating grass carp control

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ABSTRACT

Invasive fish species disrupt ecosystems and cause economic damage. Several methods have been discussed to control populations of invasive fish including the release of YY-males. YY-males are fish that have 2 male chromosomes compared to a XY-male. When YY-males mate, they only produce male (XY) offspring. This decreases the female proportion of the population and can, in theory, eradicate local populations by biasing the sex-ratio. YY-males have been used as a population control tool for brook trout in montane streams and lakes in Idaho, USA. The YY-male control method has been discussed for grass carp in Lake Erie, North America. We developed and presented an integral projection model for grass carp to model the use of YY-males as a control method for populations in this lake. Using only the YY-male control method, we found that high levels of YY-males would need to be release annually to control the species. Specifically, these levels were the same order of magnitude as the baseline adult population (e.g., 1000 YY-males needed to be released annual for 20 years to control a baseline adult population of 2500 grass carp). These levels may not be reasonable or obtainable for fisheries managers given the impacts of YY-males on aquatic vegetation and other constraints of natural resource management.

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1. Introduction

Over the last two decades, numerous invasive fishes have established populations throughout the United States including grass carp (*Ctenopharyngodon idella*). Different control techniques have been discussed to control populations of these species either through direct mortality or reduction of their spread. Possible control methods include acoustical conditioning (Sloan et al., 2013), new piscicides (Putnam et al., 2017), commercial harvest (Colvin et al., 2012), carbon dioxide barrier (Cupp et al., 2016; Donaldson et al., 2016), and the release of YY-males that only produce male offspring (Schill et al., 2016). The YY-male approach controls populations because YY-males can only produce male offspring. If enough YY-males are in the population, the sex-ratio can become biased sufficiently that the population may collapse or be more vulnerable to other control efforts. YY-males have recently been used in montane streams and lakes in Idaho to attempt to con-

trol invasive brook trout (Schill et al., 2016). Similar management approaches have been used for other invasive and noxious species such as mosquitoes (Benedict and Robinson, 2003) although not without controversy or challenges (c.f. Knols et al., 2006). We are specifically interested in the release of YY-males for grass carp control because the method has been discussed for controlling grass carp in Lake Erie, North America.

Grass carp, like many invasive fishes, cause a wide-range of adverse economical and ecological impacts in North America (Lovell and Stone, 2005; Dibble and Kovalenko, 2009). Directly, grass carp can consume up to 40% of their weight in vegetation daily, which alters available habitats, water quality, and community composition (Sutton, 1977; Chapman et al., 2013). Indirectly, grass carp adversely affect other species ranging from plankton to waterfowl (Bain, 1993; Kolar and Lodge, 2002; Dibble and Kovalenko, 2009). These ecological impacts cause economic impacts such as declines in native fisheries and contribute to the billions of dollars of damage that invasive species cause to the economy of the United States (Pimentel et al., 2000, 2005).

Grass carp originated in eastern Asia; its native range spans from the Amur River of Russia to the West River of southern China

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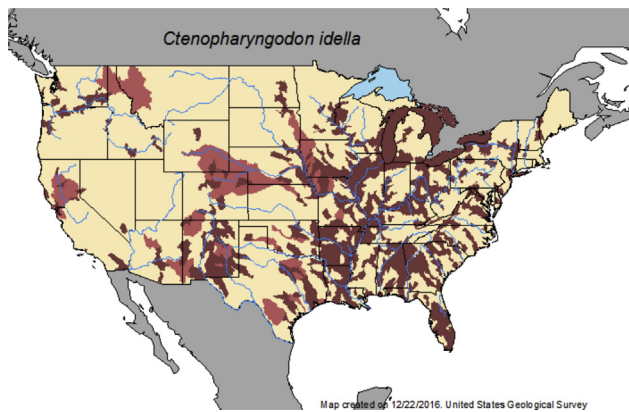
Fig. 1. Species distribution map of grass carp (*Ctenopharyngodon idella*) in the continental United States. Darker shading areas are observations from HUC 8 Level records, lighter are from HUC 6 Level Records. Map is was generated by the USGS on 22 December 2016 and accessed 23 January 2017 (https://nas.er.usgs.gov/queries/factsheet.aspx?SpeciesID=514). The figure was created by Nico, L.G., P.L. Fuller, P.J. Schofield, M.E. Neilson, A.J. Benson, and J. Li while working for the U.S. Government and is in the public domain.

(Shireman and Smith, 1983). The species feeds on aquatic vegetation and has been introduced worldwide for weed control including Malaysia, Taiwan, Japan, eastern Europe, Holland, Germany, New Zealand, and the United States (Cross, 1969; Clayton et al., 1999). First proposed for release in the United States in 1957 to control aquatic vegetation (Swingle, 1957), natural resource managers released the species 6 years later in 1963 (Bain, 1993; Mitchell and Kelly, 2006). Grass carp spread through flooding in stocked areas and additional stocking and now may be found in the Great Lakes (Chapman et al., 2013) and Mississippi River Basin (Bain, 1993) (Fig. 1).

Early studies of grass carp examined how to use the species for weed control and increase survival and recruitment of grass carp (e.g., Cross, 1969; Sutton, 1977; Mitzner, 1978; Kilambi and Robison, 1979; Ewel and Fontaine, 1982; Martyn et al., 1986; Rottmann et al., 1991; Santha et al., 1991; Spencer, 1994). Managers and scientists in the United States noticed the adverse impacts of the species and began releasing sterile, triploid grass carp as a method for limiting their adverse impact (Chilton and Muoneke, 1992). However, many viable, reproducing populations still exist throughout the United States (Raibley et al., 1995; Wittmann et al., 2014; Embke et al., 2016). Currently, some grass carp management focuses on control (Chapman et al., 2013; Wittmann et al., 2014), although regions still stock grass carp for vegetation control.

Prior to developing and implementing possible control methods, researchers and managers may want to evaluate the effectiveness of the approaches. Ecological simulations using mathematical models are one approach to compare different management methods (Caswell, 2001; Morris and Doak, 2002; Bolker, 2008). Additionally, mathematical theory can be used to "optimize" management (Lenhart and Workman, 2007), "control" the system (Friedlan, 1986), or compare different management strategies (Caswell, 2001; Morris and Doak, 2002).

Several different mathematical population models have been developed for invasive carp (e.g., silver carp, bighead carp, common carp; Lorenzen, 1995; Williamson and Garvey, 2005; Garcia et al., 2013; Tsehaye et al., 2013; Cuddington et al., 2014) including grass carp (Ewel and Fontaine, 1982; Santha et al., 1991; Spencer, 1994; Kirk et al., 2000). The life history of carp is conserved within the family Cyprinidae and these models could be re-parameterized for grass carp. Furthermore, Lorenzen (1995) presented a generic fisheries model that includes carps as an example species. However, these models do not match our management questions. First,

the models tend to be designed for specific locations and questions that differ from ours (e.g., how to release grass carp for weed control). Second, none of these models differentiate carp by sex nor do they include YY-males. Third, some of the models (e.g., Kirk et al., 2000) do not include sufficient details to easily reproduce the model, highlighting the need for documentation (c.f. Schmolke et al., 2010; Augusiak et al., 2014).

Like most fish, carp grow continuously and change in size through time. Conversely, many of the existing models were difference equations or differential equations that discretized carp size using life-stages rather than size (e.g., Lefkovitch matrix models); model age as a surrogate for size and thereby implicitly discretize size (e.g., Leslie matrix models), or completely ignored size/age structure in the carp populations. Rather than discretizing size, size can be modeled continuously using an integral projection model (Easterling, 1998; Ellner and Rees, 2006; Ramula et al., 2009; Merow et al., 2014). These models were first applied to population ecology by Easterling (1998) during his graduate work and offer advantages over matrix models when modeling discretized systems (e.g., size classes). First, integral projection models require fewer parameters than a discrete matrix of similar complexity. For example, rather than estimating a survival parameter for each life-stage, one function with two parameters can be fitted to model survival as a function of size (Easterling et al., 2000; Ellner and Rees, 2006). Second, integral projection models avoid modeling errors and artifacts caused by the choice of size structures. For example, Easterling et al. (2000) demonstrated how arbitrary choices in the number of size classes change the transient dynamics and long-term behavior of models. Integral projection models avoid this pitfall by treating size as a continuous variable rather than discretizing it.
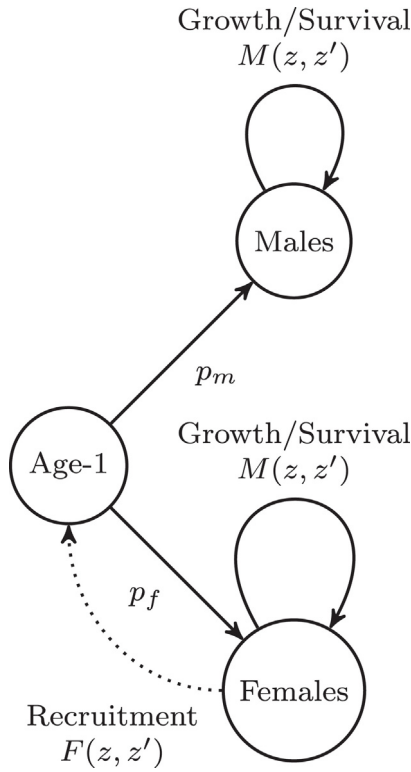
Herein, we develop an integral projection model for grass carp that includes XX-females, XY-males, and YY-males. After presenting our model and its parameterization, we conduct sensitivity analysis and compare different possible management scenarios to evaluate the possible use of YY-males. We include our "TRAnsparent and Comprehensive model Evaludation[1]" (TRACE) Documentation as a supplemental document (Schmolke et al., 2010; Augusiak et al., 2014; Grimm et al., 2014).

2. Model

2.1. Grass carp life history

Grass carp broadcast spawn in rivers, and their eggs must remain suspended in the water column until larvae are sufficiently developed to swim freely (Shireman and Smith, 1983). Males appear to have YX chromosomes and females have XX chromosomes (Wang et al., 2015). The specific requirements for successful spawning and recruitment (e.g., temperature, river discharge, and dissolved oxygen) constrain the spread of grass carps in systems such as the Great Lakes (Kocovsky et al., 2012). However, aquaculture techniques exist for spawning grass carp in captivity (e.g., Rottmann et al., 1991). We define recruitment to be from hatching until age-1 fish based upon the annual time step of our model (i.e., $t = 1$ year). Grass carp, like most species of fish, experience indeterminate growth and continue to grow throughout their life (Lagler et al., 1962). Grass carp do not reproduce until their body reaches an adequate size (Shireman and Smith, 1983). We modeled this using length as the state variable (Fig. 2). Grass carp mortality decreases as the fish increase in size because the carp are less vulnerable to predation and other stressors (Shireman et al., 1978; Shireman

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[1] "Evaludation" was intentionally invented by Grimm to cause the reader to think about the term, (V. Grimm, personal communication).

Growth/Survival
$M(z, z')$

Males

p_m

Age-1

Growth/Survival
$M(z, z')$

p_f

Females

Recruitment
$F(z, z')$

Fig. 2. Conceptual map of grass carp life history. p_f is the proportion of female recruits and p_m is the proportion of male recruits. By definition, $p_f + p_m = 1$. Adding YY–males to the system increases p_m and decreases p_f (Eq. (10)). Theoretically, if p_f becomes low enough, the population should crash. The recruitment kernel ($F(z, z')$) is defined in Eq. (4). The growth/maturation kernel ($M(z, z')$) is defined in Eq. (1). Our model seeks to alter this ratio through time with the introduction of YY-males. Growth/maturation is the annual increase in fish length. Recruitment is the successful spawning and development of eggs to produce age-1 fish. Recruitment does not occur from females until they become of sufficient length.

and Smith, 1983; Kirk and Socha, 2003). Grass carp spawn multiple times during their lifetime and larger grass carp produce more eggs than smaller grass carp (Shireman and Smith, 1983; Ashraf and Fairgrieve, 1998). The sex-ratio of grass carp eggs appears to be 1:1, however, some studies of adults have observed more females than males in field populations (Shireman and Smith, 1983). The sex-ratio data appears to be inconclusive or non-existent for grass carp in North America. Grass carp can be prolific recruiters and population density limits their growth in aquaculture (Kilambi and Robison, 1979; Kilambi, 1980). In North America outside of captivity, biomass of available food appears to limit invasive carp densities (Williamson and Garvey, 2005).

2.2. Equations

We used an integral projection model to describe the life history of grass carp. We refer readers who are unfamiliar with integral projection models to recent summary and tutorial articles (e.g., Ellner and Rees, 2006; Ramula et al., 2009; Merow et al., 2014). The populations of female grass carp ($P_f(z, t)$), male grass carp ($P_m(z, t)$), and YY-male grass carp ($P_{YY}(z, t)$) are continuous functions of a length variable z for each (discrete) time t. The variable z generally ranges over the domain Ω, which is usually an interval of possible lengths. The integral

$$\|P_f(\cdot, t)\| = \int_\Omega P_f(z, t) dz$$

gives the total population size of female carp for each time t, and similarly for male grass carp and YY-male grass carp.

In traditional matrix population models, the population vector is multiplied on the left by a matrix to project population size and distribution from one time step to next. In an integral projection model, an integral kernel (i.e., a function that projects the population number and length from one time step to another) $K(z, z')$ is used as an analogue to a matrix, where the population at time $t + 1$ is found via an integral of the form

$$P(z', t + 1) = \int_\Omega K(z, z') P(z, t) dz$$

for each time t. In many ecological settings one can partition the kernel into two kernels, a kernel for growth and maturation and a kernel for fecundity/recruitment (Ellner and Rees, 2006). The maturation and growth kernel, M, projects how fish increase in length through time (i.e., a fish at time t with length z will have length z' at time $t + 1$). This kernel includes survival ($S(z)$), which is a function of length at time t (z), and growth ($G(z, z')$), which is a function of the current length (z at t) and length at the next time step (z' at $t + 1$):

$$M(z, z') = S(z)G(z, z'). \tag{1}$$

The survival function is a logistic function with four parameters: a minimum survival rate, s_{min}; a maximum survival rate, s_{max}; an intercept parameter, α_s; and a slope parameter, β_s (Bolker, 2008):

$$S(z) = s_{min} + \frac{s_{max} - s_{min}}{1 + e^{\beta_s(\log(z) - \log(\alpha_s))}}. \tag{2}$$

The growth function is a two-variable normal distribution centered around a modified von Bertalanffy function of the length at time t (z). Whereas the von Bertalanffy function usually denotes the relationship between time and length, we took the derivative of the length with respect to length (i.e., how length change as a function of length). This produced a mapping between current size at time t (z) and size at the next time step $t + 1$ (z'). The function includes two parameters for the modified von Bertalanffy equation: k_g and a_g, and a standard deviation σ_g:

$$G(z, z')$$
$$= \text{Prob}(z'|z, k_g, a_g, \sigma_g) = \text{Normal} \quad \text{PDF}((1 - k_g)z + k_g a_g, \sigma_G). \tag{3}$$

The fecundity/recruitment kernel, F, is a function of the probability of an egg transitioning to become a recruit, e_t; the probability of females surviving from the previous year, $S(z)$; the probability of females spawning, $P_r(z)$; the number of eggs produced per female, $E(z)$; and the initial recruit length distribution, $J(z')$:

$$F(z, z') = e_t S(z) P_r(z) E(z) J(z). \tag{4}$$

$S(z)$ and $P_r(z)$ are both logistic functions, while $E(z)$ is the function of eggs produced by fish based upon her length, using the length–weight relationship. The input, female fish length z, is converted to biomass based upon the relationship between weight and length from Wanner and Klumb (2009):

$$\log_{10}(\text{biomass}) = \alpha_{lw} + \beta_{lw} \log_{10}(\text{length}), \tag{5}$$

which is integrated for the entire female population. This is then multiplied by the eggs produced per kg of female (e_{kg}). The minimum probability of spawning is r_{min}; the maximum probability of spawning is r_{max}; the probability of spawning intercept parameter is α_r; and the probability of spawning slope parameter is β_r. The recruit length distribution is the length distribution of recruit and is a log-normal distribution with mean μ_J and standard deviation σ_J. The egg transition probability to recruits includes the eggs fertilization, survival, and recruitment to age-1 fish.

Table 1
Parameter symbols, names, values, and sources used for grass carp integrated population model. All units are on an annual time step. Lengths are in cm and weights in kg.

Symbol	Name	Value	Parameter source
Length–weight model			
α_{LW}	Intercept for	−4.33	Wanner and Klumb (2009)
β_{LW}	Slope	2.77	Wanner and Klumb (2009)
Growth function, $G(z, z')$			
a_G	Maximum length	180	US Fish and Wildlife Service (2014)
k_G	Growth rate	0.15	Shireman and Smith (1983)
σ_G	Growth σ	10	Shireman and Smith (1983)
Logistic survival function, $S(z)$			
s_{min}	Minimum survival	0.10	Kirk and Socha (2003)
s_{max}	Maximum survival	0.90	Kirk and Socha (2003)
α_s	Inflection point	40	Shireman et al. (1978)
β_s	Slope	−5	
Density function			
a	Multiplier parameter	1	
b	Rate parameter	Scenario specific	
e_t	Egg transition	3×10^{-3}	
Probability of successful spawning and recruitment			
$p_{recruit}$	Probability	Beta($\alpha = 0.25$, $\beta = 0.25$)	(P. Kocovsky, expert judgment)
Logistic spawning probability function, $P_r(z)$			
r_{min}	Min spawning prob	0	Shireman and Smith (1983)
r_{max}	Max spawning prob	1.0	Shireman and Smith (1983)
α_r	Spawning infection point	40	Shireman and Smith (1983)
β_r	Spawning slope	−4	
e_{kg}	Eggs produced per kg	5×10^3	Ashraf and Fairgrieve (1998)
Length distribution of age-1 fish $J(z)$			
μ_J	Mean	log(10)	Shireman and Smith (1983)
σ_J	Standard deviation	log(2)	
Sex distribution at birth			
p_f	Proportion females	0.5	Shireman and Smith (1983)
p_m	Proportion males	$1 - p_f$	

Table 2
Parameter inputs for sensitivity analysis. Parameter details may be found in Table 1.

Symbol	Inputs
a_G	{100, 180, 200, 220, 400}
k_G	{0.075, .0135, 0.15, 0.165, 0.3}
σ_G	{5, 9, 10, 11, 20}
s_{min}	{$1 \times 10^{-4}, 1 \times 10^{-3}, 1 \times 10^{-2}, 1 \times 10^{-1}, 2 \times 10^{-1}$}
s_{max}	{0.50, 0.56, 0.62, 0.68, 0.74, 0.81, 0.87, 0.93, 0.95, 0.99}
e_t	{$1 \times 10^{-3}, 2.7 \times 10^{-3}, 3 \times 10^{-3}, 3.3 \times 10^{-3}, 4 \times 10^{-3}$}
e_{kg}	{$2.5 \times 10^3, 4.5 \times 10^3, 5 \times 10^3, 5.5 \times 10^3, 1 \times 10^4$}
p_f	{0.001, 0.054, 0.106, 0.159, 0.264, 0.316, 0.369, 0.421, 0.474, 0.500, 0.526, 0.579, 0.631, 0.684, 0.736, 0.789, 0.841, 0.894, 0.946, 0.999}

The year-to-year projection for YY-males is the simplest approach because the only recruitment is from pulse releases in each year, $\mathbf{P}_{YY}(z, t)$ and maturation kernel, $M(z, z')$:

$$P_{YY}(z', t + 1) = \int_{\Omega} (M(z, z')P_{YY}(z, t))dz + \mathbf{P}_{YY}(z, t). \quad (6)$$

The pulse function, $\mathbf{P}_{YY}(t)$, is the number and lengths of YY-males released each year. It is a length distribution for each year of release. The year-to-year projection for males includes maturation and new recruits, as well as the proportion of males produced (p_m, $p_m = 1 - p_f$). The proportion of spawning and successful recruitment during a given year is drawn from a beta-distribution, $p_{recruit} \sim \text{Beta}(\alpha, \beta)$, and depends on population density, d. The effect of density is calculated using the total biomass of carp (i.e., the sum of the weight for all individuals carp), using Eq. (5). This biomass cal-

culation is then used in a negative exponential function to calculate the decrease in fecundity caused by grass carp density:

$$d = ae^{-b\text{biomass}}. \quad (7)$$

These terms are combined to make the (now density-dependent) male kernel:

$$P_{male}(z', t + 1)$$
$$= \int_{\omega} (M(z, z')P_{male}(z, t) + F(z, z')P_{female}(z, t)p_m^{\star} \, dp_{recruit})dz. \quad (8)$$

The female year-to-year projection is similar to the male kernel:

$$P_{female}(z', t + 1)$$
$$= \int_{\omega} (M(z, z')P_{female}(z, t) + F(z, z')P_{female}(z, t)p_f^{\star} \, dp_{recruit})dz. \quad (9)$$

The sex ratio at hatching is a function of the population size of YY-males and regular males:

$$p_f^{\star} = \frac{p_f \|P_m(\cdot, t)\|}{\|P_m(\cdot, t)\| + \|P_{YY}(\cdot, t)\|}. \quad (10)$$

Our model makes two important assumptions about grass carp and the impacts of sex. First, our model assumes that XY-males and females survive and grow at the same rate. We made this assumption because data do not exist for the growth and survival of each sex individually. Second, we assume YY-males are the same biologically as XY-males, i.e., the YY-males have the same demographic parameters such as lifespan, probability of successfully spawning with females, etc. We made this assumption because YY-males have not yet been created and data does not exist on their possible survival rate. We would expect decreasing YY-male survival to

decrease the effectiveness of their use as a management tool. However, given our results, we did not feel this scenario was needed.

2.3. Parameters

We found parameter values for our model from the literature (Table 1). In general, we choose parameters from North American grass carp populations whenever possible. Our justifications for choosing specific parameters are documented in our TRACE Documentation (Supplemental Materials).

2.4. Analysis and implementation verification

We conducted numerical sensitivity analyses to examine the importance of different parameters to the system (Table 2). We did this because we were interested in how a range of parameter input values impacted the model's results both from a parameterization perspective (e.g., which parameter values require more attention to details because of their impact of the system?) and a management perspective (e.g., which portions of the grass-carp life cycle have the largest impact on total population size, based upon the corresponding parameter values within the model?). We choose sensitivity analyses (i.e., using absolute parameter value changes) rather than elasticity analysis (i.e., using relative changes) because we were interested in the specific parameter values rather than a relative difference.

We specifically examined two end points. First, we numerically calculated the sensitivity of the annual change in population (λ, $\lambda = \frac{\|P_{\text{Total}}(\cdot, t)\|}{\|P_{\text{Total}}(\cdot, t-1)\|}$) to the changes in a parameter. For example, the sensitivity of λ to a generic parameter x would be

$$S_\lambda = \frac{\partial \lambda}{\partial x}. \tag{11}$$

This analysis was based upon previous sensitivities of integral projection models (Easterling et al., 2000).

Second, we examined the population's recovery time from stocking with YY-males and how sensitive this end point was to different parameters. We specifically calculated the time it took for the population to recover to its pre-YY-male release size. We used 0.99 of this population to account for possible numerical rounding errors. For these simulations, we ran the simulation 50 years and then released 10,000 YY-males per year for 20 years. The model was then allowed to run for 130 additional years (a total of 200 years of simulations) to allow the model to return to equilibrium. We have included a longer description of our sensitivity and recovery time analysis in our TRACE Document (supplemental materials).

We verified our numerical implantation using two approaches. First, we used the `R CMD build` and `R CMD check` function to check our code for errors such as missing or extra variables. The checks also ensured our documentation included all parameters and did not include extra parameters. We also used the `devtools` and `roxygen2` packages to develop and document our package (Wickham and Chang, 2016; Wickham et al., 2015). Second, we had a test script that explored model behavior and allowed for qualitative verification of our code. We have included the outputs from the test script as part of our TRACE Documentation.

2.5. Numerical methods

We numerically solved our integrals using the mid-point rule using large approximating matrices (Burden and Faires, 2005). The mid-point rule has been used in recent integral projection models because of its simplicity and effectiveness (Ellner and Rees, 2006; Ramula et al., 2009; Merow et al., 2014). During the course of model development, we explored different step sizes for the mid-point

rule and found that about 200 points provided numerically stable results. We integrated over lengths from 0 cm to 240 cm. The upper limit was chosen based upon numerical stability and consistency of the system (e.g., avoiding "eviction" or the loss of individuals due to numerical errors; Williams et al., 2012).

We coded our model as an R package (R Core Team, 2016). We have published the R package, `carpIPM`, on the USGS BitBucket Page (http://dx.doi.org/10.5066/F7DJ5D4H; https://my.usgs.gov/bitbucket/users/rerickson_usgs.gov/repos/carpipm/) in complacence the USGS Open Code Policy. We have also included the code used in this article and the TRACE Documentation on the USGS BitBucket Page.

2.6. Simulation scenarios

We examined three different scenarios of grass carp on Lake Erie because the population size of grass carp is currently unknown (P.M. Kocovsky, expert judgment). The total population size of each scenario varied by an order of magnitude based upon the density term, b. Scenario 1 had about 2500 adults (individuals >45 cm) in the deterministic scenario using $b = 1 \times 10^{-4}$. Scenario 2 had about 20,000 adults (individuals >45 cm) in the deterministic scenario using $b = 1 \times 10^{-5}$. Scenario 3 had about 100,000 adults (individuals >45 cm) in the deterministic scenario using $b = 3 \times 10^{-6}$. We were able to ignore spatial structure in the population because there is currently only one known spawning tributary for grass carp in Lake Erie (Embke et al., 2016). For our deterministic scenarios, we compared different annual stocking levels of YY-males. Scenario 1 had annual stocking levels of 100, 1000, and 10,000 individuals. Scenarios 2 and 3 had annual stocking levels of 100, 1000, 10,000, 100,000, and 200,000 individuals. We also ran reference scenarios without any stocking of YY-males. For all deterministic stocking scenarios, we ran the model for 25 years to allow transient dynamics to dissipate. We then stocked YY-males for 20 years and then ran the simulation for another 55 years to examine long-term dynamics.

We included environmental stochasticity for the level of spawning and recruitment success because grass carp require high-flow events for successful spawning and recruitment (Stanley et al., 1978). In recent years, this has occurred every other year, but this could occur every year or every few years. Additionally, the partial success allows consideration of multiple-spawning events during a single year (Jennings, 1988; Pflieger, 1997), which has occurred with grass carp in Lake Erie (e.g., during 2015 eggs were captured on 5 dates from 3 spawning events during June and July; P.M. Kocovsky, personal observation). Note that our model has an annual time-step so 2 spawning events producing 10 recruits each would be the same as 1 spawning event producing 20 recruits. We choose a beta distribution with a bimodal distribution with modes near 0 and 1 (Table 1). This allowed most years to either have high or low levels of success, but also for some years to be have moderate success. We choose stocking-levels that were approximately 10% of the quasi-stationary distribution for the stochastic scenarios. We selected this stocking-level to explore the model's behavior and because it provides insight into the possible use of YY-males for grass carp management. We also ran a reference scenario without any stocking. For all stochastic stocking scenarios, we ran the model for 25 years to allow transient dynamics to dissipate. We then stocked YY-males for 20 years and then ran the simulation for another 55 years to examine long-term dynamics. We ran 1000 stochastic simulations for each stocking level and scenario.

We chose a quasi-extinction threshold of 1000 adults for two reasons. First, if the population were to be smaller than this, demographic stochasticity would likely become important (Morris and Doak, 2002) and another modeling approach such as branching process models (Caswell, 2001; Erickson et al., 2015) would be more appropriate. Although this threshold is higher than the suggested

(a)

(b)
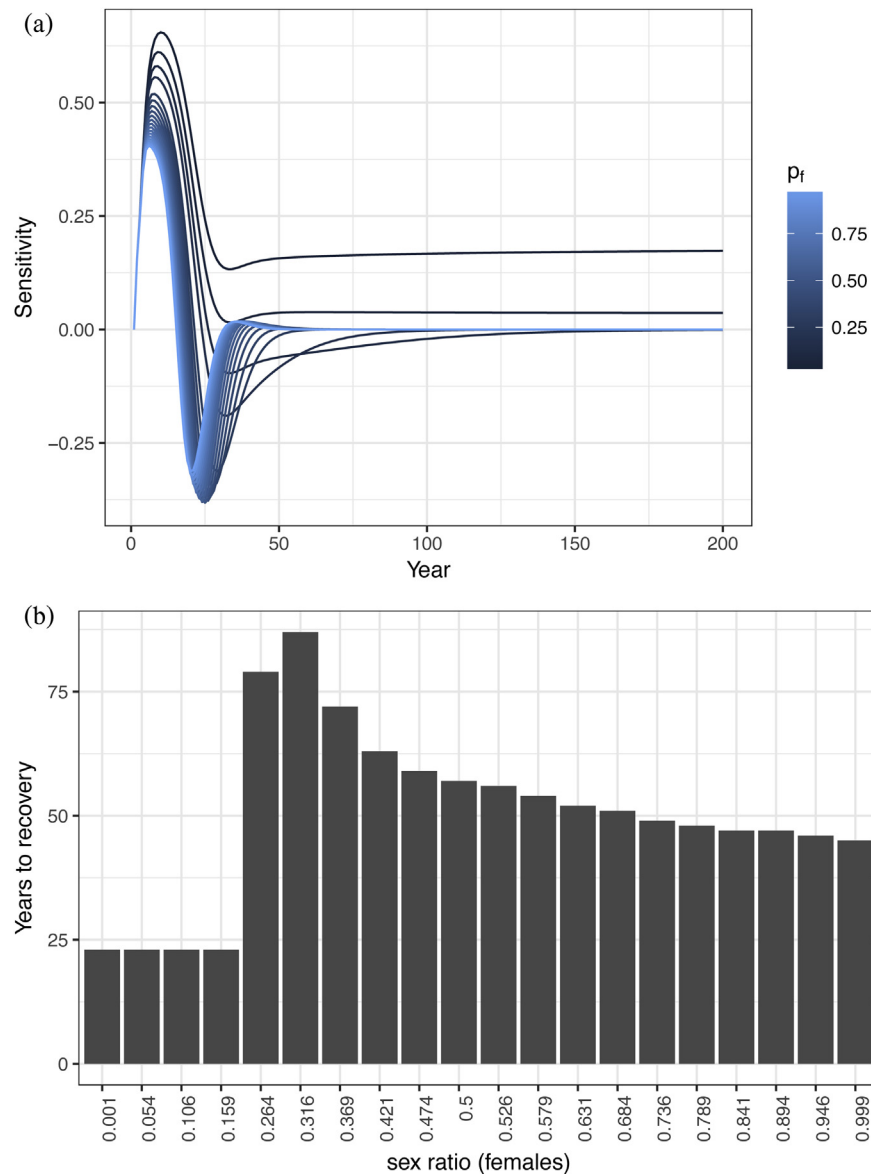
Fig. 3. Sensitivity analysis results for the proportion of females at birth (p_f) parameter.

minimum population size necessary for an invasive carp population in the Great Lakes (e.g., Cuddington et al., 2014), reducing a population to this small would likely either allow the population to be eradicated using other methods or for the population to be undetectable and have minimal ecological impacts for the duration of the population's suppression. Second, numerically modeling extinction can be challenging because the population must reach numerical zero (e.g., 0.0000000 for 8 digit floating numbers) and the population would recover even if only 0.0000001 individuals were present. For all scenarios, we focus on reporting the qualitative dynamics of the system, rather than exact numeric results to reflect uncertainties in the model and our system (Allen, 2007, 2011; Bolker, 2008).

3. Results

3.1. Model analysis

We conducted sensitivity analysis on both the annual population growth rate and the time to recover (Fig. 3 depicts representative results, see our TRACE Documentations in supple-

mental materials for the complete results). Small changes to the model's parameters generally caused small changes the model's sensitivity and recovery. Conversely, large changes to parameters sometimes produced non-linear and seemingly counterintuitive results. For example, slightly increasing the maximum survival parameter decreased the recovery time and slightly decreasing the maximum survival parameter increased the recover parameter. However, large changes had the opposite effect because changing the parameter shifted the model's equilibrium. For example, the maximum adult survival parameter had a longer recovery time because the model had a higher equilibrium population size that required more time for recovery.

The sensitivities of the proportion of females at birth (p_f) is also worth noting because of this parameter's importance with respect to YY-males (Fig. 3). The annual population growth rate was the 4th out of 8 for most sensitive parameters, which indicates that other parameters have larger impacts on the model. The parameter also required large changes to impact the recovery time. Overall, both the annual population growth rate and recovery time were most sensitive to the egg transition parameter (e_t).
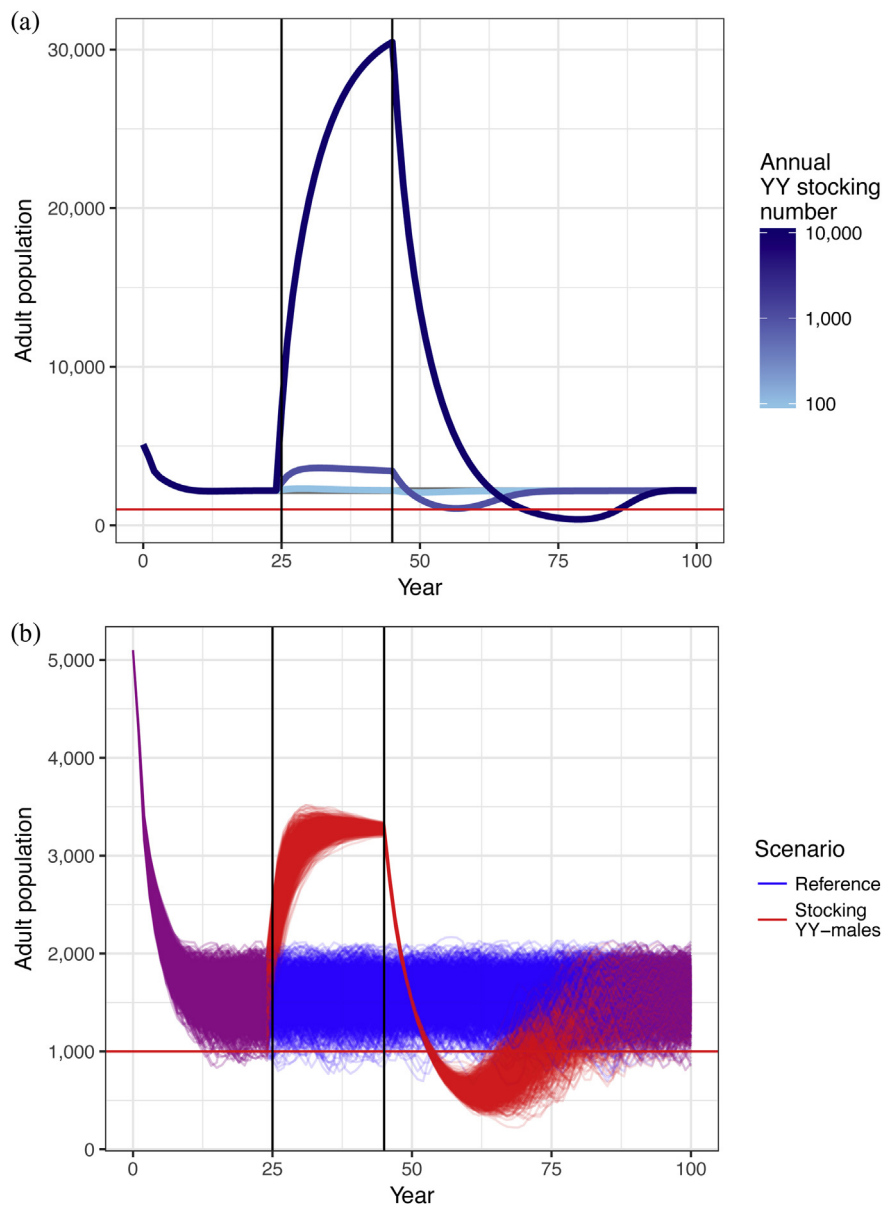
Fig. 4. Outputs from Scenario 1. The adult population are those individuals >45 cm. The redline is 1000 individuals. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

3.2. Management simulations

The deterministic Scenario 1 simulations reached the quasi-extinction threshold for the two highest stocking levels, 1000 and 10,000 per year (Fig. 4a). However, with both stocking levels, the population was able to rebound to pre-stocking levels by the end of the simulation. Additionally, the release of YY-males increased the total population size to be much greater than the population size in the reference scenario.

Some stocking scenarios increased the total population size. The 1000 YY-males per year stocking level increased the adult population from ~2500 to ~8000. The 10,000 YY-male per year stocking level increased the adult population from ~2500 to ~32,000. The 100 YY-male per year stocking level had almost no noticeable impact on the dynamics of the system. The stochastic simulations had a reference population size that ranged from ~1000 to ~1500 (Fig. 4b). As the number of YY-males increased, the total population size increased and the variability decreased. This decrease in

variability occurred because recruitment became less important as the population became more male.

The deterministic Scenario 2 simulations reached the quasi-extinction threshold for the two highest stocking levels, 100,000 and 200,00 per year (Fig. 5a). However, with both stocking levels, the population was able to rebound by the end of the simulation. Additionally, the release of YY-males increased the total population size to possibly biologically un-realistic levels for the two highest levels of release. The 100,000 YY-males per year stocking level increased the adult population from ~20,000 to ~530,000. The 200,000 YY-male per year stocking level increased the adult population from ~20,000 to ~630,000. The 10,000 YY-male per year stocking level increased the adult population from ~20,000 to ~35,000. The 1000 and 100 YY-male per year stocking level had no noticeable impact on the dynamics of the system. The stochastic simulations had a reference population size that ranged from ~10,000 to ~25,000 (Fig. 5b). As the number of YY-males increased, the total population size increased and the variability decreased.
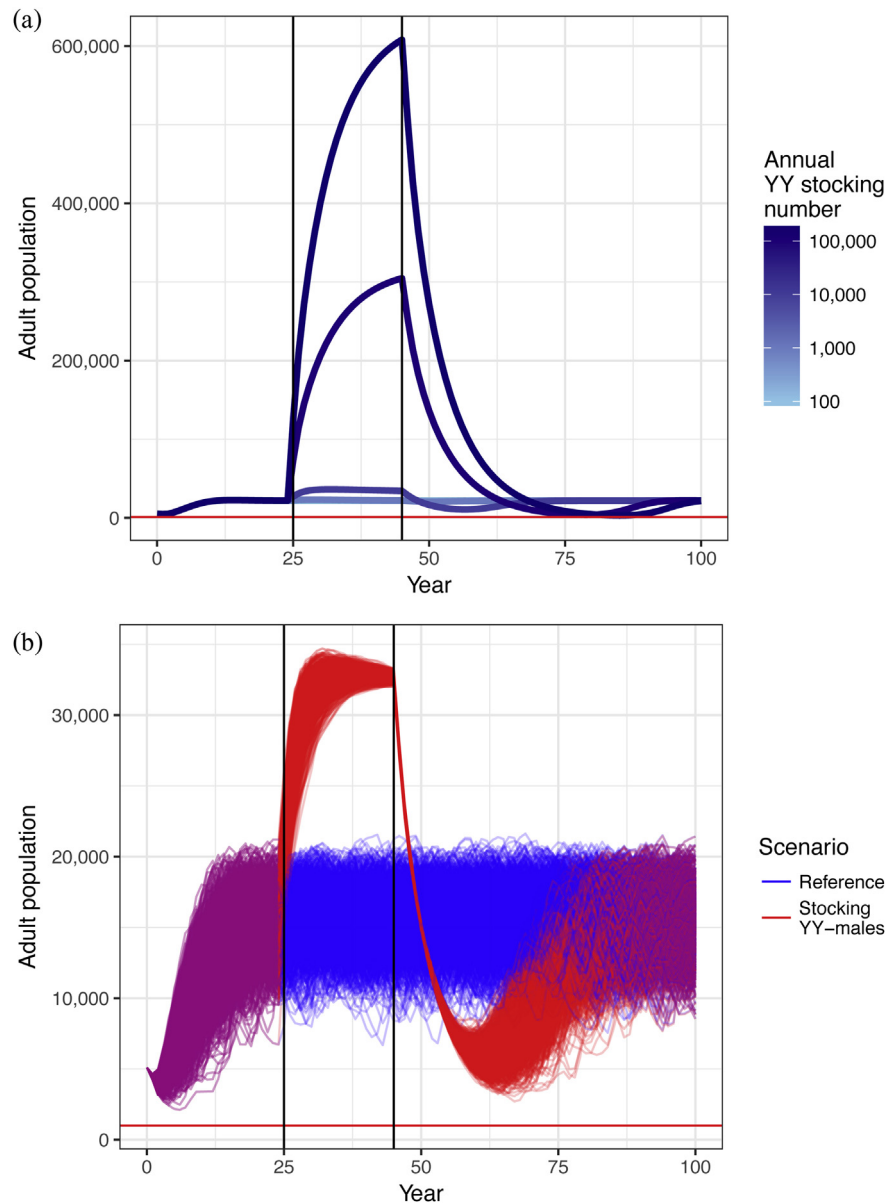
Fig. 5. Outputs from Scenario 2. The adult population are those individuals >45 cm. The redline is 1000 individuals. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

This decrease in variability occurred because recruitment became less important as the population became more male.

The deterministic Scenario 3 simulations did not reach the quasi-extinction threshold for any stocking (Fig. 6a) and the populations recovered from the addition of YY-males from all stocking levels. The release of YY-males increased the total population size to biologically impacting levels and possibly un-realistic levels for the two highest levels of release. The 100,000 YY-males per year stocking level increased the adult population from ~100,000 to ~530,000. The 200,000 YY-male per year stocking level increased the adult population from ~100,000 to ~630,000. The 10,000 YY-male per year stocking level slightly increased the adult population from ~100,000 to ~110,000. The 1000 and 100 YY-male per year stocking level had no noticeable impact on the dynamics of the system. The stochastic simulations had a reference population size that ranged from ~38,000 to ~77,000 (Fig. 6). As the number YY-males increased, the total population size increased and the variability decreased. This decrease in variability occurred because recruitment became less important as the population became more male.

However, in this scenario, the model outputs for the YY-release simulations fell within the distribution of the reference simulations.

4. Discussion

We developed an integral projection model to evaluate the use of YY-males as a control strategy. We specifically examined controlling grass carp in Lake Erie because this control approach has been discussed for that lake. Broadly, we found that smaller populations of grass carp would be easier to control than larger populations, although this finding should not be surprising. We also observed that reducing the ratio of females to a level low enough to cause population decline requires the release of a large number of YY-males. This is in agreement with Knols et al. (2006) who has highlighted this point as a criticism of sterile mosquito release and an important limitation to its use in management. Additionally, Knols et al. (2006) noted that the release of sterile mosquitoes can be un-popular unless only males are released because female mosquitoes bite and cause other adverse impacts
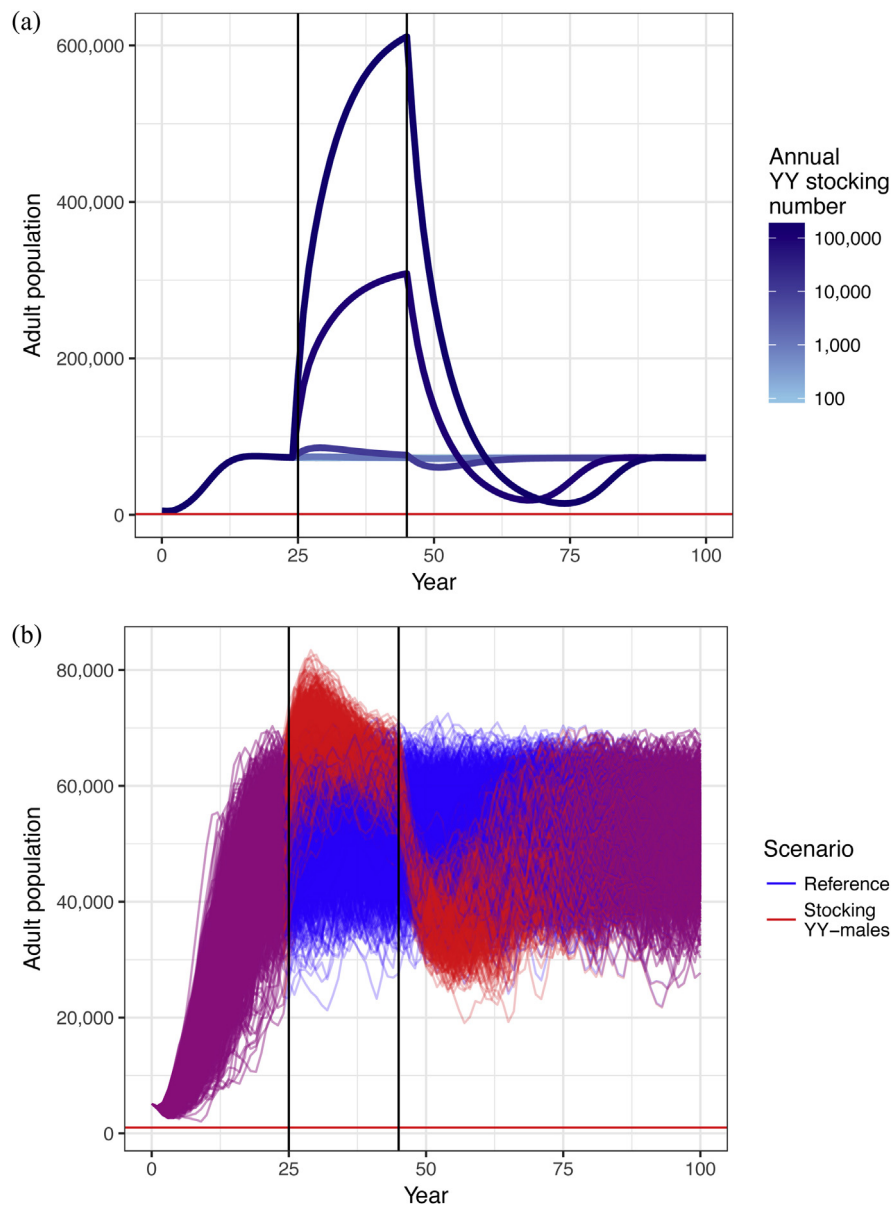
Fig. 6. Outputs from Scenario 3. The adult population are those individuals >45 cm. The redline is 1000 individuals. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

such as disease transmission. This highlights another downside to the release of YY-male carp. Sterile male mosquitoes are relatively benign compared to YY-male carp. The sterile male mosquitoes feed on non-animal sources and are short-lived (i.e., a lifespan measured in months) whereas YY-male carp cause the same ecological damage as females and can be long-lived (i.e., a lifespan measured in years if not decades). Furthermore, the release of sterile mosquitos has faced hurdles. First, the public may simply be opposed to releasing a vector species. Second, the public may be opposed to releasing genetically modified organisms, such as sterile mosquitoes (Adalja et al., 2016). Similar hurdles face the release of YY-male carps. Although not genetically modified (the discussed method used to make YY-male grass carp is hormonal; Schill et al., 2016), YY-males are still modified and a noxious species. The release of grass carp could be unpopular because it is a modified organism and because the YY-males would cause ecological harm over many years (Krynak et al., 2015). Last, releasing the YY-males into the Great Lakes would require coordination with state, provincial, and bi-national agencies across Canada and the

United States and any one of these agencies could potentially halt the release of YY-males (Lodge et al., 2016). We observed higher variability in the larger simulated stochastic populations than in the smaller scale simulated populations. A difference between the stochastic and deterministic model was that fewer YY-males were necessary to have a larger impact of population, owing to the partial success of recruitment in some years. This modeling observation highlights the importance of better understanding of conditions that allow for invasive carp to successfully spawn and recruit new females (Kocovsky et al., 2012). The increased impacts of YY-males in a stochastic model also agree with existing population ecology research that has found increasing stochastic variability also increases the chance of a population going extinct (Lande et al., 2003; Allen, 2011).

Additionally, our model had transient dynamics before the population reached a stable-length distribution. This was observed for all three scenarios, but is most pronounced for the two scenarios with higher carrying capacities. This suggests the transient dynamics of grass carp in locations such as the Great Lakes may currently

be more important than the long-term dynamics of the quasi-stationary equilibrium. Previous research has demonstrated the important of transient dynamics when studying invasive species and highlighted how it is still an open research question in population ecology (e.g., Hastings, 1996; Parker, 2000; Ezard et al., 2010).

Our results also illustrate how integral projection models can be used for fisheries management. The use of integral projection models in ecology is still less than 20 year old (Easterling, 1998). Furthermore, most applications have either been ecological studies (e.g., Ellner and Schreiber, 2012; Eager et al., 2013, 2014) or methods papers (e.g., Merow et al., 2014; Moore et al., 2016; Smallegange et al., 2017; Schreiber and Ross, 2016) rather than applications to resource management (e.g., Jongejans et al., 2011; Wallace et al., 2013; Yau et al., 2014) or proposed applications to resource management (e.g., Ainley et al., 2017). Future research to demonstrate the use of integral population modeling within fisheries management would highlight the potential for these models as a management tool.

The model we developed also suggests areas for future study. Our model could be adapted to compare integrated pest management strategies. Integrated pest management applies multiple stressors to control undesirable species (e.g., sea lamprey; Sawyer, 1980). Other stressors for carp might include barriers to limit migration (Sloan et al., 2013), novel carpicides (Putnam et al., 2017), commercial harvest (Colvin et al., 2012), and novel applications of pesticides (e.g., carbon dioxide poising under ice) (Cupp et al., 2017). The use of models, such as ours, could provide natural resource managers with initial direction or guidance for the management of invasive species. Integrated pest management of carp would benefit from the models such as ours because it could help guide management decisions of the species. Management scenarios could also be "optimized" using either optimization theory (Lenhart and Workman, 2007) or control theory from applied mathematics (Friedlan, 1986). Grass carp management in particular would likely be most effective if it either targeted recruitment (e.g., the egg transition parameter in our model) or adult survival based upon our preliminary model analysis.

From a fisheries perspective, our model raises interesting questions about the behavior and life history of YY-males. For example, do grass carp randomly or non-randomly mate? Schindler et al. (2013) theoretically demonstrated that nonrandom mating can be important for population growth. Grass carp broadcast spawn (Shireman and Smith, 1983), which would suggest random mating. Although YY-male grass carp do not exist, sterile triploid grass carp do exist. Two ongoing studies in Lake Erie and Truman Reservoir (Missouri, U.S.) may provide insight into this question using diploid ("normal" grass carp) and triploid (theoretically sterile grass carp). Researchers and managers surgically-implanted acoustic transmitters that permitted identification of individuals. A receiving array detects fish movement into spawning areas. The results from these studies would provide insight into the behavior of modified males and their interactions with females. Currently, we are unaware of any studies that examined if sterile fish try to spawn with fertile fish or if females can differentiate between diploid and triploid males. This demonstrates a case where empirical ecology lags behind theoretical ecology. We choose to assume equal mating probabilities of YY-males and normal males to model a "best-case" scenario for the YY-male release approach. We demonstrated that the release of YY-males likely would not be feasible management strategy. Had we found contrary evidence through modeling (i.e., YY-males likely be a feasible management strategy), we would have challenged this assumption in the model.

Another interesting fisheries management question about grass carp is "where does density limit growth?" We assumed spawning habitat limited the grass carp population in Lake Erie. Lake Erie is a large lake (~1300 km shoreline), but only grass carp are only known to spawn on a short reach (<2 km long) of the Sandusky River in Freemont, Ohio, U.S. However, grass carp consume a large amount of vegetation biomass in the Great Lakes and this impact is amplified because grass carp eat early season vegetation biomass thereby eliminating aquatic plants before they can grow and produce more biomass (van der Lee et al., 2017). Releasing large numbers of YY-males would almost certainly drive an ecological cascade caused by widespread elimination of vegetation. However, we demonstrated that releasing a large number of YY-males would only have limited success. If managers wanted to release a large number of YY-males, considering both the inter- and intraspecific density effects would be important not only from a modeling perspective, but also a managerial perspective.

The grass carp population we examined lacked spatial structure, but many invasive carp populations have distinct spatial structures (Lohmeyer and Garvey, 2009). Integral projection models can incorporate spatial dynamics (e.g., the use of spatial integral projection models for plants by Jongejans et al., 2011). Furthermore, an integral projection model could be inserted into existing network-node models rather than the difference equations or matrix models that have currently been used (Taylor and Norris, 2010; Erickson et al., 2014). A spatial structure would increase the complexity of grass carp management and likely require the release of more YY-males. Including spatial structure would also facilitate the modeling of other invasive carps.

5. Conclusion

We have presented an integral projection model of grass carp. We applied the model to examine different YY-male release strategies. We found that controlling a large population of grass carp, such as the population found in Lake Erie, would require more YY-males to be released than currently exist in the system. This level of release may not be practical given the ecological impact of the releases as well as social and political implications of the releases.

Acknowledgments

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.ecolmodel.2017.07.030.

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