

TRACE document

This is a TRACE documentation (“TRANSPARENT and Comprehensive model Evaluation”), which provides supporting evidence that our model presented in:

Erickson RA, Eager EA, Bray MK, Hansen MJ, and Kocovsky PM. An integral projection model with YY-males and application to evaluating grass carp control. *Ecological Modelling*.

was thoughtfully designed, correctly implemented, thoroughly tested, well understood, and appropriately used for its intended purpose.

The rationale of this document follows:

Schmolke A, Thorbek P, DeAngelis DL, Grimm V. 2010. Ecological modelling supporting environmental decision making: a strategy for the future. *Trends in Ecology and Evolution* 25:479-486.

and uses the updated standard terminology and document structure in:

Grimm V, Augusiak J, Focks A, Frank B, Gabsi F, Johnston, Liu C, Martin BT, Meli M, Radchuk V, Thorbek P, Railsback SF. 2014. Towards better modelling and decision support: documenting model development, testing, and analysis using TRACE. *Ecological Modelling* 280:129-139

and

Augusiak J, Van den Brink PJ, Grimm V. 2014. Merging validation and evaluation of ecological models to ‘evaluation’: a review of terminology and a practical approach. *Ecological Modelling*. 280:117-128

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1 Problem Formulation

This TRACE element provides supporting information on: The decision-making context in which the model will be used; the types of model clients or stakeholders addressed; a precise specification of the question(s) that should be answered with the model, including a specification of necessary model outputs; and a statement of the domain of applicability of the model, including the extent of acceptable extrapolations.

Summary:

Grass carp (*Ctenopharyngodon idella*) are native to eastern Asia. The fish have been transported outside of their native range for weed control and have escaped into native habitats. As an invasive species, grass carp disrupt native ecosystems and vegetation. Controlling the species is important for conservation biology and fisheries management. Population models are one tool for guiding carp control efforts and better understanding carp life history. Possible management activities include containment through barriers, harvest, releasing YY-males, and developing carpicides. All of these approaches would benefit from population models to guide management. The objective of our model is assist in the control of grass carp. The objective of the corresponding paper is to present and analyze our model. We also apply the model to compare different management scenarios with YY-males.

Grass carp are native to eastern Asian and range from the Amur River of eastern Russia to the West River of southern China (Shireman and Smith, 1983). The range also gives it another common name, white Amur. The species feeds on aquatic vegetation and has been introduced around the world, including Malaysia, Taiwan, Japan, eastern Europe, Holland, Germany, and the United States of America (Cross, 1969). Although effective at weed control, the species has also escaped into the wild and disrupts native ecosystems (Chapman et al., 2013). The species decimates native macrophyte communities, which in turn alter ecosystem function, habitat structure, community process, and food web dynamics (Dibble and Kovalenko, 2009). Within North America, grass carp were first proposed to be released in 1957 (Swingle, 1957) and first released six years later (Bain, 1993). Grass carp quickly spread from release sites and have dispersed to other systems including the Mississippi River (Bain, 1993) and Great Lakes (Chapman et al., 2013) (Figure 1).

Grass carp management has changed in the United States and North America through time. Initial management of grass carp actually focused on increasing individual survival because the species was (and still is to some) a desirable aquatic weed control species (e.g., Cross, 1969; Mitzner, 1978; Kilambi and Robinson, 1979; Rottmann et al., 1991). Shortly after the first grass carp were introduced to North America, managers noted adverse effects of grass carp and the introduction of sterile individuals (e.g., triploids) were used to limit the impact of introduced carp (Chilton II and Muoneke, 1992). Management of grass carp in many areas of North America has now changed to focusing on limiting invasions, monitoring invasion, and controlling the species (Chapman et al., 2013; Wittmann et al., 2014). Several different species of carp have been introduced to North America and control techniques developed for these and other fishes may also be applicable to grass carp as well. Possible tools include acoustical conditioning (Sloan et al., 2013), new carpicides (Putnam et al., 2017), commercial harvest (Colvin et al., 2012), and the release of YY-males that only produce male offspring (Schill et al., 2016). Prior to the expensive development and implemen-

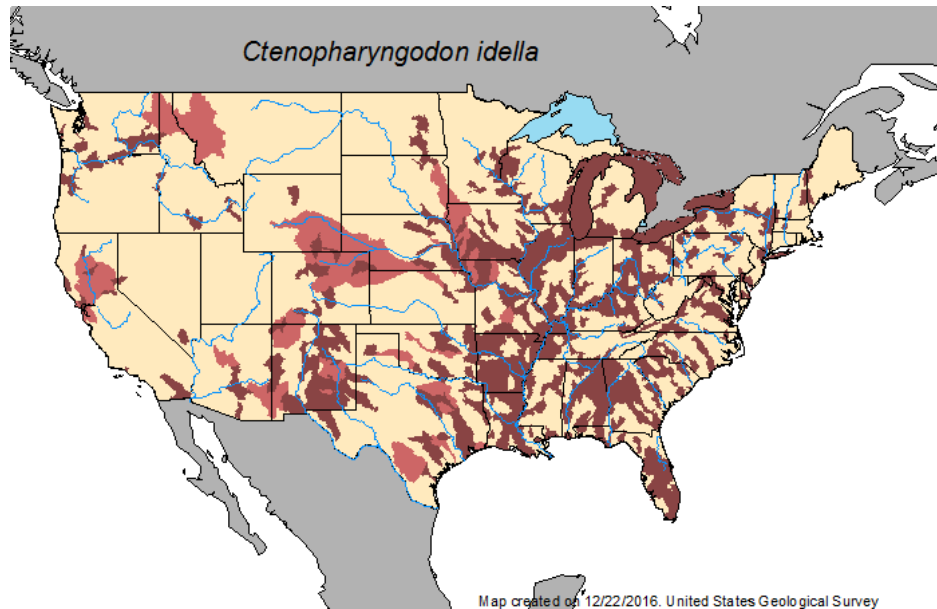


Figure 1: Species distribution map of grass carp (*Ctenopharyngodon idella*) in the continental United States. Map is was generated by the USGS on 22 December 2016 and accessed 23 January 2017 (<https://nas.er.usgs.gov/queries/factsheet.aspx?SpeciesID=514>). The figure was created by Nico, L.G., P.L. Fuller, P.J. Schofield, M.E. Neilson, A.J. Benson, and J. Li while working for the US Government and is in the public domain.

tations of these and other possible management options, managers and researchers may wish to evaluate the effectiveness of the approaches. Mathematical models are one method for running ecological simulations (Bolker, 2008). Additionally, mathematical theory can be applied to “optimize” management (Lenhart and Workman, 2007) or at a minimum, allow different management strategies to be compared (Caswell, 2001; Morris and Doak, 2002).

Mathematically, several population models have been developed for invasive carp (e.g., silver carp, bighead carp, common carp; Lorenzen, 1995; Williamson and Garvey, 2005; Tsehaye et al., 2013; Cuddington et al., 2014) including grass carp (Kirk et al., 2000). The life history of carps (family Cyprinidae) is likely conserved enough that these models could be re-parameterized for grass carp and Lorenzen (1995) presents a generic fisheries model that includes carps. However, these models are not applicable to our management questions. First, the models tend to be designed for specific locations and questions that differ from ours. Second, none of these models differentiate carp by sex nor do they include YY-males. Last, the grass carp model Kirk et al. (2000) does not include sufficient details to reproduce the model, highlighting the need for documentation such as TRACE and ODD (Schmolke et al., 2010; Augusiak et al., 2014). These modeling gaps point to the need for a new carp model that can be readily adapted to new management scenarios. Our model was designed to explore different population-level management options of grass carp by resource managers. Possible organizations that might use our model include international organizations (e.g., the Great Lakes Fisheries Commission), national management agencies (e.g., the US Army Corps of Engineers, the US Fish and Wildlife Service, Environment Canada), state/provincial agencies, and other groups (e.g., NGOs, local governments). The model could also be used to help guide conservation of the species in its native range, where the species has declined due to overfishing (Shireman and Smith, 1983)

As an additional modeling consideration, previous models have tended to be difference equations or differential equations that discretize carp size (e.g., matrix models) or ignore size/age structure. However, carp, like most fish, grow continuously and change in size through time. Hence an integral projection model would more accurately reflect the life history of the species (Ellner and Rees, 2006; Ramula et al., 2009; Merow et al., 2014).

Our model produces two state-variables for a population: the population number (e.g., 1,000 carp at year 10) and the population size distribution (e.g., the length of the fish at year 10 was a binomial distribution with modes at...). We specifically designed the model to answer the following question:

1. How many YY-males must be released to cause quasi-extinction for a population? and
2. How long will the stocked males persist in the environment?

Answering these questions will help managers evaluate the potential for using YY-males to control grass carp.

2 Model description

This TRACE element provides supporting information on: The model. Provide a detailed written model description. For individual/agent-based and other simulation models, the ODD protocol is recommended as standard format. For complex submodels it should include concise explanations of the underlying rationale. Model users should learn what the model is, how it works, and what guided its design.

Summary:

Our model is an integral projection model. The model is designed to guide control of the species. This section describes the model's equations and lists the sources for the model's parameters.

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2.1 Purpose

Our model exists to allow managers and researchers to compare different grass carp management scenarios, specifically, the use of YY-males to control grass carp. However, the model could be applied to other carp species through reparameterization and other management scenarios by including those sources of mortality. Additionally, our parameter values were chosen to reflect management of grass carp in Lake Erie, but the model could be adapted to other locations.

2.2 Entities, state variables, and scales

Our model's entity is a single population of grass carp. The state variables are the number of carp in a population and their size distribution. The population is broken down into three sub-populations: females, males, and YY-males. The model's scale is based upon the biomass capacity of the system. Different scenarios were examined because of uncertainty about the number of carp in Lake Erie.

2.3 Process overview and scheduling

Mathematically, our model has an annual time step. First, the total biomass is calculated based upon the relationship between length and weight. Next, the population from the previous year matures based upon the growth kernel (i.e., individuals grow or shrink in length). The population from the previous year survives and produces recruits. The number of recruits produced depends upon the probability of reproducing, which is a function of size; the number of eggs produced, which is a function of size; the adult survival for the

current year; and the egg transition to age-1 fish parameter (this parameter includes successful spawning, fertilization, and first-year survival). The number of eggs produced is mapped to new individuals by a distribution of initial recruit length. The process can also include stochastic spawning pulses. The new recruits are divided into males and females based upon a sex ratio. The sex ratio is altered by the ratio of YY-males to XY-males in a linear relationship.

2.4 Design concepts

2.4.1 Basic principles

Fish experience asymptotic growth and continue to grow throughout their lives (Lagler et al., 1962). Integral projection models (IPMs) are a mathematical methods for describing this biological process (Ellner and Rees, 2006; Merow et al., 2014). In turn, IPMs form the background of this model. This also assumes that grass carp’s life history is a function of their size. Specifically, this means that the survival, eggs produced, and probability of spawning change as a function of size.

2.4.2 Emergence

Our model does not contain any emergence behavior.

2.4.3 Adaptation

Our model does not contain any adaptive behavior.

2.4.4 Objectives

We do not have an adaptive trait with objectives in the current version of the model.

2.4.5 Learning

This model does not contain “learning” (e.g., individuals changing and adapting based upon their experiences).

2.4.6 Prediction

The model assumes a static future and does include internal or external updates. Grass carp spawning events can be stochastic, but the events are random within the model. YY-males that can be released are predetermined and a set number may be released each year.

2.4.7 Sensing

No sensing occurs within the model.

2.4.8 Interaction

Density dependency occurs within the model where the total biomass of all individuals decreases the reproductive output. A negative exponential relationship is used model this interaction (Bolker, 2008).

2.4.9 Stochasticity

Within the model, spawning events and successful recruitment may be stochastic events. The frequency of spawning events can greatly change the model's output and population size. Additionally, the simulated populations may be more likely to reach a quasi-extinction threshold when the frequency of spawning and successful recruitment increases. Currently, stochastic spawning and recruitment is an important event in the life history of grass carp, but a paucity of data exists on the occurrence of spawning and recruitment in the Great Lakes.

2.4.10 Collectives

The model assumes a single grass carp population. This assumption was made because of a lack of data about grass carp in the Great Lakes and specifically Lake Erie. Depending upon population structures, a spatial-explicit meta-population may be appropriate. However, only one tributary is currently known to have grass carp spawning within Lake Erie and hence, the meta-population dynamics might not be important (P. Kocovsky, personal observation).

2.4.11 Observation

The grass carp population numbers and lengths are the endpoint kept from the model.

2.5 Initialization

The initial grass carp population is the initial settings for our model. This population has three important attributes: size distribution (i.e., "what lengths are the fish?"), sex distribution, and number. The transient dynamics of the system are important for the system and can change the behavior of the system. The initial conditions were not parameterized because the initial release(s) and escape(s) of grass carps into the Great Lakes are unknown. Additionally, the stochastic probability of spawning occurring is an important initial condition, although the model eventually reaches a quasi-stationary distribution. We used a lognormal distribution with a mean of $\log(50)$ and standard deviation of 0.2 for our population's initial distribution.

2.6 Input data

Grass carp are a highly studied species because of their dual importance as an aquaculture species and invasive species. In aquaculture, grass carp are an important species for vegetation control (Chilton II and Muoneke, 1992). In conservation biology and fisheries management, grass carp have large impacts as an invasive species by disrupting native vegetation communities and out-competing native fish (Chapman

et al., 2013; Wittmann et al., 2014). Because of this, many studies have been conducted that provide specific parameters as well as large-scale synthesis pieces that cover the life-history of the species (e.g., Shireman and Smith, 1983). This rich literature source has provided a source of parameter values for the model (Table 1). In this section, we walk through the different parameters used for the integral projection model.

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, personal observation)
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 inflection 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_f	Proportion males	$1 - p_f$	

2.6.1 Length-weight relationship

Several studies exist that examine the relationship between length and weight of grass carp (e.g., Dhanze and Dhanse, 1997). Most of these relationships are for populations outside of North America in aquaculture settings. We choose to use the relationship parameterized by Wanner and Klumb (2009). Wanner and

Klumb (2009) examined the length weight relationship for three species of invasive carps in the Missouri River including grass carp. The study examined carps at two reaches, Gavins Point and Interior Highlands, using a log-log relationship:

$$\text{Log}_{10}\text{weight} = \alpha_{\text{LW}} + \beta_{\text{LW}}\text{Log}_{10}\text{length} \quad (1)$$

The relationship between \log_{10} length and \log_{10} weight was statistically indistinguishable between reaches. We used the relationship estimated for Interior Highlands because it has a larger samples size ($n = 78$ versus $n = 33$; Table 1). This data fit the model well ($r^2 = 0.88$) for observational field data.

2.6.2 Growth-rate

We assumed that grass carp grew using following a von Bertalanffy curve (Bolker, 2008) The maximum length of grass carp has been reported to be 150 cm (US Fish and Wildlife Service, 2014). We choose the asymptotic limit in our model, a_g , to be 180 cm, because this causes the maximum length of most grass carp to about 100 cm or less, which is similar to size distributions reported in the literature (Shireman and Smith, 1983; Martyn et al., 1986). We calculated the annual growth rate, k_g , and standard deviation, σ_g , using lengths summarized by Shireman and Smith (1983). The standard deviation was increased because Shireman and Smith (1983) only included means as part of their work. The standard deviation is on the scale of the length whereas the growth is an annual percentage.

2.6.3 Survival

Many studies of grass carp survival examine rearing the fish in aquaculture conditions (e.g., Stott and Cross, 1973; Kilambi, 1980; Shelton et al., 1981; Cassani and Caton, 1986). Fewer studies exist that examine grass carp survival in wild settings (Shireman and Smith, 1983). In general, grass carp experience higher mortality at smaller size (Shireman and Smith, 1983). At smaller sizes, carp face intraspecific competition and predation risk (Shireman and Smith, 1983), with carp size being an important limitation to predation in North America (Shireman et al., 1978). As grass carp grow larger, predation risk decreases and by the time grass carp are longer than 45cm, predation risk decreases greatly (Shireman et al., 1978).

Our model includes young-of-the-year grass carp survival into the egg transition parameter e_t . No data exists for this parameter, although the model results are extremely sensitive to the parameter's values. Once eggs transition to first-year individuals, survival increases with size. Grass carp can be a long-lived fish species with individuals living greater than 20 years (Shireman and Smith, 1983). A reservoir-based study found annual mortality rates ranging from 22% to 39% meaning that 10% of a cohort could persist for 5 to 9 years (Kirk and Socha, 2003). For post-egg grass carp, we choose the minimum survival rate to be 10% and the maximum to be 90% The inflection point for the logistic curve was chosen to be 40 cm, which reflects the increase in survival as individuals grow larger. The slope parameter was selected because it yields reasonable function behavior.

2.6.4 Density

Density affects the ability of grass carp to successfully produce offspring (Kilambi and Robison, 1979; Shelton et al., 1981) and we modeled the effects of density exclusively on off-spring survival. The number of carps found in our target system are unknown and we explored this uncertainty with different carrying capacities for the system.

2.6.5 Egg production and transition to recruits

The probability of spawning increases as grass carp increase in size. The smallest carp have no probability of spawning and we assumed a maximum probability of spawning to be 1.0 (Shireman and Smith, 1983). The inflection point was chosen to be 40 cm, which assumes 1/2 of all carp reach sexual maturity by the time they grow to be 40 cm. The slope was chose to be -4 for the logistic function.

The number of eggs produced per female is a function that uses the length-weight function to convert length to weight and then uses the the eggs per kg to calculate the eggs produced by females. We used a value of 5,000 egg kg^{-1} for e_{kg} based upon production and fertilization rates reported by Ashraf and Fairgrieve (1998).

The initial size of recruits was a lognormal distribution with a mean of $\log(10)$ and standard deviation of $\log(2)$ based upon values reported by Shireman and Smith (1983).

2.6.6 Sex ratio

We assumed a sex ratio of 50% for the initial population and new recruits because of a paucity of evidence to indicate another ratio (Shireman and Smith, 1983). This ratio can be changed through the introduction of YY-males into the population. We explored this assumption in our sensitivity analysis.

2.7 Stochastic spawning and recruitment

Based upon observations from Lake Erie (P. Kocovsky, personal observation), we choose to model the probability of successful spawning and recruitment during a given year as a beta distribution with $\alpha = 0.75, \beta = 0.75$. This produces a bimodal distribution with mostly boom or bust years (i.e., almost all or none of the population successfully spawns and produces recruits), but allows for some years with partial success.

2.8 Submodels

The backbone of our model is an integral projection model. Integral projection models are still relatively new to population ecology, especially applied ecology, and we refer readers who are unfamiliar with them to recent summary and tutorial articles (e.g., Ellner and Rees, 2006; Ramula et al., 2009; Merow et al., 2014). The state variables for our model are the populations of female grass carp ($P_f(z, t)$), male grass carp ($P_m(z, t)$), and YY-male grass carp ($P_{YY}(z, t)$), which are continuous functions of a size variable z for each

(discrete) time t . The variable z generally ranges over the domain Ω , which is usually an interval of possible sizes. 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 $K(z, z')$ 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 size z will have size z' at time $t+1$). This kernel includes survival, which is a function of current size ($S(z)$), and growth, which is a function of the current size and size at the next time step ($G(z, z')$):

$$M = S(z)G(z, z'). \quad (2)$$

The survival function is a logistic function with four parameters: a minimum survival rate, s_{\min} ; a maximum survival rate, s_{\max} ; a slope parameter, α_s ; and an intercept parameter, β_s (Bolker, 2008). The growth function is a two-variable normal distribution centered around a modified von Bertalanffy function of the current size, z . The function includes two parameters for the modified von Bertalanffy equation: k_g and a_g , and a standard deviation σ_g :

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

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 size distribution, $J(z')$:

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

$S(z)$ and $P_r(z)$ are both logistic functions, while $E(z)$ is the function of eggs produced by fish based upon their size, using the length-weight relationship. The input, female fish length z , is converted to biomass using Equation 1, which is integrated for the entire female population. This is then multiplied by the eggs produced per kg of female (e_{kg}). The minimum survival is s_{\min} ; the maximum survival is s_{\max} ; the survival slope parameter is α_s ; and the survival intercept parameter, β_s . The minimum probability of spawning is r_{\min} ; the maximum probability of spawning is r_{\max} ; the probability of spawning slope parameter is α_r ; and the probability of spawning intercept parameter, β_r . The recruit size distribution is the size 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 eggs fertilization, survival, and transition to age-1 fish.

The year-to-year projection for YY-males is the simplest because the only recruitment is from the pulse releases during each year, $\mathbf{P}_{YY}(t)$, and maturation kernel, M :

$$P_{YY}(z', t+1) = \int_{\Omega} (M(z, z') P_{YY}(z, t)) dz + \mathbf{P}_{YY}(z, t). \quad (5)$$

The pulse function, $\mathbf{P}_{YY}(t)$, is the number and size of YY-males released each year. It is a size 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 each year from a beta-distribution, $p_{\text{spawn}} \sim \text{Beta}(\alpha, \beta)$; 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), where the relationship between weight and length is taken from Wanner and Klumb (2009):

$$\log_{10}(\text{weight}) = \alpha_{lw} + \beta_{lw} \log_{10}(\text{length}). \quad (6)$$

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

$$d = ae^{-bbiomass}. \quad (7)$$

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

$$P_{\text{male}}(z', t+1) = \int_{\omega} (M(z, z') P_{\text{male}}(z, t) + F(z, z') P_{\text{female}}(z, t) p_m^* d p_{\text{spawn}}) dz. \quad (8)$$

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

$$P_{\text{female}}(z', t+1) = \int_{\omega} (M(z, z') P_{\text{female}}(z, t) + F(z, z') P_{\text{female}}(z, t) p_f^* d p_{\text{spawn}}) dz. \quad (9)$$

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

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

Our model makes some important assumptions about grass carp and the impacts of sex. First, our model assumes that normal males and females survive and grow at the same rate. We made this assumption because data does not exist for the growth and survival of each sex individually. Second, we assume YY-males are the same biologically as normal males. We made this assumption because YY-males have not yet been created and data does not exist on their possible survival rate.

The transient dynamics of our model also depend upon the initial conditions. We chose a log-normal distribution to model the initial size distribution of individuals for both males and females.

We used the mid-point rule to numerically solve the system of integrals (Burden and Faires, 2005) using large approximating matrices. Most recent IPM models have used this approach because of its simplicity (Ellner and Rees, 2006; Ramula et al., 2009; Merow et al., 2014).

3 Data evaluation

This TRACE element provides supporting information on: The quality and sources of numerical and qualitative data used to parameterize the model, both directly and inversely via calibration, and of the observed patterns that were used to design the overall model structure. This critical evaluation will allow model users to assess the scope and the uncertainty of the data and knowledge on which the model is based.

Summary:

Our model used published parameter values, as described in §2.6. We did not have observed trends for Lake Erie and were unable to formally calibrate our model. We discuss limitation of our data in this section and the impact of the limitations on our model. We also discuss how our data is similar to a published study that examined length through time.

Portions of this section could be redundant with §2.6. We therefore focus on the quality of data within this section. Grass carp are a well studied species because of their importance in aquaculture and their impact as an invasive species. We therefore had a large range of literature to draw upon. First, we discuss the limitations of lacking a relative population estimate for our species. Second, we compare our model outputs of length to those from a study published in the literature.

Given our goal of examining the feasibility of releasing YY-males to control grass population in Lake Erie, the great data limitation facing our model is the lack of a reliable population estimate for the lake. Without knowing the order of magnitude for the population, we were forced to explore different population scenarios. We specifically choose to examine three different grass carp population scenarios: a low abundance with about 1,000 adults; a medium abundance with about 10,000 adults; and a high abundance with about 100,000 adults. Obviously, understanding the population size is critical for using YY-males. The YY-male control strategy depends upon “diluting” the amount of females present as a method for decreasing recruitment.

Qualitatively, our model outputs were similar to length distributions reported by Martyn et al. (1986). Martyn et al. (1986) sought to evaluate grass carp a control for aquatic weeds. As part of their methods, 270,000 grass carp were socked into an 8,100 ha reservoir located near Houston, TX over 2 years. The length of the fish were recored prior to release and also twice during the study as part of rotenone based sampling. The fish lengths for distinct modes for each release period (Figure 11 in Martyn et al., 1986). Additionally, these frequency plots of length are qualitatively similar to our model’s outputs.

Quantitatively, we would expect our model to have a slower growth rate than the carp observed by Martyn et al. (1986). Martyn et al. (1986) examined carp in the southern United States, near Houston, TX, which is a sub-tropical region. Our model is for Lake Erie, which is a temperate, continental climate region. Although we did not parameterize our model with parameters specific to Lake Eric, our parameter sources were from temperate regions of the former USSR. This qualitative agreement lends additional support to our model.

4 Conceptual model evaluation

This TRACE element provides supporting information on: The simplifying assumptions underlying a model's design, both with regard to empirical knowledge and general, basic principles. This critical evaluation allows model users to understand that model design was not ad hoc but based on carefully scrutinized considerations.

Summary:

Our model is based upon the life history of carp. Although specifically designed for grass carp, the model should work for any species of carp.

Grass carp, like most species of fish, experience asymptotic growth and continue to grow throughout their life (Lagler et al., 1962). Individual females also produces more eggs as they increase and larger individuals are more likely to spawn than smaller individuals. Additionally, larger individuals of both have higher survival rates than smaller individuals (Shireman and Smith, 1983). These characteristics create a species that would be well described by an integral projection model (Ellner and Rees, 2006; Ramula et al., 2009; Merow et al., 2014).

We created an integral projection model that matches the life history of grass carp (Figure 2). The fish become recruits that survive the first year. Then, the individuals grow. Following a logistic curve, the probability of females spawning and producing recruits increases with their size. Similarly, survival follows a logistic curve with longer individuals being more likely to survive than smaller individuals.

We also included YY-males within the model. These individuals decrease the sex ratio of the offspring and skew it towards male. The goal of this management strategy is to decrease the population growth rate by decreasing the number of females (Schill et al., 2016). This individuals are assumed to be the same demographically as XY-males. Although no YY-males have yet been created, triploid carps have been released to control vegetation. These individuals appear to have similar lifespans based upon research from reservoirs in the southeastern United States (Kirk and Socha, 2003) and anecdotal evidences from pond owners who have released them (<http://forums.pondboss.com/ubbthreads.php?ubb=showflat&Number=146930>).

5 Implementation verification

This TRACE element provides supporting information on: The simplifying assumptions underlying a model's design, both with regard to empirical knowledge and general, basic principles. This critical evaluation allows model users to understand that model design was not ad hoc but based on carefully scrutinized considerations.

Summary:

The model was programmed as an R package. This was checked using the R CMD check and R CMD build functions. Test functions were also used to examine the model's output and verify the outputs behaved as expected.

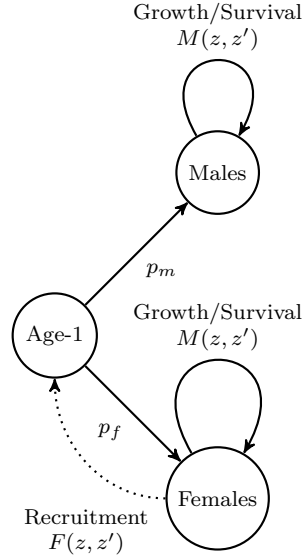


Figure 2: Conceptual map of grass carp life history. p_f is the proportion of recruits who are female and p_m is the proportion who are male. By definition, $p_f + p_m = 1$. Our model seeks to alter this ratio through the introduction of YY-males. Growth/maturation is the annual increase in fish length. Recruitment is the successful spawning and development of eggs to produce age-1 fish. Recruitment does not occur from females until they increase in length.

Our model was coded as an R package. The first tests our code went through were the R `CMD check` and the R `CMD build` functions. These functions build the package and make sure it can pass the CRAN Tests for documentation. They also ensure the examples work. Our second round of verification examined the model's behavior under different test conditions. These conditions start simple and expand upon the simulations complexity.

5.1 Examine growth without mortality

The first scenario had no mortality (Figure 5a) or recruitment and examined how grass carp would grow through time (Figure 3b). The initial population size distribution was log normal (Figure 3c).

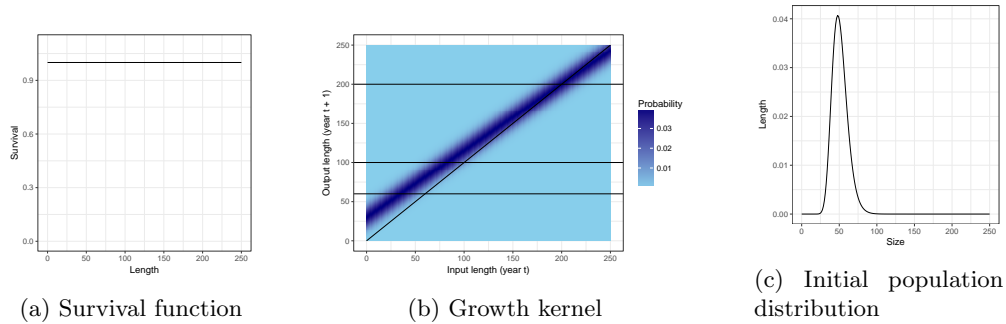


Figure 3: Input functions for Scenario 5.1.

The dominant eigenvalue of this system is 1. If it was not, then there might be problems with the numerical methods or the mesh size may need to be adjusted. The output population is constant (Figure 4a). If the population changed or the leading eigenvalue was not 1, there may be numerical problems or wrong parameters used. For example, when debugging the mid-point rule, individuals would be lost because the dominant eigenvalue was 0.998. The size distribution grows until a stable distribution is reached (Figure 4b). This is important because it indicates the growth function is behaving as expected.

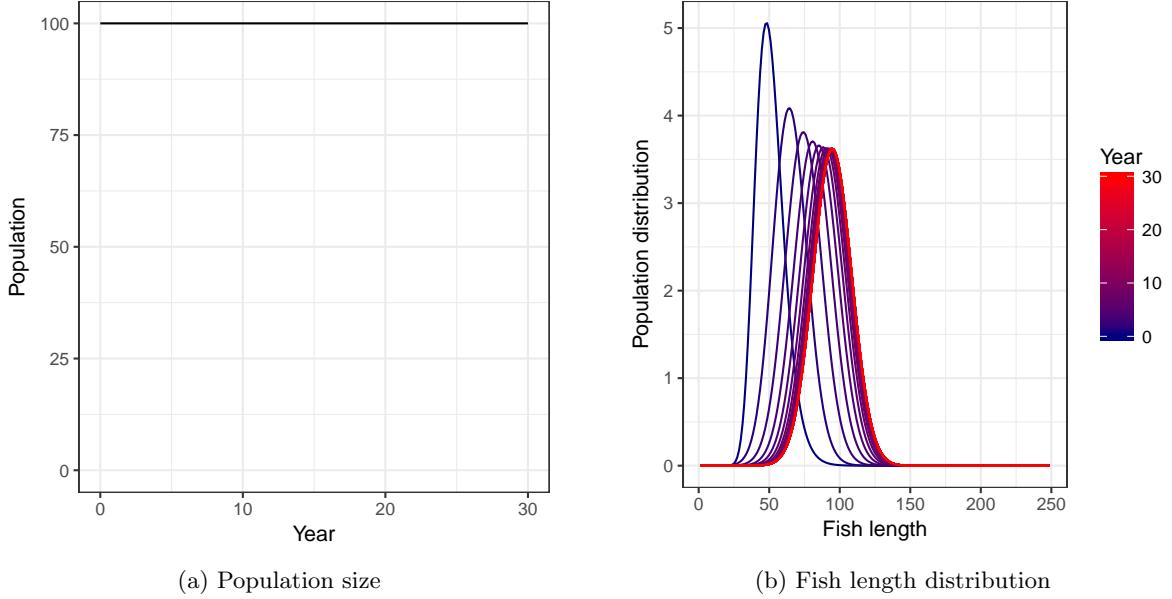


Figure 4: Models outputs for Scenario 5.1.

5.2 Examine growth with mortality

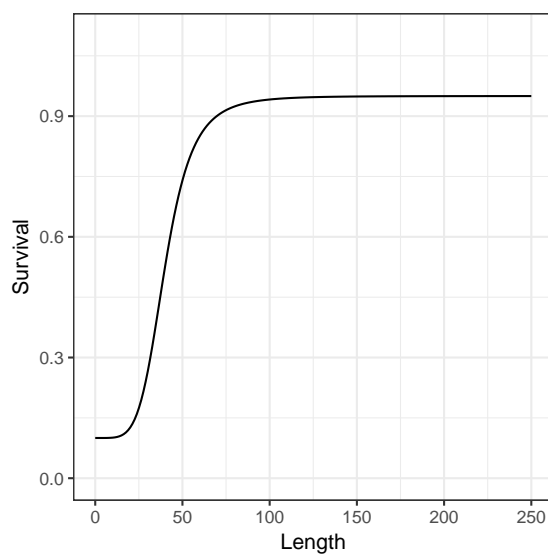
Next, we build upon §5.1 and include mortality as a function of length. All other parameters and functions were held constant and were the same as §5.1 (Figure 5).

In this scenario, the dominant eigenvalue is $0.909+0i$. The population size decreases through time (Figure 6a). The size of individuals in the population increase through time, but the population is shrinking through time (Figure 6b). These are the expected outcomes for the model under these scenarios.

5.3 Examine linear model

Next, births are added into the model. All other parameters and function are the same, but some new parameters are required. An egg transition to recruits parameters is required. A value of 1×10^{-4} was used for this parameter. The initial size distribution of new recruits is required (Figure 7a).

This population is not limited and grows towards infinity (Figure 8a). The dominant eigenvalue is $1.23+0i$. The population reaches a stable size distribution as the number of individuals in the population goes towards infinity (Figure 8b).



(a) Survival function

Figure 5: Input functions for Scenario 5.2.

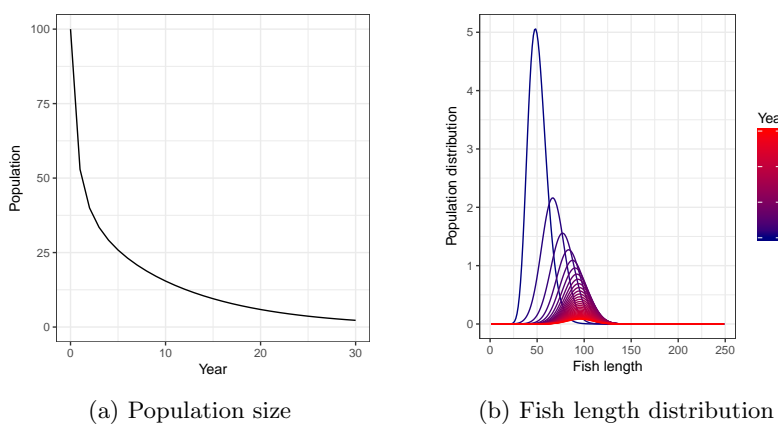


Figure 6: Models outputs for Scenario 5.2.

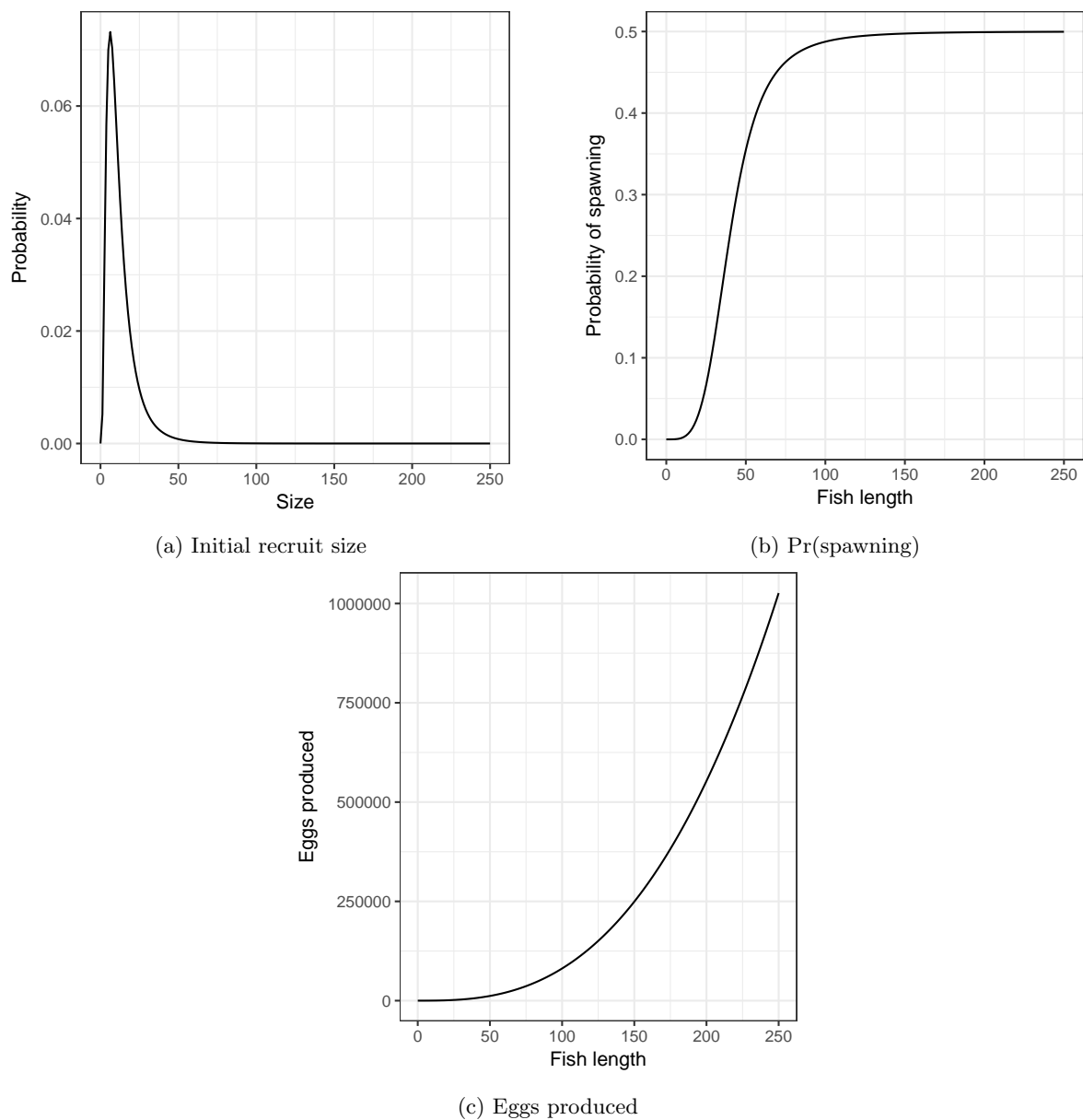


Figure 7: Input functions for Scenario 5.3.

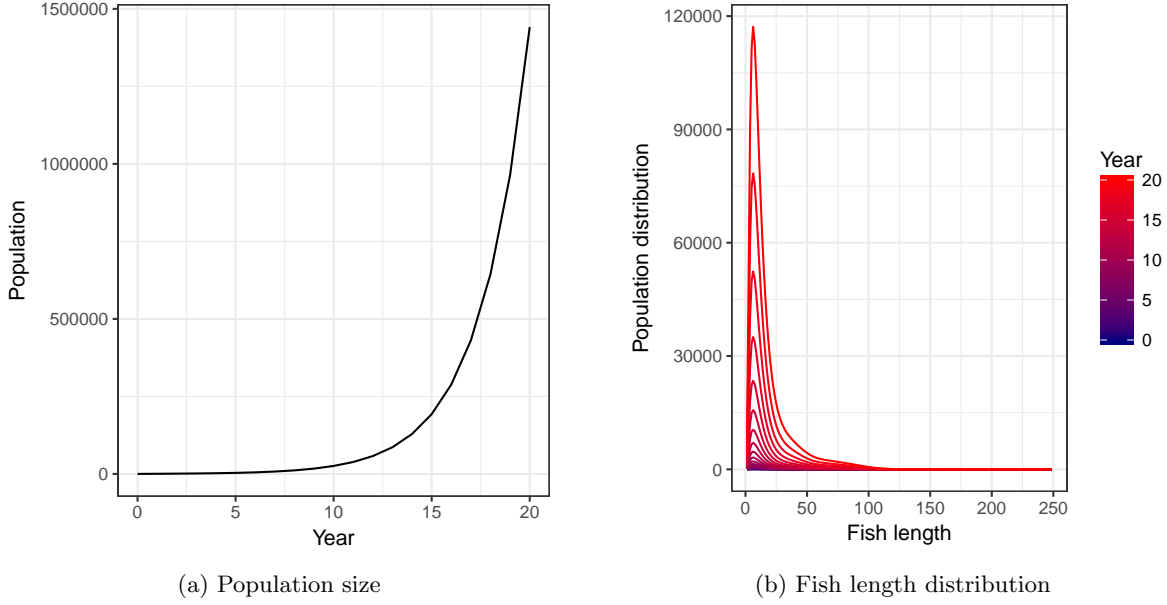


Figure 8: Models outputs for Scenario 5.3.

5.4 Include density within the model

The next step is to include density within the model. The model is the same, other than two new functions are needed. First, a relationship between length and weight is needed. An existing relationship was used from work by Wanner and Klumb (2009):

$$\log_{10}(\text{weight}) = \alpha_{lw} + \beta_{lw}\log_{10}(\text{length}). \quad (11)$$

This equation fit well ($r^2 = 0.87$). A negative-exponential function is used to model how increasing biomass decreases recruitment (Figure 9b; Bolker, 2008).

This system can be used to produce deterministic results (Figures 10a and 10b) as well stochastic (Figures 10c–10e). The stochastic functions have a randomly generated chance of spawning occurring. The models are more biological realistic but come with a tradeoff of less analytical tractability.

5.5 Females, males, and YY-male model

The last portion of the model involves modeling males and YY-males in addition to females. This model allows for control scenarios to be explored. The inputs are the same as before other than sex-ratios that are needed for spawning and the initial conditions. The outputs can be broken viewed as female, male, YY-male, and the total population. This population cannot go extinct numerically unless the population reaches numeric zero (i.e., 0s to the floating point decimal, which is difficult to obtain).

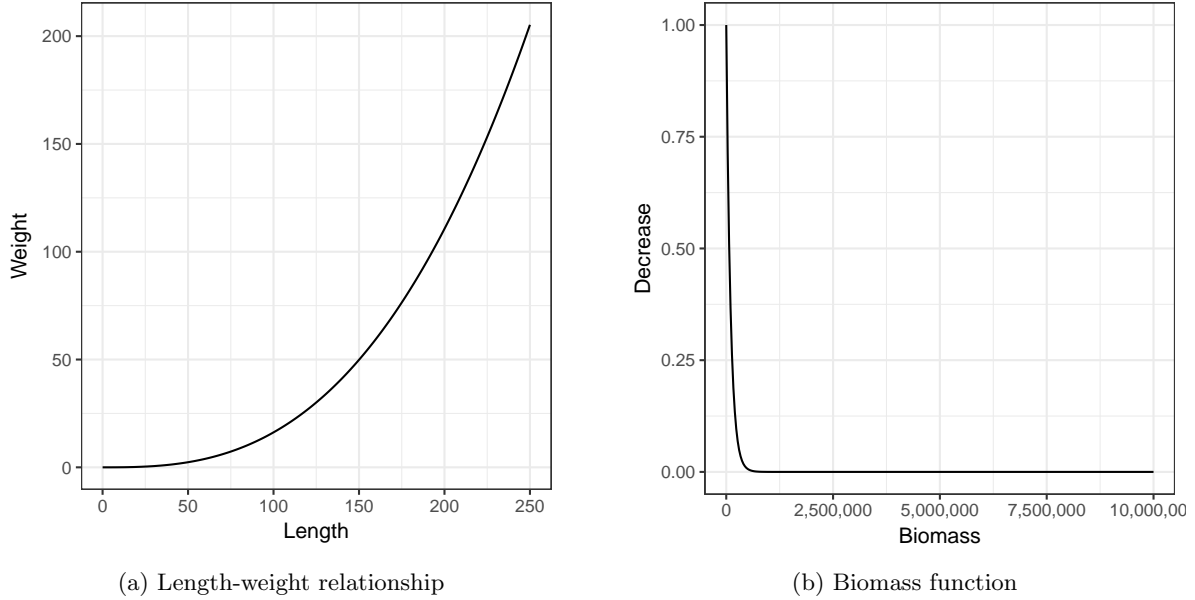


Figure 9: Input functions for Scenario 5.4.

6 Model output verification

This TRACE element provides supporting information on: (1) how well model output matches observations and (2) how much calibration and effects of environmental drivers were involved in obtaining good fits of model output and data.

Summary:

Our model was unable to be formally parameterized. However, we qualitatively compared our model's outputs to existing data and discuss this realism.

We were unable to formally parameterize our model. We were able to qualitatively compare our results to a study by Martyn et al. (1986) who examined the length distributions of grass carp following their release into a reservoir. Additionally, §5 agrees with observations that would be expected based upon first principles of fish population dynamics.

7 Model analysis

This TRACE element provides supporting information on: (1) how sensitive model output is to changes in model parameters (sensitivity analysis), and (2) how well the emergence of model output has been understood.

Summary:

We conducted formal sensitivity analysis by changing input parameters and examining the impacts on the annual population growth rate λ . Furthermore, we

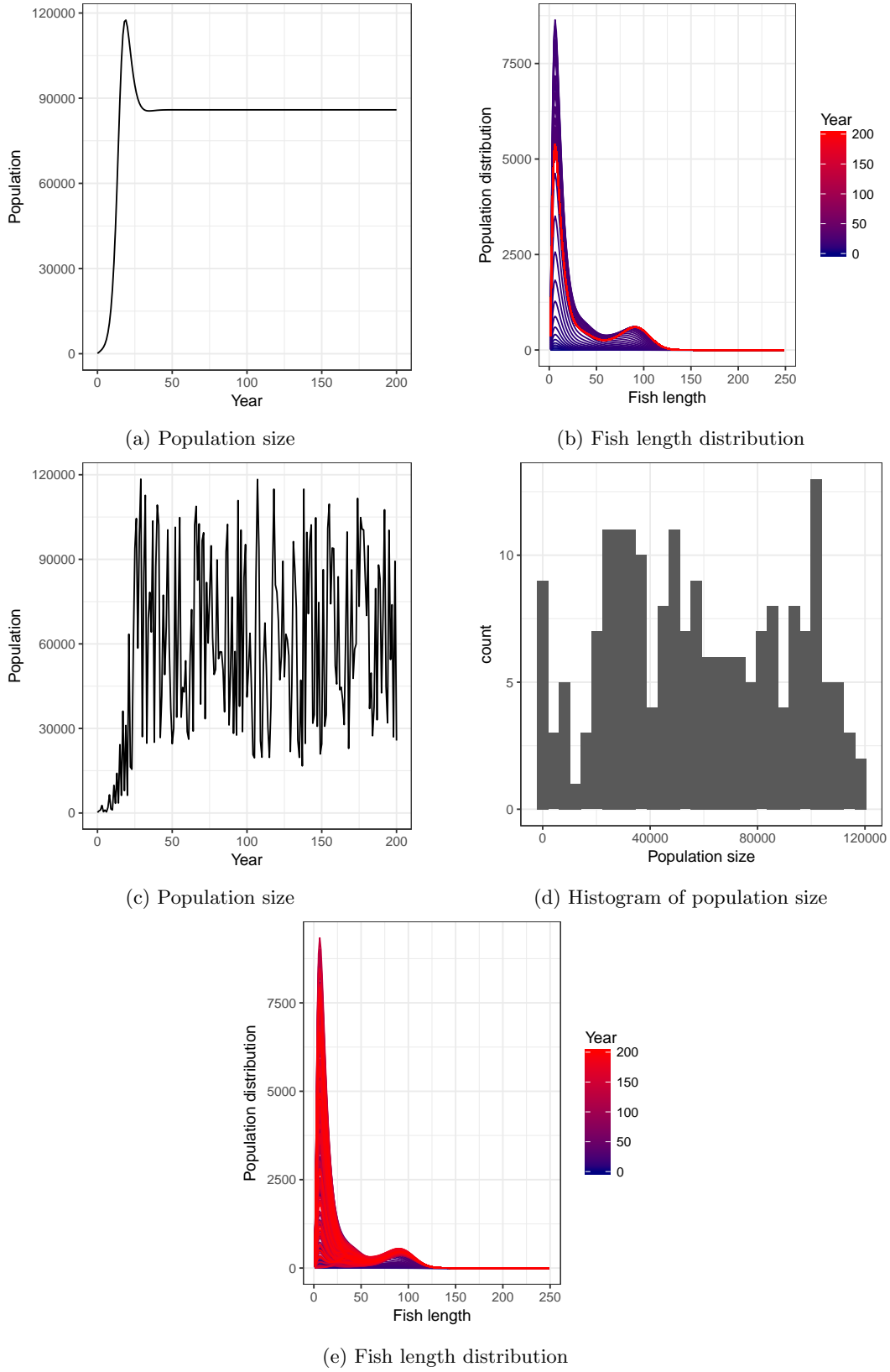


Figure 10: Models outputs for Scenario 5.3, with and without stochastic birth pulses.

examined how different parameters changed the recovery time from YY-males releases.

We examined the sensitivity of the population's growth rate through time. We conducted this analysis to understand how different management actions might be able to change the dynamics of the system and also gain insight into the importance of different parameters. We based our analysis upon that of Easterling et al. (2000) and Caswell (2001), but adapted it for the non-linearities of our system to address our specific question. We specifically examined how the annual population growth λ , changed through time relative to the reference parameter combination. This was done for each time step. We scaled the change in λ by the magnitude of the parameter changed (Table 2). For example λ 's sensitivity parameter x 's would be

$$S_x = \frac{\partial \lambda}{\partial x}. \quad (12)$$

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

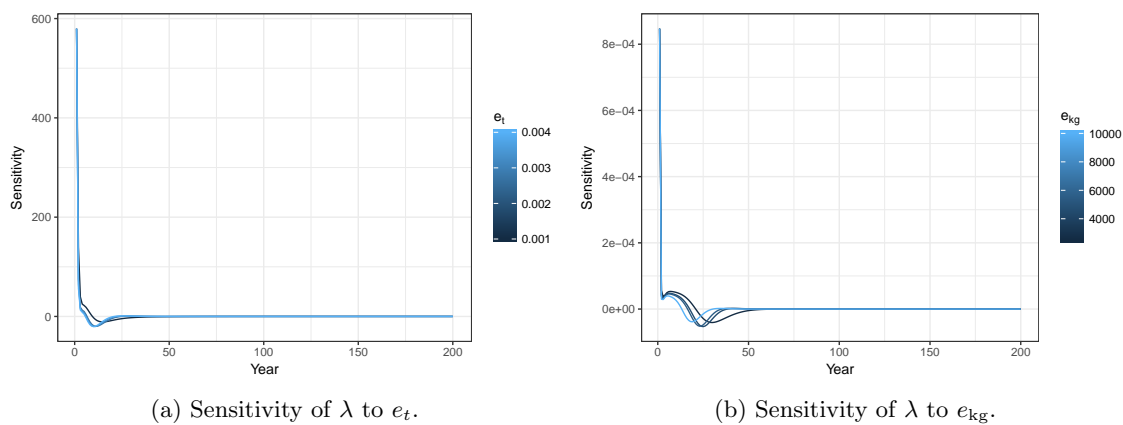
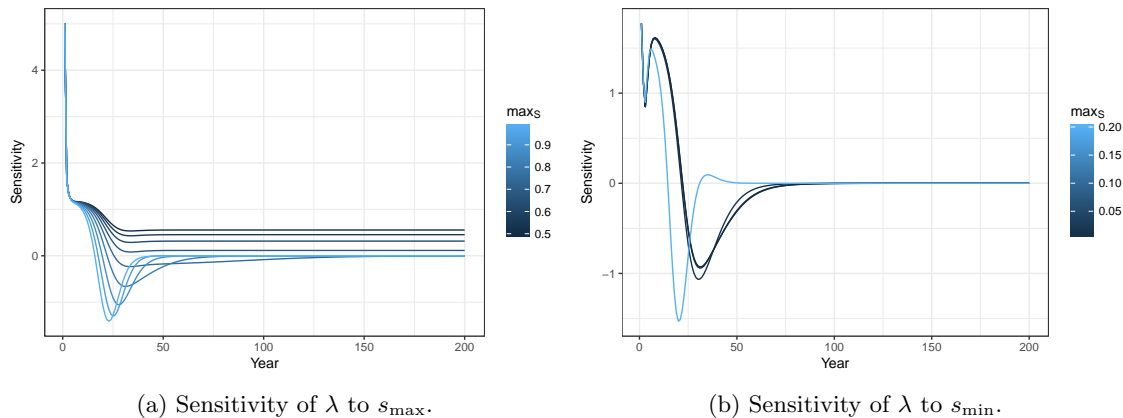
Symbol	Inputs
a_G	$\{100, 180, 200, 220, 400\}$
k_G	$\{0.075, .0135, 0.15, 0.165, 0.3\}$
σ_G	$\{5, 9, 10, 11, 20\}$
s_{\min}	$\{1 \times 10^{-4}, 1 \times 10^{-3}, 1 \times 10^{-2}, 1 \times 10^{-1}, 2 \times 10^{-1}\}$
s_{\max}	$\{0.50, 0.56, 0.62, 0.68, 0.74, 0.81, 0.87, 0.93, 0.95, 0.99\}$
e_t	$\{1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

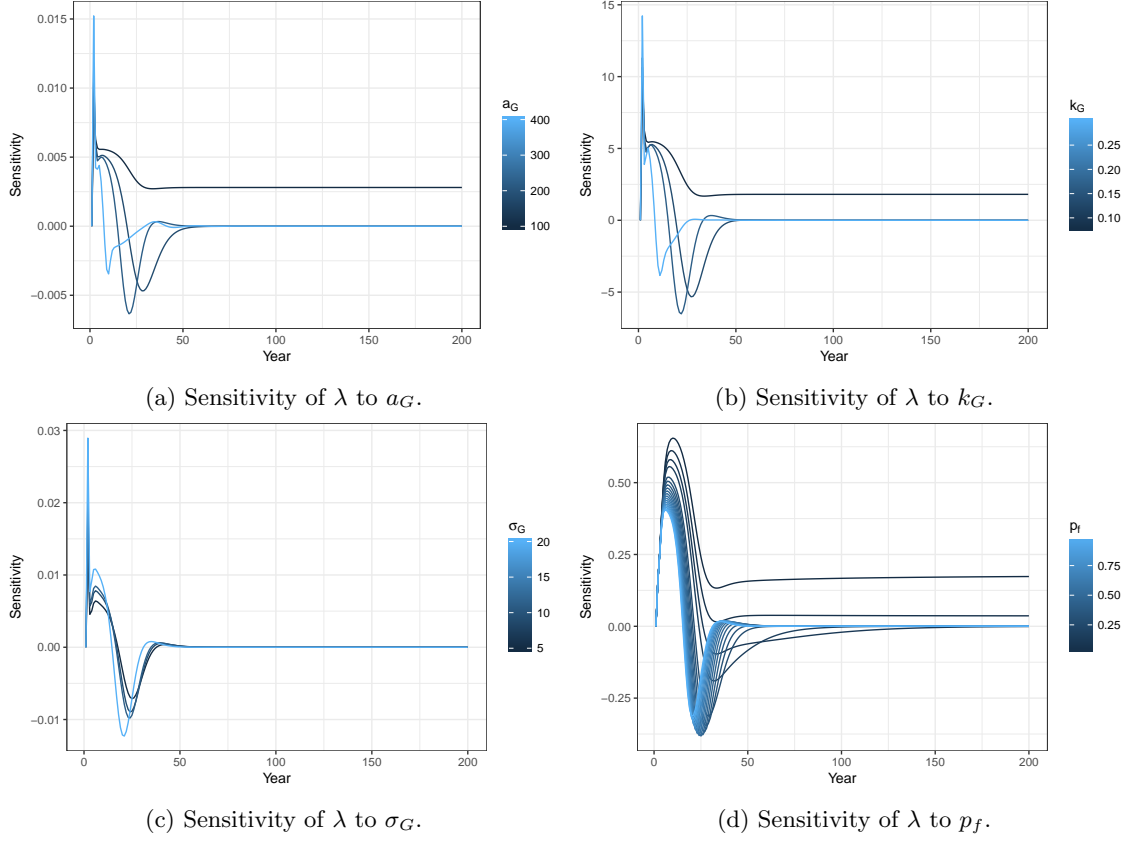
We examined the sensitivity of λ to the egg parameters and minimum and maximum survival parameters (Figure 12). The egg transition parameter, eggs per kg of adult female parameter, and minimum survival rate parameters' sensitivities all converged. The maximum survival rate sensitivity did not converge. The model was the most sensitive to the egg transition parameters and then the maximum survival rate parameters. The egg per female parameter had an almost trivial sensitivity.

We also examined the sensitivity of λ to the fish growth parameters and the proportion of female sex ratio (Figure 13). Of these parameters, the maximum fish length parameter was the most sensitive, which is likely a modeling artifact. Specifically, if fish do not get long enough to reproduce in the model, there is a lower population growth. However, biologically, fish have shown the ability to adapt to harvesting large fish to the loss of large individuals (e.g., harvesting large fish; Birkeland and Dayton, 2005).

In addition to sensitivities we also examined how different parameters changed the recovery time. 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 addition years (a total of 200 years of simulations) to allow the model to return to equilibrium.

In general, the small changes to parameters had small effects on the recovery time (Figure 14). The effects of larger changes varied by parameter. The results for the egg transition parameter, e_t , and the eggs per female

Figure 11: Sensitives of λ (S_λ) of egg parameters through time.Figure 12: Sensitivities of λ to egg and survival parameters.

Figure 13: Sensitivities of λ to fish growth parameters and proportion of female sex ratio.

kg were straight forward as expected (Figures 14a and 14b). The results for the two length parameters, a_g and k_g , behaved as expected for the small changes near the reference parameter value (Figure 14c and 14d). Larger changes however, dramatically reduced the recovery time and both the largest and smallest values. Although similar outcomes, these reflect two different outcomes. The parameter values that increased the populations growth rate caused the population to recover more quickly. Conversely, the parameters values that decreased the population growth rate had a lower equilibrium population size that required less to return to. Decreasing the standard deviation of growth parameters, σ_g caused the time to recover to increase, which was expected (Figure 14e). This is because a larger standard deviation allows some individuals to become big quicker and these individuals therefore reproduce more quickly.

The effects of the female sex ratio at birth, p_f , generally behaved as expected (Figure 14f). The populations with a higher female ratio recovered more quickly. However, at the lowest sex ratios, the recovery time for the mostly male population becomes quicker. This occurs for two reasons. First, these populations have a smaller equilibrium population size. Second, stocking YY-males has minimal effect on the sex ratio because it is already low. This also illustrates the difficulties of stocking with YY-males to reduce a population.

The maximum survival parameter, s_{\max} , had local sensitivities that were reasonable and intuitive (Figure 14g). Small decreases increased recovery time and small increases decreased recovery time. Conversely, larger changes had the opposite effect. When the maximum survival rate was highest, recovery time was longer, which reflects a larger equilibrium population that requires more time for recovery to occur. Similarly, simulations with smaller maximum adult survival rates had smaller equilibrium population sizes, which required less time to for recovery to occur.

Compared to the maximum survival, recovery time was less sensitive for the minimum survival parameter, s_{\min} (Figure 14h). However, all of these changes had effects that would be expected. The decreases all increased recovery time and the increases all decreased recovery time. These changes also reflect the high recruitment strategy (e.g., an r versus k species; Gotelli, 2008) of this species, specifically, if most small carp die, further decreasing this survival will not have as large of impact compared to a long-lived species.

In summary, our model was most sensitivity to the egg transition parameters, which specifically control recruitment based upon both the sensitivity analysis and the recovery time analysis. The sex ratio was not important for the sensitivity analysis, but was important for recovery time. Although seemingly paradoxical, this reflects the biology of the species and management scenario. The sex ratio affects the population's growth rate and its equilibrium size. Hence, if it is altered too much, the simulated population has a much smaller equilibrium size and can recover quickly. Additionally, from a management perspective, the sex ratio could only be change as long as YY-males are release, not permanently as was done with the recovery time analysis. Furthermore, one female grass carp can produce 100,000s to 1,000,000s of eggs, which means even one female can have a large impact on the population.

8 Model output corroboration

This TRACE element provides supporting information on: How model predictions compare to independent data and patterns that were not used, and preferably not even known, while the model was developed, parameterized, and verified. By documenting model output corroboration, model users learn about evidence which, in addition to model output verification, indicates that the model is structurally

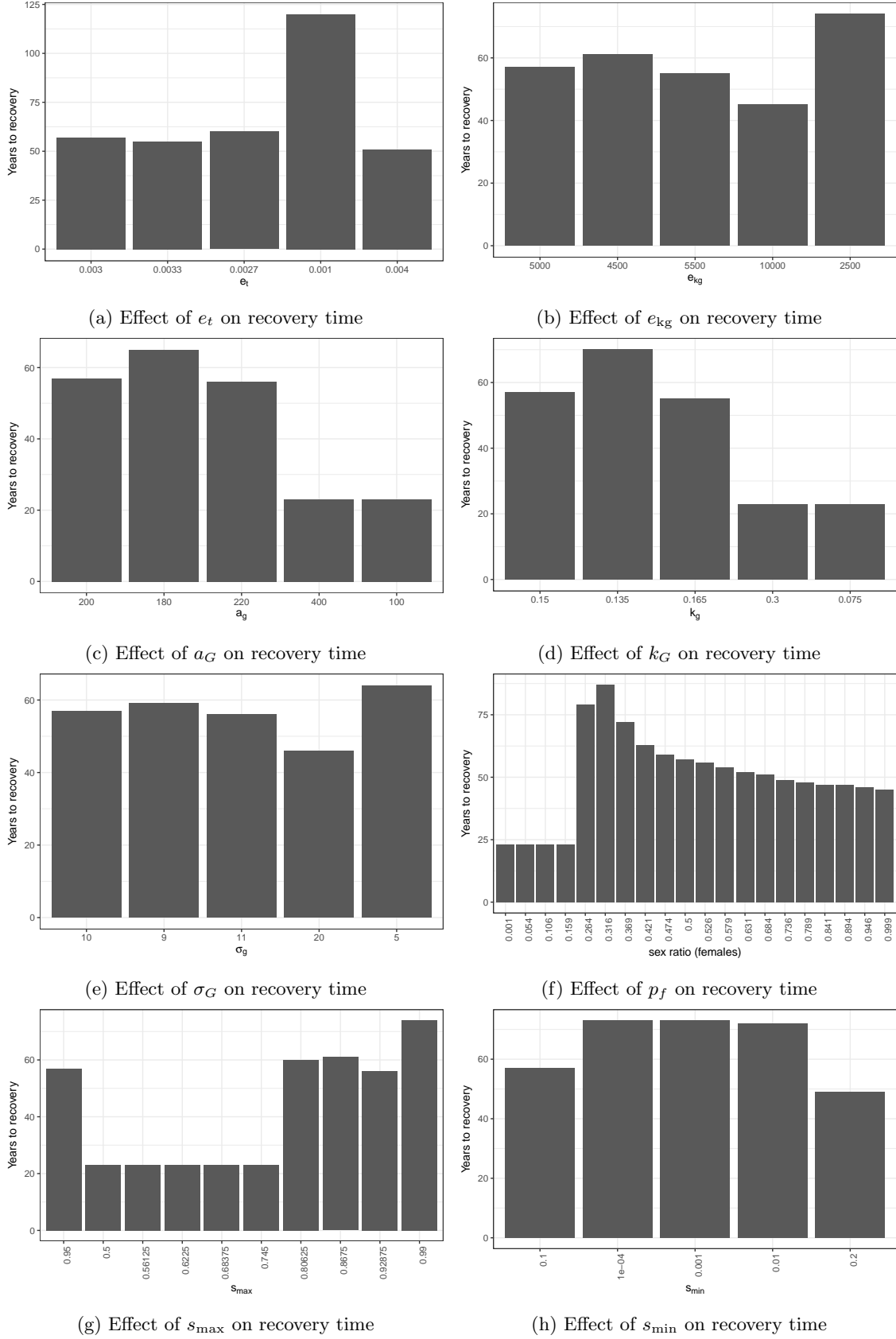


Figure 14: Sensitivities of recovery time. The parameter value farthest to the left is generally the reference value parameter.

realistic so that its predictions can be trusted to some degree.

Summary:

We were unable to formally corroborate our model to any datasets. We discuss a qualitative corroboration to a previously study and why existing datasets do not allow for corroboration.

No datasets exist that examine our system or a similar system through time. Qualitatively, our results were similar Martyn et al. (1986) as noted in §3. In both our model and their system system, the population of carps grows in length through time. However, robust field observations of large-scale grass carp invasions are sparse. A long-term data exists that examines how grass carp have spread up the Mississippi River system (Ickes et al., 2014) that can be used to estimate population trends (e.g., Erickson et al., 2017). However, the spread of this population through a complex river systems differs greatly from the homogenous population that our model assumes. This spatial diffusion and movement would need to be incorporated for a population model to capture the population dynamics of an invasive species in system such as the Mississippi River.

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