TRACE document

This is a TRACE documentation ("TRAnsparent and Comprehensive model Evaludation"), which provides supporting evidence that our model presented in:

Erickson RA, Eager EA, Long, KR, Kocovsky PM, Glover D, et al. A spatially discrete, integral projection model and its application to invasive carps. 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 'evaludation': a review of terminology and a practical approach. *Ecological Modelling.* 280:117-128

Contents

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:

Resource managers and ecologists often seek to understand and model spatial dynamics of invasive species. These models can be applied to both the management of species (e.g., "how many do we need to kill?") and development new control methods (e.g., "is approach X a feasible tool that should be further developed?"). Furthermore, management activities often target organisms of a specific size (e.g., harvest may only target large fish or a barrier may limit the movement small fish but not large fish). We developed a spatially explicit, integral projection model that can be used to help managers. We demonstrate the use of the modeling framework on a lake-tributary system and a series of river pools for grass carp. We did not parameterize our system to any specific system of grass carp. More broadly, our model could readily be adapted to other species (aquatic or terrestrial).

Decision making context: Resource managers use population models to guide management. For example, conservation biologists use population models to prevent the extinction of endangered species, fish and game biologists use population models to management fisheries and game species, ecotoxicologists use population models to assess population-level risks, and invasion biologists use population models to control invasive species (Morris and Doak, 2002). For invasive species, population models provide can provide guidance for the control of species. For example, how many fish of what size should be harvested when and where (e.g., Tsehaye et al., 2013)? Also for invasive species, population models can guide the development of control tools. For example, would YY-males be a feasible control tool for a specific fish species (e.g., Erickson et al., 2017c; Schill et al., 2017)? When the spatial dynamics of the populations are important, the models must consider these dynamics as well (Strasser et al., 2012). We created our model specifically for resource managers seeking to compare control techniques and management scenarios for species that live in discrete spatial populations. That being said, our model should apply to any species with discrete spatial populations that has either continuous growth (i.e., one can use an integral projection model to describe the species life history) or discrete size or age stages (i.e., "matrix model" style growth). Although we do not consider the second life history within this presentation, our code is generalizable enough to include this situation because "matrix models" (i.e., difference equations) are a special case of integral projection models (Ellner et al., 2010).

Model clients or stakeholders: Our specific presentation of a spatially explicit integral projection model targets resource managers controlling invasive fish species. These clients would include state/provincial agencies (e.g., the Michigan or Illinois Department of Natural Resources), national agencies (e.g., the United States Fish and Wildlife Service or Environment Canada), NGO seeking to control invasive species, or private companies developing new control methods (e.g., YY-males or sterile male fish). With our specific system,

we assume the fish exhibit some form of spatially discrete habitat this use. This could be seasonal migration in and out of tributaries or discrete pools on a river due to dams or other impediments

Model questions: We presented our model as a broad, theoretical framework. With our case studies we examined two situations. First, we examined the use of modified fish as a control tool in a system with a lake and two tributaries. The broad management goal for this system is to eradicate the invasive fish species. We specifically asked two questions:

1. How many sterile males would need to be released to cause the population to go extinct?

2. Would modifying the released sterile males to have a shorter lifespan decrease their population size while still producing similar control results as the above question?

Second, we examined a riparian system that was comprised of a series connected pools. The management goal for this system is to decrease the population in the uppermost node. For example, fisheries managers seek to prevent the spread of invasive carp from the Illinois/Mississippi Rivers system to the Great Lakes or fisheries managers week to prevent the spread of invasive carp from the Lower Mississippi River into the Upper Mississippi River or other waterways in Minnesota. We specifically ask four questions with this system:

1. What level of carp harvest is necessary to decrease the the population in the upper most pool?

2. Where should this harvest occur? i.e., the upper pools or the lower pools?

3. Does the harvest size matter? i.e., does the ability to only harvest large organisms change the effects of harvest?

4. What impact does including a barrier have on managing the population?

Our model tracks the population number and size distribution in each node and keeps track of the fish sex groups for the first objective. We did not parameterize our model specifically for these systems because these parameterizations would be beyond the scope of this manuscript.

Domain of applicability of the model: As presented, our model directly applies to fisheries management. The case studies highlight this specific application. Our model could readily be adapted to other aquatic species that are demographically similar to *Cyprinids*. More broadly, our model creates a framework for demographic, spatially explicit population models that account for the full-annual life cycle. We extend the full-annual cycle work for Hostetler et al. (2015). We also extend the network-node framework developed by Taylor and Norris (2010). The model also demonstrates population dynamics such as the "knock-on-effect", which was described by (Betini et al., 2015). Our work also ties into resent work for creating broad, spatially explicit models for migratory species that emerged from a NIMBioS Working group (e.g., Wiederholt et al., 2017; Sample et al., 2017; Erickson et al., 2017a; Bieri et al., 2018). Our model could be adapted to a wide range of species given minor adjustments.

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 recom-

mended 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 a network-node model with integral projection models as the population model within each node. Our model is designed to guide control of the invasive fish species. This section describes the model's equations and lists the sources for the model's parameters.**

Model description contents

2.1 Purpose

We created this model to allow managers and researchers to compare different spatially explicit and size specific management approaches. We were specifically motivated by managers wanting to compare different management scenarios and new, theoretical technologies (e.g., YY-males, sterile-males, or other modified organisms) for invasive carps. Our model allows for the comparison of different management strategies (e.g., harvest, barriers) and new control technologies to meet this need. We also sought to create a generalizable framework as we addressed these needs.

2.2 Entities, state variables, and scales

Our model's entities are "groups" of carp. Groups occupy nodes, which are connected via edges. The groups are roughly analogous to age- or stage-classes in a matrix model. We choose the term "group" because "class" has a special meaning in the Python programming language (and, more broadly, most Object Orientated programming languages). The state variables are the number of carp in a group and their size distribution. The amount of biomass in each node scales the system (i.e., controls the population size).

2.3 Process overview and scheduling

Mathematically, our model has an annual time step. We present the model with two different process options. One model has time periods within each year (i.e., seasons). The second model does not have time periods within season. Each of these models have similar process, with the seasonality introducing an extra step. In pseudo-code, the two models have the following flow through:

2.3.1 Model with time periods

1. Year loop

    (a) Time period loop (e.g., "Spring" $\rightarrow$ "Summer" $\rightarrow$ "Fall" $\rightarrow$ "Winter")

        i. Move individuals among nodes

        ii. Node loop

            A. Calculate node biomass

            B. Calculate sex-ratio or other relevant ratios for reproduction (e.g., decrease in fecundity)

            C. Group loop (within node)

- Project group growth

- Project group recruitment

2.3.2   Model without time periods

1. Year loop

   (a) Move individuals among nodes

   (b) Node loop

      i. Calculate node biomass

      ii. Calculate sex-ratio or other relevant ratios for reproduction (e.g., decrease in fecundity)

      iii. Group loop (within node)

         - Project group growth

         - Project group recruitment

2.4   Design concepts

2.4.1   Basic principles

Many species, including 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. Furthermore, many species exist in discrete habitat patches that are connected and network-node models are one method for modeling these systems (Wiederholt et al., 2017; Sample et al., 2017; Erickson et al., 2017a; Bieri et al., 2018). Network-node models are one method for modeling these systems. We used a network-node model with integral-projection models as the population model within each node.

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

Our model is a deterministic population model. There is no forcing within the model (e.g., no climate, temperature, or other outside conditions that impact the model).

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

As presented, our model was deterministic and does not include stochasticity.

2.4.10   Collectives

Our model includes a spatial structure within a network-node framework. One set of scenario assumes a lake-tributary system (Figure 1) and the other set of scenarios assumes a series of river pools (Figure 2).

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 and Mississippi River Basin 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.
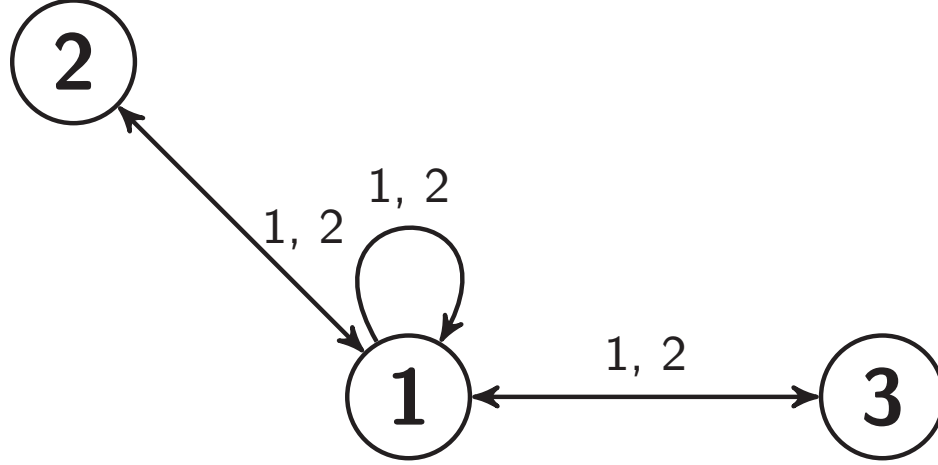
Figure 1: Spoke-and-hub network model used to describe a grass carp population that spends most of its life cycle in a lake (Node 1), but spawns in nodes 2 and 3. Nodes are illustrated with circles and lines represent temporal movements with their corresponding numbers indicating which time periods the lines are used. The model has two time periods: Summer (time period 1) and winter (time period 2). Some grass carp migrate seasonally to spawn during summer, while others stay in node 1. During the winter, all grass carp move into node 1.

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.

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:

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

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 lager samples size ($n = 78$ versus $n = 33$; Table 1). This data fit the model well ($r^2 = 0.88$) for observational field data.
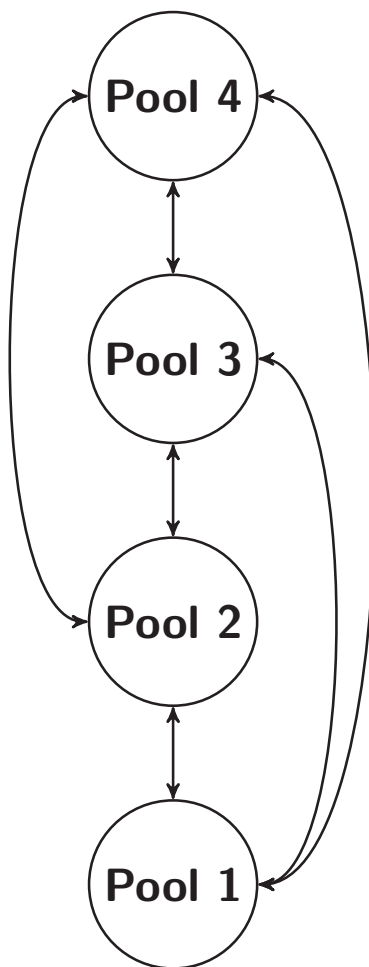
Figure 2: A series of connected pools that form the river system used for the second case study. Transitions that "skip" pools are possible because fish can move among multiple pools during the course of an annual time step. The model ignores transitions that occur if a fish ends in the same pool it begins in. For example, if a fish starts in Pool 1, swims to Pool 2, and then swims back to Pool 1, the model would not record any transitions for the 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 Serivce, 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 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_f	Proportion males	$1 - p_f$	

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 Serivce, 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 Submodels

2.7.1 Integral Projection Model

We modeled the life history of carp using an integral projection model based upon previous work by Erickson et al. (2017c). Our model presentation closely followes that of Erickson et al. (2017c). Recent work provides overviews, introductions, and tutorials of integral projection models for readers who are unfamiliar with their basic application (e.g., Ellner and Rees, 2006; Ramula et al., 2009; Ellner et al., 2010; Merow et al., 2014). The continuous-length distribution of individuals within populations form the basic foundations of the model (Figure 4). We model the length of individuals (z) within the population through discrete time (t). The variable z ranges over an interval of possible lengths Ω, with considerations for unintentional eviction (Williams et al., 2012). Our specific time step differs between case studies, reflecting the different amounts of biological data for the case studies. By default, we include 2 fixed population sex-classes within the model: females $P_{\mathrm{f}}(z,t)$) and males $P_{\mathrm{m}}(z,t)$ of size z at time t). Our model includes the option to add additional sex-classes such as YY-males (Erickson et al., 2017c) or genetically modified sterile individuals (Knols et al., 2006) or ignore sex-structure within the populations. We include some of these variations within this paper.

An integral gives the total population size of female carp at each time step t

$$||P_{\mathrm{f}}(\cdot, t)|| = \int_{\Omega} P_{\mathrm{f}}(z,t) dz,$$

with similar equations existing for males and other possible sex classes (e.g., sterile males or YY-males). Using matrix population models, one "projects" the population size and distribution from one time step to the next by multiplying a population vector with a matrix. Using integral projection models, one "integrates" the integral kernel (i.e., the function from one time step to the next) $K(z, z')$ to calculate the population size through time:

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

for each time t. Note that if z is the current length at time t, then z' is the length at time $t+1$. The kernel often can be split into two kernels: a kernel for recruitment/fecundity and a kernel for growth and maturation
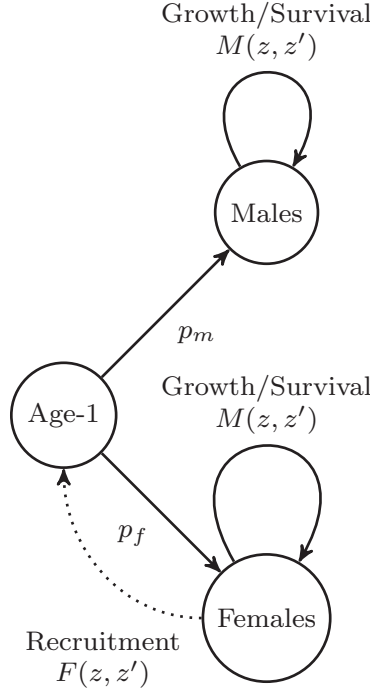
Figure 3: Conceptual map of carp life history. p_f is the proportion of female recruits and p_m is the proportion of male recruits. By definition, $p_f + p_m = 1$. The recruitment kernel ($F(z, z')$) is defined in Equation 5, where z is size at the current time, t and z' is the size at the next time step $t+1$. The growth/survival kernel ($M(z, z')$) is defined in Equation 2. Growth/maturation is the annual increase in fish length including the survival. 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. Figure is reprinted from Erickson et al. (2017c) and is in the public domain because it was created by a US Government Employee as part of his official duties.

(Ellner and Rees, 2006). Additionally, we include immigration, $I(z)$, and emigration, $E(z)$, kernels modeling connections among subpopulation as a function of fish size. These terms include both movement mappings and survival (i.e., they indicate the probability of a fish both moving between nodes and surviving the move). Non-moving fish have a different survival function. The growth and maturation kernel, M, models how fish grow in length as a function of time and includes both survival, $S(z)$, and growth, $G(z, z')$.

$$M(z, z') = S(z)G(z, z'). \tag{2}$$

We used a four-parameter logistic function for survival: 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):

$$S(z) = s_{\min} + \frac{s_{\max} - s_{\min}}{1 + e^{\beta_s(\log(z) - \log(\alpha_s))}}. \tag{3}$$

We modified and derived a von Bertalanffy function to model growth. First, we took the derivative of the length with respect to length (i.e., how length changes as a function of length) because the von Bertalanffy function usually denotes the relationship between time and length. Second, we assumed the function was centered around a modified normal distirbution. We created a mapping between current size at time t (z) and size at the next time step $t + 1$ (z'). Our new function included two parameters for the modified von Bertalanffy equation: k_g and a_g, and a standard deviation σ_g:

$$G(z, z') \quad = \quad \text{Prob}(z'|z, k_g, a_g, \sigma_g) = \text{Normal PDF}((1 - k_g)z + k_g a_g, \sigma_G). \tag{4}$$

Our 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, $Egg(z)$; and the initial recruit length distribution, $J(z')$:

$$F(z, z') \quad = \quad e_t S(z) P_r(z) Egg(z) J(z). \tag{5}$$

$S(z)$ and $P_r(z)$ are both logistic functions, while $Egg(z)$ 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):

$$\log_{10}(\text{biomass}) = \alpha_{\text{lw}} + \beta_{\text{lw}}\log_{10}(z), \tag{6}$$

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 recruits 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.

The proportion of spawning and successful recruitment during a given year, p_{recruit} 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 Equation 6. This biomass calculation is then used in a negative exponential

function to calculate the decrease in fecundity caused by grass carp density:

$$d = ae^{-b\text{biomass}}. \tag{7}$$

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

$$P_{\text{male}}(z', t+1) = \int_\omega (M(z, z')P_{\text{male}}(z, t) + F(z, z')P_{\text{female}}(z, t)p_m; d\ p_{\text{recruit}} + I(z) - E(z))\ dz. \tag{8}$$

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

$$P_{\text{female}}(z', t+1) = \int_\omega (M(z, z')P_{\text{female}}(z, t) + F(z, z')P_{\text{female}}(z, t)p_f\ d\ p_{\text{recruit}} + I(z) - E(z))\ dz. \tag{9}$$

Our model makes an important assumptions about grass carp and the impacts of sex. Our model assumes that XY-males and females survive, grow, and are produced at the same rate. We made these assumptions because data do not exist for the growth and survival of each sex individually. For models with sterile males, we either assumed the sterile males had the same survival as normal males or had reduced survival. This was done to explore potential modified organisms as a control tool.

For scenarios with harvest, we assumed harvest either had a uniform distribution across size or a 4-parameter logistic equation (similar to Equation 3), but with different parameter values. The logistic harvest model allowed for larger fish to have a higher probability of harvest because these fish are easier to harvest.

2.7.2 Network-node model

Taylor and Norris (2010) presented a network-node framework for examining populations dynamics through space that could readily be adapted to also include time (e.g., Erickson et al., 2014; Wiederholt et al., 2013; Erickson et al., 2016). This framework describes nodes that are connected by edges to form a network. The framework follows the migratory path (i.e., the set of all nodes and edges) a group of individuals use through time. The network model assumes groups do not change paths, allowing for paths to go extinct, but not be re-populated. Taylor and Norris (2010) originally considered species with forced migration (e.g., migratory birds with non-overlapping summer and winter habitat), but their framework readily generalizes include partial migration (e.g., some groups do not migrate) and no migration (e.g., the model does not impose migratory dynamics) (Erickson et al., 2017b). We further generalize their framework to use IPMs within each node. Our model can include "time periods" such as seasons (e.g., summer, winter) or within-year discretizations of time. These time periods do not need to be the same length (e.g., time period 1 could be 2 months and time period 2 could be 10 months), but the units within each time period must have consistent units (e.g., events per 2 months for all parameter in time period 1).

Broadly, we attempted to avoid using formal notation for nodes and edges unless absolutely necessary because it complicates the equations. When necessary, we used forward subscripts for locations (e.g., parameter or variable X for node 1 would be $_1X$) and edges (e.g., parameter or variable X for the edge between nodes 2 and 3 would be $_{2,3}X$). We were able to avoid this notation in our code by using an object-orientated programing approach.

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 intentionally present our model as theoretical, hence it matches no exact population. However, our broad, qualitative findings agree with other another Asian carp population models developed for the Illinois River System (D. Glover, personal observation). 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.

Broadly, one of the largest hurdles to our model and any population modeling effort used to guide resource is density, how it limits population growth, and estimating these two effects. We assumed only recruitment was impacted by density, a seemingly reasonable assumption for this system and one made another modeling team examining this system (D. Glover, personal observation). However, scaling the population size is difficult because no reliable population estimates exist for grass carp populations in systems such as Lake Erie or the Mississippi River system and its tributaries (e.g., Illinois River, Missouri River).

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.

Quantitively, 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. More broadly, our model should apply to any species that lives in discrete habitat patches. Our implementation of the network-node model and IPM allow for life- and age-stages to be included within the model as well.**

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 4). 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 allow the model to include modified groups of fish such as sterile males (included in the case study) or yy-males (previously described in Erickson et al., 2017c). The sterile males decrease the recruitment of viable individuals. The goal of management strategy is to cause a population collapse by stopping recruitment. It has been used as a method for mosquito control (e.g., Benedict and Robinson, 2003). We compared two different release scenarios for the modified organisms. First, we assumed the modified organisms were the same as normal males. Second, we explored using modified organisms that had half maximum survival rate as normal males. The sterile males 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). These individuals are assumed to be the same demographically as XY-males for one set of scenarios and have decreased survival for a second set of scenarios. Although no YY-males or sterile 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).

Our model also allows other control tools to be included. Proportional harvest (e.g., 10% of the population) can be included within the model. The model also allows tools such barriers to be examined. Barriers work by decreasing carp movement among nodes.
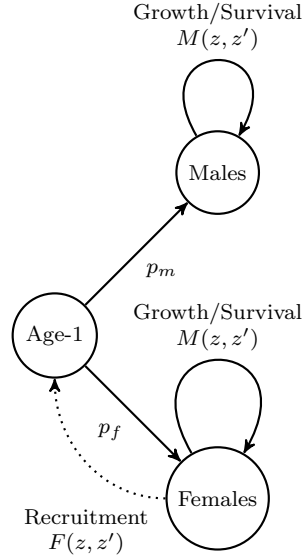
Figure 4: Conceptual map of grass carp life history. p_f is the proportion of recruits who are female and p_m is the proportion who are male. By definition, $p_f + p_m = 1$. Our model seeks to alter this ratio through the introduction of YY-males. Growth/maturation is the annual increase in fish length. 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.

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:

> **We build the model using Python. We included formal unit testing and version control as part of our model building. We also included non-unit testing to check our code's plotting function. Additionally, we created a Universal Modeling Language (UML) diagram of our model's code.**

We build our model using unit testing, using the `unittest` module in Python. These tests ensure functions behave as expected and provide coverage of most of the model's code. We have included this test code as part of our `git` repository. We also ensured our mesh size did not gain or lose fish (Williams et al., 2012). We also created a Universal Modeling Language (UML) diagram of our model's code design.

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 aggress 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 did not conduct formal sensitivity analysis within this project. However, we did examine how changing treatments impacted the population dynamics of the system. We plan formal sensitivity analysis as part of future research on this model.

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 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, he population of

carps grows in length through time. However, robust field observations of large-scale grass carp invasions are sparse.

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