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A matrix population model to aid agency response to grass carp (*Ctenopharyngodon idella*) in the Great Lakes Basin - Lake Erie

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Abstract

Managers and researchers have identified a reproducing population of grass carp (*Ctenopharyngodon idella*) in the western basin of Lake Erie, generating concern over the potential threat to ecosystem function in the Great Lakes Basin. Capture histories indicate that grass carp may be present at low levels in other areas of Lake Erie, necessitating a large scale, multi-jurisdictional response. As a result, a group of experts and decision makers began a structured decision making exercise to collaboratively address the threat and identify potential response actions. To aid this process, we developed a spatially-explicit periodic matrix population model to project grass carp abundance, and probabilistically evaluate specific management actions. We evaluated four potential management response actions ranging from no action, diffuse removal efforts, and concentrated removal efforts with and without a barrier on the Sandusky River to reduce spawning success. Based on our current knowledge, concentrated removal including a barrier on the Sandusky River provides the most likely path to achieving and maintaining a management target of no more than 10 fish per hectare. Our understanding of grass carp ecology in Lake Erie is growing. This model and parameter development methods were designed to flexibly accom-

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modate new information as our understanding of grass carp ecology evolves, or management objectives change. Ultimately, this modeling framework and use of Bayesian methods could facilitate management response efforts for other invasive species occurring over large scales and multiple jurisdictions.

Keywords: Matrix model, periodic, spatial, Bayesian, adaptive management

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Introduction

Grass Carp (*Ctenopharyngodon idella*) pose a threat to ecosystem function in the Great Lakes Basin, especially Lake Erie (Cudmore et al., 2017). Grass carp, an herbivorous fish native to East Asia, was brought to the U.S. in 1963 as a potential management tool for nuisance aquatic vegetation (Guillory and Gasaway, 1978). Recently, management concerns arose after the majority of Lake Erie grass carp captures in the western Basin during 2013-2017 were found to be diploid (Wittmann et al., 2014; Wieringa et al., 2016; Gertzen et al., 2017), successful reproduction was confirmed in the Sandusky and Maumee rivers (Chapman et al., 2013; Embke et al., 2016; USGS, 2019), and reproductively advantageous thermal and hydrologic conditions were found in other Lake Erie tributaries (Kocovsky et al., 2012; Murphy and Jackson, 2013). Lake Erie grass carp present a large-scale multi-jurisdictional challenge, as fish have been captured in all five of Lake Erie's management jurisdictions (Ohio, Michigan, New York, Pennsylvania, and Ontario), while connectivity among Laurentian Great Lakes and the presence of suitable habitats suggest a potential for spread and establishment to other parts of the Great Lakes Basin (Guillory and Gasaway, 1978; Wittmann et al., 2014; Cudmore et al., 2017). This concern was later supported after one fish, tagged in Lake Erie with an acoustic transmitter, was observed moving into lower Lake Huron - an adjacent Great Lake (Harris et al., 2019). As a result, a diverse group of experts and decision makers initiated a structured decision-making (SDM) exercise to coordinate and guide future management actions.

The initial SDM exercise took place over a series of workshops spanning December 2016 to September 2017 (Robinson et al., 2020). During the exercise the group identified a need to "develop a strategy for controlling grass carp in Lake Erie to socially and environmentally acceptable levels." To accomplish this task, the group established four fundamental objectives (Gregory et al., 2012; Runge et al., 2013), one of which, "fulfill public trust and social responsibility", directly addressed grass carp population dynamics through a means objective, "minimize risk of spread and abundance." A recent bio-energetics study indicated that at low densities grass carp would have minimal negative impacts on vegetated aquatic environments (van der Lee et al., 2017). Through discussion, the group established a management target of no more than 10-fish/hectare within low-marsh habitats of Lake Erie (Gertzen et al., 2017). Thus our goal was to develop a quantitative model (Robinson and Fuller, 2017) that mimicked existing grass carp population dynamics and allowed researchers to evaluate a variety of potential response actions, for their performance relative to this target.

The Lake Erie grass carp population presents a challenging modeling scenario, as the information surrounding demographic parameters and seasonal ecology is sparse. Grass carp are long-lived, highly mobile fish that seasonally move between habitat types (i.e., wetland and riverine) during foraging and reproductive periods (Shireman and Smith, 1983), and exchange among lakes within the Great Lakes Basin is possible (Harris et al., 2019; Whitledge et al., this issue). As a result, successful management may require testing an integrated approach including a suite of spatially-temporally distinct actions targeting specific life stages - similar to the integrated pest management strategy used for sea lamprey (*Petromyzon marinus*) in the Great Lakes (Christie and Goddard, 2003). The knowledge about grass carp ecology and effectiveness of management actions in Lake Erie is incomplete but currently growing. Therefore, it is important to have a model that allows flexibility in the application of management actions, makes it easy to update model parameters as new information is gathered, and accounts for projection uncertainty, all of which will facilitate an adaptive management approach (Runge et al., 2013). Matrix population models can accommodate life history and management complexities, while propagating uncertainty, and informing management actions (Caswell, 2001; Mantzounia et al., 2007). Additionally, Bayesian statistical methods can be used to develop and update demographic parameter estimates under sparse data conditions.

The objective of our study was to generate a spatially- and temporally-explicit matrix population model for grass carp that would: 1) mimic the ecology of grass carp within Lake Erie's western basin, 2) take advantage of all available information to develop demographic parameter estimates, 3) propagate uncertainty from demographic parameters to projected abundance, and 4) allow the probabilistic evaluation of response scenarios. Ultimately, the model and associated parameter development methods, while specific for Lake Erie grass carp, provide a framework for evaluating management actions for grass carp in other waters (both in the Great Lakes and beyond) and for other aquatic invasive species.

Materials and methods

Study system

Lake Erie is composed of three basins, with the western basin being the shallowest, warmest, and most productive (Ryan et al., 2003). The upper Great Lakes feed into Lake Erie via the St. Clair and Detroit River System, and Lake Erie is connected to Lake Ontario by the Niagara River and the Welland Canal. Both of these connections provide opportunity for the movement of grass carp and other species into the other Great Lakes from Lake Erie. Recent modeling work has indicated that three rivers in the western Basin, the Sandusky River, Maumee River, and River Raisin, provide potential spawning habitat for grass carp (Kocovsky et al., 2012), and reproduction has been confirmed in the Sandusky and Maumee rivers (Embke et al., 2016; USGS, 2019). In addition, the bulk of grass carp captures in Lake Erie have come from the western basin (USGS-NAS, 2018, November 16). Along with these recent findings, the Binational Grass Carp Risk Assessment indicated that Lake Erie was at high risk for grass carp establishment and negative impacts, and that response actions implemented in Lake Erie could reduce these risks (Cudmore et al., 2017). As such, we chose to focus our model on the western basin of Lake Erie.

Data

We used information from three sources to structure the Lake Erie grass carp matrix model and develop demographic parameters. Beginning in 2012, researchers and management agencies began collecting and recording capture and biological information on Lake Erie grass carp. As a result, a database was created that included age, sex, maturity, ploidy, total length, and weight information for most of the 109 captures, between 2012 and 2017. We used these data to directly inform the *likelihood* portion of subsequent demographic parameter estimates. Additionally, between December 2016 and February 2018, researchers and managers from fifteen state, provincial, federal, and academic entities participated in an SDM exercise (including four in-person meetings and one virtual meeting) to collaboratively establish grass carp response goals and objectives. During these meetings, participants shared thoughts, experiences, and updated information on grass carp monitoring and research activities within and outside of Lake Erie (Robinson et al., 2020). This participatory modeling framework (Robinson and Fuller, 2017) informed the matrix model's temporal and spatial structure, demographic parameter development, and grass carp movement ecology. Open and transparent discussion during these workshops was integral to the development of this model, and will be invaluable to productive collaborations and successful management of Lake Erie grass carp moving forward. Finally, we scoured the literature for grass carp demographic information, and used several sources to help develop Lake Erie specific parameter estimates (Table 1). In general, literature values were used to develop *prior* distributions for subsequent demographic parameter estimates. Although we recognized up front that the available data were limited, we structured the model to accommodate future information under the assumption that continued data collection and research would increase knowledge over time.

Matrix model

The Lake Erie grass carp matrix population model builds on previous work (Jones et al., 2017a) by adding seasonal and spatial components. The simulation model projected age-specific abundance of diploid grass carp across a 60-year time horizon for 3 known areas and 1 "unknown" area (i.e., Michigan-Raisin, Ohio-Maumee, Ohio-Sandusky, and "unknown"). Each area included 2 habitat types (i.e., river and lake; Figure 1), for a total of 8 "regions" ($R = 1, 2, 3, 4, 5, 6, 7, 8$), where 1-4 correspond to lake regions and 5-8 to river regions. Within each year (t), 4 seasons (i.e., spring, summer, fall, and winter; $S = 1, 2, 3, 4$) were represented, as well as movement among "regions". We consider fish to migrate among the three known areas (i.e., western basin of Lake Erie) and the fourth "unknown" area, mimicking potentially unknown, yet established, populations elsewhere or inputs to the system from an unknown source. Five age groups (a) were included in the model ranging from age-1 to age-4 juveniles, and one age-5+ group representing all reproductively viable adults. The initial construction, computation, and evaluation of this matrix population model was carried out using basic *R* functions, loops, and matrix notation (R Core Team, 2018).

Model overview and calculations

Matrix model components

The model is constructed of population vectors ($n^R(t, S)$) and two matrix types: population projection (A_R^S), and movement (M_{RR}^S) matrices. These components were combined to project region-specific abundances through time on a seasonal scale including four seasons per year (Figure 2). Matrix and parameter notations are described in (Table 2).

Population vectors ($n^R(t, S)$)

Population vectors including 5 age groups (a) were created for each region (R), totaling 8 individual vectors, and projected over 60 years (t) and across four seasons (S). Initial abundance, was estimated by simply multiplying current catch (USGS-NAS, 2018, November 16) at each age by 10. The decision to multiply by 10 was based on expert opinion and group consensus, as little information on actual population size existed. Our reasoning was that: 1) it was unlikely we captured the entire population; therefore, it must be larger than the number of captures, and 2) given the potential spatial extent of the population and presumed low catchabiltiy, multiplying by 10 seemed like a conservative starting point. This resulted in an initial population size of approximately 2,640 grass carp, and we distributed them evenly across the lake habitats in the three known areas (i.e., Michigan-Raisin, Ohio-Maumee, and Ohio-Sandusky) and one unknown area (i.e., Regions 1-4) during the spring season. We used age structure from the existing capture data (i.e., $P_a = percent-at-age$) to inform initial population age structure in each region (e.g., $2640 \div 4 \times P_a$) resulting in 150, 120, 100, 90, 200 age-1 through age-5+ fish in each lake region:

$$n^R(0,1) = \begin{bmatrix} 150 \\ 120 \\ 100 \\ 90 \\ 200 \end{bmatrix}, R = 1,2,3,4.$$

Initial abundances in the river regions ($R = 5,6,7,8$) were set to zero. Regional abundances were updated annually and seasonally through future projections. Although we assumed the initial grass carp population was low, this remains a critical uncertainty that was difficult to address using traditional abundance estimators because most sampling efforts at the time had resulted in limited or zero captures.

Population projection matrices (PPM, A_R^S)

A 5×5 matrix (accommodating 5 age groups) was created for each region (R) and season (S), totaling 32 individual PPMs. These PPMs include survival (s), reproduction (r), stochastic uncertainty in reproduction (su), and movement

(m) parameters, providing for the projection of the current population to the next season. Survival (s) represents the proportion of fish at age from one season surviving to the next, and is assumed 100% for all seasons except for winter. Reproduction (r), is characterized by a stock-recruitment function and only occurs during the summer. Movement (m) represents the proportion of fish moving from a region (R), while $(1 - m)$ represents the proportion that remain in the current region. Therefore, $(s(1 - m))$ represents the proportion of fish that survived and remained in a region. Within a year, we used matrices with diagonal elements to transition fish from spring to winter without aging:

$$A_R^S = \begin{bmatrix} s(1-m) & 0 & 0 & 0 & r(su) \\ 0 & s(1-m) & 0 & 0 & 0 \\ 0 & 0 & s(1-m) & 0 & 0 \\ 0 & 0 & 0 & s(1-m) & 0 \\ 0 & 0 & 0 & 0 & s(1-m) \end{bmatrix}, S = 1, 2, 3$$

At the end of the year (i.e., winter), we used matrices with off-diagonal elements to transition fish from winter to the following spring while aging by one year:

$$A_R^4 = \begin{bmatrix} 0 & 0 & 0 & 0 & r(su) \\ s(1-m) & 0 & 0 & 0 & 0 \\ 0 & s(1-m) & 0 & 0 & 0 \\ 0 & 0 & s(1-m) & 0 & 0 \\ 0 & 0 & 0 & s(1-m) & s(1-m) \end{bmatrix}$$

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Within a year, we assumed 100% survival, and applied the annual survival (s) estimate to all ages during the winter to spring transition. We estimated survival, reproduction, and movement parameters from a combination of existing Lake Erie population data and literature values (see below). For each region and season, a PPM updates the population vector in concert with multiple movement matrices.

Movement matrices (M_{RR}^{S})

A 5×5 movement matrix (accommodating 5 age groups) was created for each potential movement scenario between regions, where M_{31}^{S} represents movement from region 3 to region 1, for example. Similar to the PPMs, these included survival (s), and movement (m) parameters. However, here $s(m)$ represents the number of fish that survive and move from the current region to a destination region. Again, survival is assumed 100% for all seasons except for winter. In total, we created 224 movement matrices representing all of the between-region and through-season movement scenarios. Similar to the PPM, we used a matrix with diagonal elements for within year movements from spring to winter in which fish remained the same age:

$$M_{RR}^{S} = \begin{bmatrix} s(m) & 0 & 0 & 0 & 0 \\ 0 & s(m) & 0 & 0 & 0 \\ 0 & 0 & s(m) & 0 & 0 \\ 0 & 0 & 0 & s(m) & 0 \\ 0 & 0 & 0 & 0 & s(m) \end{bmatrix}, S = 1, 2, 3,$$

However, we used a matrix with off-diagonal elements to transition fish from winter to the following spring while aging by one year:

$$M_{RR}^{4} = \begin{bmatrix} 0 & 0 & 0 & 0 & 0 \\ s(m) & 0 & 0 & 0 & 0 \\ 0 & s(m) & 0 & 0 & 0 \\ 0 & 0 & s(m) & 0 & 0 \\ 0 & 0 & 0 & s(m) & s(m) \end{bmatrix}$$

Additionally, we assumed 100% survival within year, and applied the annual survival estimate during the winter to spring transition. For each region and season, there are seven movement matrices that transition fish from the other regions to the region of interest.

Seasonal projections

The region-specific PPMs (A_R^S) and among region movement (M_{RR}^S) matrices described above were combined to form 8×8 seasonal block matrices (B_S) with each row and column representing a region:

$$B_S = \begin{bmatrix} A_1^S & M_{21}^S & M_{31}^S & M_{41}^S & M_{51}^S & M_{61}^S & M_{71}^S & M_{81}^S \\ M_{12}^S & A_2^S & M_{32}^S & M_{42}^S & M_{52}^S & M_{62}^S & M_{72}^S & M_{82}^S \\ M_{13}^S & M_{23}^S & A_3^S & M_{43}^S & M_{53}^S & M_{63}^S & M_{73}^S & M_{83}^S \\ M_{14}^S & M_{24}^S & M_{34}^S & A_4^S & M_{54}^S & M_{64}^S & M_{74}^S & M_{84}^S \\ M_{15}^S & M_{25}^S & M_{35}^S & M_{45}^S & A_5^S & M_{65}^S & M_{75}^S & M_{85}^S \\ M_{16}^S & M_{26}^S & M_{36}^S & M_{46}^S & M_{56}^S & A_6^S & M_{76}^S & M_{86}^S \\ M_{17}^S & M_{27}^S & M_{37}^S & M_{47}^S & M_{57}^S & M_{67}^S & A_7^S & M_{87}^S \\ M_{18}^S & M_{28}^S & M_{38}^S & M_{48}^S & M_{58}^S & M_{68}^S & M_{78}^S & A_8^S \end{bmatrix}$$

Similarly, the region-specific population vectors ($n^R(t,S)$) described above were combined to form 8×1 block population vectors, with each row representing a region:

$$N(t,S) = \begin{bmatrix} n^1(t,S) \\ n^2(t,S) \\ n^3(t,S) \\ n^4(t,S) \\ n^5(t,S) \\ n^6(t,S) \\ n^7(t,S) \\ n^8(t,S) \end{bmatrix}$$

We multiplied the seasonal block matrices (B_S) and block population vectors ($N(t,S)$) to project age-specific abundance for each region-specific population through seasons and across years. This process included a set of nested matrix multiplications. For example, $B_S N(t,S)$ initially results in the multiplication of the first row of B_S by the column $N(t, S)$ producing a vector of matrix multiplications for spring through fall ($S = 1, 2, 3$):

$$A_1^S n^1(t, S), M_{21}^S n^2(t, S), M_{31}^S n^3(t, S), \ldots, M_{R1}^S n^R(t, S)$$

Each matrix multiplication produced an age specific abundance, where $A_1^S n^1(t, S)$ is the abundance of fish surviving and remaining in region 1 and $M_{R1}^S n^R(t, S)$ is the abundance of fish surviving in region R and migrating to region 1. Age-specific abundances from each matrix multiplication (8 total) were summed to produce age-specific regional abundances in the following season:

$$n^1(t, S+1) = A_1^S n^1(t, S) + M_{21}^S n^2(t, S) + M_{31}^S n^3(t, S) +, \ldots, + M_{R1}^S n^R(t, S)$$

To complete the block matrix multiplication, the calculations were repeated for each region (i.e., row) finishing one seasonal transition. When moving from winter to spring, we used PPMs (A_R^4) and movement (M_{RR}^4) matrices with off-diagonal elements to project abundances into the following year:

$$n^1(t+1, S+1) = A_1^S n^1(t, S) + M_{21}^S n^2(t, S) + M_{31}^S n^3(t, S) +, \ldots, + M_{R1}^S n^R(t, S)$$

Although reproduction, in reality, occurred in rivers during the summer, we delayed adding recruits to the population until the following spring, when age-1 fish moved from river habitats to adjacent lake regions. To accomplish this, we added the river-specific matrix multiplication for reproduction to the spring block matrix rows associated with each lake region.

Quantifying uncertainty in demographic parameters

We used Lake Erie capture data, literature values, expert opinion, and additional unpublished data to inform grass carp survival, reproduction, and seasonal movements. Given the limitations of available data, we sought to capture uncertainty in these demographic parameters and propagate it through the matrix model into abundance estimates. Additionally, we estimated some values using Bayesian methods that will facilitate updating our knowledge as additional Lake Erie data are collected. All Bayesian analyses were performed in *Stan* (Carpenter et al., 2017), a modeling language that allows the incorporation of prior information and produces probabilistic parameter estimates in the form of random variables. *Stan* was linked to *R* (R Core Team, 2018), a statistical and graphic environment, through the package *rstan* (Stan Development Team, 2018). Detailed descriptions of each parameter estimate are provided below.

Survival (s)

We pooled age data from 58 grass carp captures in Lake Erie between 2014 and 2017, and performed a catch curve analysis (Quinn and Deriso 1999) to estimate survival (Eq. 1);

$$ln(C_a) = Za + b \tag{1}$$

where C_a is catch-at-age, a is age in years, Z is the slope of the line among ages recruited to the sample gear, and b is the y-intercept. The absolute value of Z is equivalent to total instantaneous mortality, while $s = e^{-Z}$ (i.e., survival). Given the relatively few captures and pooling across multiple cohorts, we believed that the Lake Erie-specific survival estimate might be biased. Therefore, we reviewed the grass carp literature and used 16 mortality estimates to develop the mean and standard deviation for a prior value on Z. Literature values included introduced triploid populations from large lake and reservoir systems in the southeastern U.S., and a native population from the Amur River, Russia (Table 1). We combined the raw Lake Erie data (*likelihood*) and literature information (*prior*) in a Bayesian analysis to generate a weighted Lake Erie survival estimate (*posterior*).

Reproduction (r)

We used a Ricker stock-recruitment model (Eq. 2; Quinn and Deriso 1999) to characterize reproduction (r) for each river; assuming age-1 production was related to age-5+ abundance (i.e., the spawning stock; SS) in the previous year.

$$r = \alpha SSe^{-\beta SS}e^{\sigma^2} \tag{2}$$

Where α represents the slope of the curve near the origin (i.e., at low abundance), with higher values indicating higher productivity. The parameter β indicates the degree of density-dependent compensation, with higher values indicating an increased degree of compensation, and σ^2 represents the degree of inter-annual variation in recruitment. There were no published stock-recruitment relationships for grass carp; therefore, we used methods described by Myers et al. (1999) and information on habitat carrying capacity to estimate reasonable values for α and β.

Myers et al. (1999) found that $\tilde{\alpha}$, the maximum lifetime reproductive rate, was relatively constant across species. This value ($\tilde{\alpha}$) is a standardized version of α from the Ricker model that takes into account spawner-per-recruit at unfished equilibrium ($SPR_{F=0}$; Goodyear 1993). We used estimated $\tilde{\alpha}$ values from four freshwater and marine species that had similar maximum age ranges (~25 years) and/or migrate and reproduce in freshwater rivers like grass carp (i.e., striped bass [*Morone saxatilis*], walleye [*Sander vitreus*], northern pike [*Esox lucius*], and lake trout [*Salvelinus namaycush*]). We used the mean and standard error of these values, and a Bayesian hierarchical model with a common global prior, to produce a weighted average $\tilde{\alpha}$, and converted $\tilde{\alpha}$ back to α ($\alpha = \tilde{\alpha}/(SPR_{F=0}(1-s))$); see Myers et al. 1999), where s is survival.

We calculated spawner-per-recruit (SPR) value as

$$SPR = \sum_{a=1} Rec_a mat_a, \tag{3}$$

where mat_a was the average proportion mature at age, and Rec_a was the proportion of recruits surviving to age (Goodyear, 1993). Proportion of recruits surviving to age (Rec_a; Eq. 4) was determined by iteratively applying our survival estimate (s) to successive age classes (i) of the same cohort, where number at age-1 equaled one:

$$Rec_a = \prod_{i=2} Rec_{i-1} s. \tag{4}$$

There were little data on Lake Erie grass carp maturity; therefore, we used 54 maturity values from 29 peer-reviewed articles for other populations to estimate maturity-at-age. These included male and female maturity values from populations across native and introduced ranges within temperate climates. These studies typically gave a single value for 50% maturity-at-age. We assumed for all studies that age-0 and -1 fish were immature (0), and all age-10+ fish were mature (1). Additionally, for each study, we coded the age prior to reported maturity as immature (0), and the reported age of maturity as mature (1). We pooled all age data together and used a logistic regression (Eq. 5) to determine probability of maturity across ages:

$$logit(mat_a) = \gamma_1 a + \gamma_2, \tag{5}$$

where $logit(mat_a)$ is the log-odds ($ln(mat_a/1 - mat_a)$) of the estimated proportion mature at age, with a as age, γ_1 as the slope, and γ_2 as the y-intercept.

Similar to α, we had no data and minimal literature information to directly inform the compensation parameter (β) for the Ricker stock-recruitment curve. Therefore, we indirectly estimated this value based on inventoried low-marsh vegetated habitats in Lake Erie's western basin (Gertzen et al., 2017), and grass carp consumption rates (van der Lee et al., 2017). Gertzen et al. (2017) used GIS layers of coastal wetland inventories to estimate the amount of low-marsh habitat in the Great Lakes Basin. Low-marsh habitat was defined as, "areas that are permanently inundated, support SAV [submerged aquatic vegetation], and support fish spawning and foraging," and represented the habitat most likely to be negatively affected by herbivorous grass carp Gertzen et al. (2017). Within the Michigan and Ohio waters of Lake Erie's western basin, Gertzen et al. (2017)

estimated between 3,602 and 17,373 ha of low-marsh habitat, with most of that occurring in Sandusky Bay of the Ohio-Sandusky area. Using this information and expert opinion on Sandusky Bay vegetation coverage expressed during the SDM exercise (Robinson et al., 2020), we assumed that Michigan-Raisin and Ohio-Maumee areas each held 1,500 ha, while the Ohio-Sandusky area held 3,000 ha of low marsh habitat. A bioenergetics study on the effects of grass carp consumption on Great Lakes wetlands indicated that adult densities (ages-5+) greater than 16 fish/ha would cause a greater than 50% reduction in a wetlands initial biomass (van der Lee et al., 2017). Therefore, we assumed that densities of this magnitude would have a compensatory effect on recruitment due to the reduction of foraging and nursery habitats. Using these two pieces of information along with the α estimated above, we identified unique β parameters for each region which established equilibrium abundance (EA; Eq. 6) at 16 fish/ha for each region:

$$EA = log(\alpha)/\beta. \tag{6}$$

These calculations resulted in a point estimate for β, so we used mean and standard error values for 54 β estimates reported in Goodwin et al. (2006) to estimate a typical coefficient of variation (cv) for the parameter. We used the cv value to scale the standard deviation of β parameters to the point estimate mean. Additionally, we used the mean and standard deviation from 54 estimates of inter-annual recruitment variation (σ^2) reported in Goodwin et al. (2006) to inform variation in the grass carp stock-recruitment model.

Stochastic uncertainty in reproduction (su)

Successful reproduction is dependent on stochastic environmental conditions, that is, the annual availability of optimal thermal and hydrological conditions in rivers. Each river system responded differently to regional weather patterns, causing optimal conditions to occur at different inter- and intra-annual frequencies. We accounted for stochastic uncertainty in reproduction by adjusting reproductive success in each river using the annual frequency of “high quality events”, making the simplifying assumption that reproduction occurred each year but the magnitude and uncertainty were dependent on the percentage of “high quality events” in each system. According to Kocovsky et al. (2012), the Sandusky River experienced thirteen, and the Maumee River sixteen “high quality events” between 1990 and 2009, representing 69 and 84% of years respectively. This study did not include River Raisin, but based on its hydrologic history (USGS-NWIS, 2018, November 16) we assumed that at least one year over this period might have supported grass carp reproduction, representing 5% of years. We used reported frequencies, the number of projected years (60), and a binomial distribution to determine the probable number of years that would support successful reproduction within each system. This produced a binomial distribution of counts, which we divided by 60 to create a percentage with uncertainty. This percentage (su) was used to curb the magnitude of annual reproduction, $r(su)$ in PPM A_R^S and movement M_{RR}^S (see below). In effect, reproduction (i.e., number of recruits) within each year and realization was adjusted by a value (i.e., percentage) randomly drawn from the su distribution.

Movement (m)

We relied heavily on a general understanding of grass carp ecology, preliminary information from an ongoing telemetry study, and expert opinion to inform grass carp seasonal movements. In general, grass carp spawn in large river systems during warm seasons and elevated flow conditions (Shireman and Smith, 1983). Studies in Lake Erie have indicated that successful reproductive conditions (i.e., thermal and hydrologic) occur in select Lake Erie tributaries during summer months (Kocovsky et al., 2012; Murphy and Jackson, 2013). Additionally, initial findings from the telemetry project indicated that adult grass carp can make large-scale movements across open-lake areas to access tributaries during the spawning period, and that these movements typically occurred during the spring and fall leading up to and following spawning (Harris et al., 2019). Therefore, we initiated our model with all grass carp occupying open-lake habitats during the spring, simulating use of coastal wetland habitats and/or large-scale movements in open water.

Spring to summer - During the spring to summer transition we moved 4% of all adults (age-5+) from each area into the River Raisin [Mig->RR], 62% into the Maumee River [Mig->MR], and 31% into the Sandusky River [Mig->SR] to reproduce. The proportion of adults (age-5+) moving into each river was based on the propensity for a system to have optimal thermal and hydrologic conditions for spawning, which was calculated as the proportion of high quality events, as defined in Kocovsky et al. (2012), among the three river systems over a 20 year time period. Rivers with more consistent conditions received a greater proportion of spawning adults. Based on the low frequency of grass carp captures outside of Lake Erie's western basin, an additional 3% of adults were moved to an unknown region, mimicking emigration [Emig] from the system. We incorporated additional inputs [Input], simulating immigration from an unknown region or undocumented releases, by adding 5% of each age group (based on initial population abundances) to lake and river habitats in all areas. Meanwhile, all juvenile fish remained in lake habitats.

Summer to fall - During the summer to fall transition, adults moved out of the rivers back to coastal lake regions, in proportion to the available foraging habitat: 25% in both Ohio-Maumee [Mig->O-MR] and Michigan-Raisin [Mig->M-RR] areas, and 50% in the Ohio-Sandusky [Mig->O-SR] area (i.e., low-marsh habitat based on Great Lakes Low Marsh Inventory (GLLMI) layers; Gertzen et al. 2017). This again simulated a return to coastal wetland habitats and the propensity for large-scale open lake movements.

Fall to winter - There was little information on winter grass carp movements, but commercial seine catches indicated that some portion of the population may use lower river mouth habitats (T. Hartman, Ohio Department of Natural Resources, pers. comm.), whereas telemetry studies showed fish congregating in coastal areas adjacent to thermal effluent (i.e., power plants; Harris et al. 2019). Therefore, during the winter, we divided the entire population (age-1 through -5+) within each area between lake and river habitats, moving 50% into adjacent river habitats in each area.

Winter to spring - Transitioning back to spring, all adults and juveniles overwintering in river habitats (including age-1 recruits from the previous summer spawn) moved back to adjacent lake habitats within areas. Seasonal habitat use and movement information for the juvenile population (age-1 through -4) was lacking. Expert opinion indicated that juvenile movements were likely restricted (D. Chapman, U.S. Geological Survey, pers. comm.), so we only allowed age-1 individuals to move out of the river system of origin into adjacent lake habitats in the spring following reproduction. Juveniles remained in the coastal lake habitats of their natal areas until they reached adult age, at which time they began reproductively related large-scale movements. Given the lack of information on seasonal movement dynamics, all movement parameters were assumed fixed and were implemented with restricted uncertainty (i.e., SD=0 to 0.02; Table 3).

Propagating uncertainty through matrix model simulations

Using independent analyses (see above), we estimated the mean and standard deviation of as many demographic parameters as possible with the intent of propagating uncertainty through the model to projected population estimates. Within the matrix model, all demographic parameters were considered random variables characterized by an appropriate distribution. Age-specific estimates of abundance ($n^R(t, S)$) and adult reproduction (r) were treated as counts and drawn from a Poisson distribution. We used beta distributions to describe percentages such as survival (s) and stochastic uncertainty in reproduction (su). Region- and age-specific proportions of movement (m_a), which sum to one, were treated as multinomial distributions. Finally, Ricker stock-recruitment parameters (i.e., $log(\alpha)$ and β) were both drawn from normal distributions. During matrix model projections with fixed parameters, simple multiplication would be used to combine percentages and proportions (e.g., $s(m)$ or $s(1-m)$) or to update abundances. With random variable percentages, we can still perform this multiplication, but it is the individual draws from the random variables that were multiplied producing an updated probability distribution. However, when updating abundances, we had to account for an additional level of uncertainty associated with each individual draw (i.e., count) from a Poisson distribution. Rather than directly multiplying individual count and probability draws, we drew projected abundances from a binomial distribution (Eq. 7) using $n^R(t,S)$ (defined by a Poisson distribution) from the previous period as the number of trials and the product of $s(m)$ (defined by beta distributions) as the probability of success:

$$n^R(t,S+1) \sim binomial(n^R(t,S), A_R^S). \tag{7}$$

Similarly, there was a probability of successful reproduction occurring by adults ($a = 5$) during the summer ($S = 2$) of each year and in each river ($R = 5, 6, 7$) based on stochastic uncertainty in reproduction (su). We used the binomial distribution (Eq. 7) to determine the probability of successful recruitment (r; a count variable) based on the probability of optimal spawning conditions (su), where r were the trials and su were the probabilities of success. Matrix models were built in *R*, and we used the *rv* package (Kerman and Gelman, 2007) to handle and manipulate random variables and carry out matrix model simulations.

Sensitivity analysis

A sensitivity analysis clarifies how much influence model inputs (i.e. data and model parameters) have on outputs of interest (e.g., population growth rate and equilibrium abundance) (Cariboni et al., 2007). Following the recommendations in Cariboni et al. (2007), we used the Morris method (Morris, 1991), which accommodates non-linearity and high computational costs, to evaluate sensitivity of our model to input values. The Morris method generates an elementary effect for each input (x) of interest, relative to its influence on a model output (y). The elementary effects are comparable among inputs in magnitude (μ) and uncertainty (σ), where the magnitude represents the degree of influence and uncertainty represents the degree of non-linearity/interaction with other inputs. In brief, an elementary effect was generated by first taking a random draw from each input of interest (x_i - defined over its distribution), running the model, and producing an output ($y(x)$). Next, we ran the model again using the same random draws, but a single input value (x_i) was adjusted (i.e., "perturbed") by a predefined value (Δ), and generated a second output ($y(x_1, x_2, \ldots, x_{i-1}, x_i + \Delta, x_{i+1}, \ldots, x_k)$). We repeated model runs until all inputs of interest had been "perturbed" and generated a unique output ($y(x_1 + \Delta, \ldots, x_k), \ldots, y(x_1, \ldots, x_k + \Delta)$). Predefined Δ values are unique for each input, but represent a similar proportional change among inputs. For movement parameters, it was important that they summed to one within sites and time periods so when a movement input of interest was "perturbed" the accompanying movement rates were adjusted in the opposition direction to accommodate. We calculated the elementary effect ($d_i(x)$) for each input by subracting the input specific "perturbed" output from the original "unperturbed" output and dividing by the input specific delta (Eq. 8).

$$d_i(x) = [y(x_1, x_2, \ldots, x_{i-1}, x_i + \Delta, x_{i+1}, \ldots, x_k) - y(x)]/\Delta. \tag{8}$$

A distribution of elementary effects (F_i) was generated by iteratively redrawing 100 values from each input of interest (x_i) and calculating $d_i(x)$ for each iteration. The magnitude (μ) and uncertainty (σ) define the distribution of input-specific elementary effects (F_i). Inputs of interest (x_i) included parameters that could potentially be influenced by management actions: initial abundance, survival (s), stock recruitment parameters (α and β), stochastic uncertainty in reproduction (su), movement patterns (m), and immigration/illegal inputs. Outputs of interest ($y(x)$) included: 1) average population growth rate from years 2 to 20, where total annual population during spring was calculated as $N(t) = \sum_{R=1}^{8} n^R(t, 1)$ and annual population growth rate as $\lambda_t = N(t)/N(t-1)$, and 2) equilibrium abundance (average population size from years 40 to 60 - $\sum_{t=40}^{60} N(t)/21$), which are key demographic characteristics that can help us evaluate the impact of management actions. These results will help prioritize research efforts to improve parameter estimates and identify where management actions may be most effective. The sensitivity analysis was carried out in R (R

Core Team, 2018).

Evaluating response actions

Through an SDM process, we identified and evaluated four different response scenarios aimed at reducing grass carp abundance (Robinson et al., 2020). The first scenario (1) included no response, allowing the population to grow unimpeded. The second scenario (2) included a fixed annual amount of direct capture and removal effort distributed across seasons and habitats in the Michigan-Raisin, Ohio-Maumee and Ohio-Sandusky areas. We assumed that catchability changed across habitats; therefore, we used high catchabilities for river/wetland sampling and low catchabilities for open lake sampling based on literature (Bayley and Austen, 2002). This scenario represented an inefficient allocation of resources due to sampling in low catchability habitats, and in locations that were not seasonally occupied by fish. The third scenario (3) used the same amount of annually fixed direct capture and removal effort, but concentrated it in high catchability habitats believed to seasonally hold grass carp (i.e., rivers/wetlands). For example, sampling occurred in the Raisin, Maumee, and Sandusky rivers during the summer spawning runs, and River Raisin/"hot ponds" during the fall cool water period where fish are believed to aggregate in this location due to the thermal effluent from a power plant. This scenario represents an efficient allocation of resources as effort was concentrated in high catchability habitats, and in locations that seasonally hold fish. The fourth scenario (4) implemented the concentrated removal (Scenario 3) and added a moderately efficient barrier to the Sandusky River, excluding 50% of all immigrating fish during the summer spawning season and subsequently reducing spawning contributions by 50% from this system. All capture efforts were directed at large bodied individuals (age-3+), those primarily encountered with existing sampling. The four scenarios display how we can use this tool to evaluate specialized response actions moving forward.

Results and Discussion

To evaluate risk and the effectiveness of proposed response scenarios, we created a spatially-explicit periodic matrix model that accounted for uncertainty in demographic parameters including survival, reproduction, the effects of stochastic uncertainty in reproduction on reproductive success, and seasonal movements. Our treatment of uncertainty effectively generated multiple potential realizations (Figure 3–left; Scenario 1). When these individual realizations (i.e., potential future outcomes) are grouped together, we can summarize annual projections using mean and credible intervals (Figure 3–right; Scenario 1). Mean population growth and terminal abundance were low in the Michigan-Raisin population ($\sim$10,000), which was driven by the small probability of successful reproduction (5%) in the River Raisin. Mean population growth and terminal abundance were greater in the Ohio-Maumee and Ohio-Sandusky regions ($\sim$50,000 and 150,000, respectively), as these areas offered a higher probability of reproductive success (69 and 84%) and accounted for most of the preferred low-marsh habitat. Uncertainty in abundance estimates reflects the limited information available on this population and variability of ideal reproductive conditions within river systems, but the potential for the grass carp population to increase to high levels ($\sim$200,000 total individuals; Figure 3) in Lake Erie's western basin is evident (Wittmann et al., 2014; Cudmore et al., 2017). The probabilistic treatment of model parameters and projections will help managers guage establishment risks and response action efficacy.

Evaluation of four response scenarios showed that management of Lake Erie grass carp can be effective under certain conditions. First, indiscriminate capture and removal responses, that is action without knowledge, is not recommended, as effort likely will be wasted in locations and seasons in which removal of grass carp will not result in a meaningful population level reduction. We can see this by comparing the diffuse (Scenario 2) and concentrated (Scenario 3) capture and removal scenarios (Figure 4). Using the same amount of effort, concentrated removal (Scenario 3) resulted in a decreased population growth rate (Figure 4–left) and brought the terminal abundance substantially closer (3% probability) to achieving a management target ($\leq$10 fish/ha of low marsh habitat) compared to diffuse removal (Scenario 2; 0% probability; Figure 4–right). Second, using an integrated approach can have compounding effects. In Scenario 4, we duplicated the concentrated removal efforts (Scenario 3) and added a hypothetical barrier to the Sandusky River, effectively interrupting reproductive efforts in this system (50% reduction). As a result, population growth rates were substantially reduced and the probability of achieving the target density greatly improved (97%). Of course, management scenarios may have ecological or societal tradeoffs. For example, applying a barrier may negatively affect movements of native fish or interfere with recreational or commercial navigation. These types of tradeoffs were fully evaluated during a SDM exercise (Robinson et al., 2020).

Our population projections and management scenario evaluations relied on sparse data collected from the Lake Erie population and additional literature information gathered from a wide temporal and spatial range. To help inform future data collection and potential response strategies, we used a sensitivity analysis (Morris, 1991) to determine the relative influence of parameter estimates on population projections. Population growth rates and carrying capacity were most sensitive to survival (s), stock recruitment parameters (α and β), and frequency of high quality spawning conditions in each river (su), as indicated by a higher degree of uncertainty and larger mean elementary effect (Figure 5). These results showed that relatively small deviations in these parameters can have a larger effect on projected population abundances, relative to other parameters. Additionally, these results further supported our conclusion that response scenarios that reduce survival or interfere with reproduction could have positive management outcomes. In general, improving information surrounding these demographic parameters, through continued collections of age and maturity data as well as reproductive periodicity, will lead to more accurate population projections and the development of more effective response scenarios.

As indicated by the sensitivity analysis, population projections and associated uncertainty were directly dependent on demographic parameter estimates. Therefore, it was important for us to incorporate as much available information as possible into the estimated values while allowing a coherent route for their future update. The survival estimate (s), the most sensitive model parameter, provided a clear example for how we incorporated prior information using Bayesian methods and allow for future updates. Literature values on survival, taken from a range of introduced and native temperate populations, were highly variable (Figure 6). From these values, we developed a *prior* distribution for survival (mean = 0.62, sd = 0.05), and with Lake Erie data in hand, we initially estimated the *likelihood* of grass carp survival (mean = 0.78, sd = 0.03) with a catch curve analysis. Bringing these two pieces of information (*prior* and *likelihood*) together in a Bayesian analysis, our *posterior* annual survival estimate (mean = 0.75, sd = 0.03; Table 4) was intermediate to the extremes of *prior* literature values and slightly less than the *likelihood* of Lake Erie data alone (Figure 6). Although the prior literature values were variable, they provided some influence on the limited Lake Erie data by adjusting *posterior* estimates downward. Using a process called sequential Bayesian updating (Cowles, 2013) we can easily improve survival estimates, as well as other important demographic parameters. As new information is gathered, the additional data informs the *likelihood* and the *posterior* becomes the *prior*. The ability to update, of course, relies on the continued collection of age data from captured individuals to inform future survival estimates, which is ongoing in Lake Erie.

Informing the reproductive capacity of Lake Erie grass carp was a pivotal step in projecting population abundance and assessing response scenarios, but this series of calculations could be improved with additional system specific information. The very first step in this process was to estimate age-at-maturity, which was not a direct model input but influenced model structure and productivity estimates. We estimated that 58% of age-5 fish would likely be mature and capable of reproduction (Figure 7), and as a result, our matrix model made a simplifying assumption that all fish age-1 through age-4 were juveniles and all fish age-5+ were reproducing adults. This estimate and resulting model structure relied solely on literature values collected from populations over a wide spatial and temporal range. Using a sequential Bayesian updating process, as described above, this estimate can be combined with future data from the Lake Erie population to provide an improved age-at-maturity estimate and inform model structure. Therefore, we recommend continued collection of age and maturity data from captured individuals.

The sensitivity analysis highlighted the strong influence of stock-recruitment parameters on population growth rates and terminal abundance. Unfortunately, data limitations on grass carp reproductive capacity extend well beyond Lake Erie, as we were unable to find any published values. As a result, we choose to inform parameters of a Ricker stock-recruitment model (i.e., α, β, and σ^2 - Table 2) following methods outlined in Myers et al. (1999) and described above. We estimated an α value for the Ricker model ($log(\alpha)$ - mean = 1.8 (SD = 0.23); Table 4) which indicated mild recruitment at low abundance, ~ 6.2 (1.4) recruits-per-spawner annually. The availability of low-marsh habitat (Gertzen et al., 2017) and the rate of vegetation consumption by grass carp (van der Lee et al., 2017) indicated equilibrium spawning stock (age-5+) abundance of 24,000 individuals in Ohio-Maumee and Michigan-Raisin areas, and double that, 48,000 individuals, in the Ohio-Sandusky area. Using these calculations and literature reported values from other species, we identified a β value for Ohio-Maumee and Michigan-Raisin areas, and the Ohio-Sandusky area (Table 4). Because of increased habitat availability, the compensation effect (β) was smaller in the Ohio-Sandusky region allowing recruitment to double at equilibrium abundance (Figure 8). Finally, based solely on literature values, inter-annual variation (σ^2; 0.55 (0.0)) was high within all areas, leading to a high degree of uncertainty in projected recruitment (Table 4, Figure 8-right). Given that these relationships were developed primarily from other species with similar life history characteristics (i.e., striped bass, walleye, northern pike, and lake trout), we recognize they could be improved with stock-recruitment information from the Lake Erie population. As grass carp monitoring and response efforts evolve in Lake Erie, continued collection of size, age, and maturity data along with a stage specific abundance index could help inform the stock-recruitment relationship.

The quality of spawning habitats in western Lake Erie and the likelihood of successful spawning also had a strong influence on population growth rates and terminal abundance. Using percentages of "high quality events" and associated uncertainty from each system, we incorporated this random component into individual projections. For example, in each year and individual realization, X% (randomly drawn from system-specific su distribution) of potential grass carp reproduction resulted in successful recruitment. The effect of stochastic uncertainty on reproduction and population projections was evident when realizations are viewed individually, as the path of increasing abundance is erratic and difficult to precisely predict (Figure 3-left). In this way, we mimic not the complete absence (0%) or presence (100%) of reproduction and recruitment, but varying levels dependent on system specific characteristics. These values were primarily informed by a modeling exercise (Kocovsky et al., 2012); however, improved understanding between recruitment success and environmental conditions (Kocovsky et al., this issue) would help solidify these relationships.

According to our sensitivity analysis, the proportion of adults migrating into spawning rivers (Mig->RR, Mig->MR, and Mig->SR) was somewhat influential, while other movement parameters (between lake habitats [Mig->M-RR, Mig->O-MR, and Mig->O-SR], emigration [Emig], and immigration/inputs [Inputs]), had proportionally smaller effects on model outputs (Figure 5). Although these inputs were less influential, this does not suggest they are irrelevant. Movement ecology is an important component to developing and evaluating response actions (Christie and Goddard, 2003). Implementing response strategies must be cost effective and efficient, as state and federal resource dollars are often stretched thin and highly valued (Runge et al., 2013); therefore, developing a strong understanding of seasonal occupancy and movement rates is critical. We relied heavily on expert opinion and limited returns from an ongoing telemetry study to inform movement rates (Table 3). These sources suggested there were concentrations of adult (age-5+) fish in river systems during summer spawning and overwintering periods, which may facilitate targeted removal efforts. Further advancing our knowledge of Lake Erie grass carp movement ecology will help managers efficiently direct resources toward a suite of plausible response scenarios to reduce survival and reproduction. Specifically, continued use of telemetry (Coulter et al., 2018; Harris et al., 2019) to identify large and small scale movements, periods and locations of aggregation, and proportional movement rates among seasons and locations would help elucidate additional response scenarios for evaluation and update movement parameters used in the model.

Finally, identifying the current population status during an invasion or colonization can help managers assess the immediacy of risks and plan future responses (Sakai et al., 2001). Within our sensitivity analysis we evaluated the impact of starting population size (Start-pop; Figure 5), which had little influence on population growth rates or terminal abundance. We had little information to inform starting population size and without an existing estimate, it is impossible to evaluate the population's current status relative to management targets (e.g., eradication or some density threshold like 10 fish/ha). As a result, we suggest that research focus on assessing the current population size, which will help identify where grass carp in Lake Erie are on the invasion curve and help achieve a balance between response efforts and applied research to inform those efforts (Flemming et al., 2017).

Moving forward, this model can be used to probabilistically evaluate specialized response actions in an adaptive framework (Runge et al., 2013). For example, as new information on demographic parameters, movement ecology, current population size, agency resource availability, or success of past response scenarios becomes available, managers can update their knowledge of grass carp population dynamics in this system and develop plausible response scenarios. In turn, abundance projections, or derivatives thereof, can be updated and the outcomes of new response scenarios can be directly compared to current management targets. Ultimately, this model provides the flexibility to inform the development of a temporally and spatially integrated response strategy similar to that implemented for sea lamprey in the Great Lakes (see, Christie and Goddard, 2003).

Conclusion

The development of predictive models that address uncertainty for invasive species management is an important step in identifying effective response strategies (Christie and Goddard, 2003; Blomquist et al., 2010; Moore and Runge, 2012; Gannon et al., 2013; Robinson et al., 2014, 2020). This model indicated that, without management intervention, the Lake Erie grass carp population abundance and density was likely to reach levels that, according to a SDM exercise (Robinson et al., 2020), could negatively affect coastal wetland habitats. However, response scenarios that: 1) reduce survival (capture and removal), 2) interrupt spawning (barriers), and 3) efficiently distribute response efforts indicated the potential to effectively control Lake Erie grass carp to densities that result in negligible negative ecological impacts (Figure 4–right; Scenario 4). We incorporated all available knowledge and quantified uncertainty in Lake Erie grass carp demographic parameters using Bayesian methods, which allow for sequential updating as new information becomes available. As such, a focus should be placed on collecting additional system specific information to improve estimates of survival, stock-recruit relationships, system-specific productivity, maturity-at-age, length-at-age, weight-at-age, seasonal occupancy and movement rates, and current abundance. Although this model was focused on Lake Erie grass carp, methods here-in could be adapted to other invasive species populations that threaten dispersal and establishment and may require large-scale, inter-jurisdictional management (Herborg et al., 2007).

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Table 1: Summary of prior literature information used in developing Lake Erie grass carp model parameters including number of values, source, location within source, and original sources. Original sources not cited here in, but available in the cited source which is referenced.

Parameter	**Values**	**Source**	**Location**	**Original sources**
Maturity (mat_a)	10	Jones et al. (2017b)	Table 2.1	Adullayev and Khakberdiyev 1980; Abdusamodov 1986; Gorbach and Krytin 1981; Karpov et al 1989; Makeyeva 1968
Maturity (mat_a)	42	Shireman and Smith (1983)	Table 6	Opuszynski 1972; Wolny 1971; Alabama Dept. of Cons. 1968; Baily and Boyd 1971; Baily and Boyd 1973; Sneed 1971; Gorbach 1961; Makeeva 1963; Gorbach 1966; K'o-lei-hei-chin 1966; Ma-k'ai-yeh-wa, Su-yini, and Po-t'a-po-wa 1966; Vinogradov 1968; Bobrova 1972; Anon. 1970c; Martino 1974; Lin 1935; Konradt 1968; Brown 1977; Dah-Shu 1957; Yashouv 1958; Chen et al. 1969; Shrestha 1973; Lin 1965; Chen 1976
Maturity (mat_a)	2	Cudmore et al. (2004)	Section 3.3	Fedorenko and Fraser 1978; FishBase 2004
Survival (s)	1	Morrow Jr. et al. (1997)	Results text	
Survival (s)	6	Stich (2011)	Chapter 4	
Survival (s)	3	Kirk et al. (2000)	Table 1	
Survival (s)	5	Kirk and Socha (2003)	Table 1	
Survival (s)	2	Jones et al. (2017b)	Table 2.1	Abrosov and Bauer 1955; Li 1999
Survival (s)	2	Weberg (2013)	Chapter 2	
Reproduction ($\tilde{\alpha}$)	4	Myers et al. (1999)	Table 1	Myers et al. 1995
Reproduction ($sd(\beta)$)	54	Goodwin et al. (2006)	Table A1	ICES database
Reproduction (σ^2)	54	Goodwin et al. (2006)	Table A1	ICES database

Table 2: Description and summary of Lake Erie grass carp model notation.

Notation	**Description**	**Model**
$n^R(t, S)$	Region and season specific population vectors (5×1)	Matrix
A_R^S	Region and season specific population projection matrices (5×5)	Matrix
M_{RR}^S	Region and season specific movement matrices (5×5)	Matrix
B_S	Block seasonal projection matrices (8×8)	Matrix
$N(t, S)$	Block seasonal population vectors (8×1)	Matrix
S	Season - number if seasons (4)	Matrix
R	Region - number of unique area/habitat specific regions	Matrix
a	Age - number of age groups (5) or age in years	Matrix/Catch-curve
y	Years - number of projected years (60)	Matrix
s	Survival - proportion of fish surviving some period (e^{-Z})	Matrix
r	Reproduction - based on stock recruitment model	Matrix
m	Movement - proportion of fish moving from one region to another	Matrix
su	Stochastic uncertainty in reproduction - likely reproductive success	Matrix
C_a	Catch at age - based on unpublished Lake Erie capture data	Catch-curve
Z	Total mortality - slope in the catch-curve model	Catch-curve
b	y-intercept in catch-curve model	Catch-curve
SS	Spawning stock - number of adult fish (age-5+)	Ricker
α	Spawning stock productivity at low abundance - slope near origin	Ricker
β	Degree of density-dependent compensation	Ricker
σ^2	Inter-anal variation in recruitment	Ricker
$\tilde{\alpha}$	Maximum lifetime reproductive rate	α calculation
$SPR_{F=0}$	Spawner-per-recruit at unfinished equilibrium	α calculation
Rec_a	Proportion of recruits surviving to age	α calculation
mat_a	Maturity-at-age	Maturity
γ_1	Slope in maturity logistic regression	Maturity
γ_2	y-intercept in maturity logistic regression	Maturity
EA	Equilibrium abundance - spawning stock size at which the number of surviving recruits replaces the number of dying spawners in the absences of fishing mortality (F)	β calculation

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Table 3: Lake Erie grass carp model movement parameters including means and standard deviation in parentheses

Season	**Age group**	**Parameter**	**Unknown (emigration)**	**Michigan Lake**	**Ohio Lake**	**Lake Erie Islands**	**River Raisin**	**Maumee River**	**Sandusky River**
Spring to Summer	Age-5+	Michigan Lake spawners to	0.03 (0.01)				0.04 (0.01)	0.62 (0.02)	0.31 (0.01)
	Age-5+	Ohio Lake spawners to	0.03 (0.01)				0.04 (0.01)	0.62 (0.02)	0.31 (0.01)
	Age-5+	Lake Erie Island spawners to	0.03 (0.01)				0.04 (0.01)	0.62 (0.02)	0.31 (0.01)
	All	Unknown to lake (immigration)		0.05 (0)	0.05 (0)	0.05 (0)			
Summer to Fall	Age-5+	River Raisin spawners returning to lake					0.5 (0)		
	Age-5+	Maumee River spawners returning to lake						0.5 (0)	
	Age-5+	Sandusky River spawners returning to lake							0.5 (0)
Fall to Winter	All	Michgan Lake to rivers							
	All	Ohio Lake to rivers							
	All	Lake Erie Islands to rivers							
Winter to Spring	All	River Raisin returning to lake		1.0 (0)					
	All	Maumee River returning to lake			1.0 (0)				
	All	Sandusky River returning to lake				1.0 (0)			

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Table 4: Lake Erie grass carp model inputs and parameters inlcuding means and standard deviation in parentheses.

Inputs/Parameters	**Global**	**Michigan-Raisin**	**Ohio-Maumee**	**Ohio-Sandusky**
Initial population (total individuals)		660	660	660
Low marsh habitat (ha)		1,500	1,500	3,000
Annual survival (s)	0.75 (0.03)			
Ricker alpha ($log(\alpha)$)	1.8 (0.23)			
Ricker beta (β)		7.5e-05 (5.8e-06)	7.5e-05 (5.8e-06)	3.9e-05 (3.0e-06)
Ricker sigma (σ^2)	0.55 (0.00)			
Probability of spawning success (su)		0.05 (0.02)	0.84 (0.04)	0.69 (0.04)
Age-at-maturity (γ_1)	-3.2 (0.34)			
Age-at-maturity (γ_2)	0.71 (0.067)			

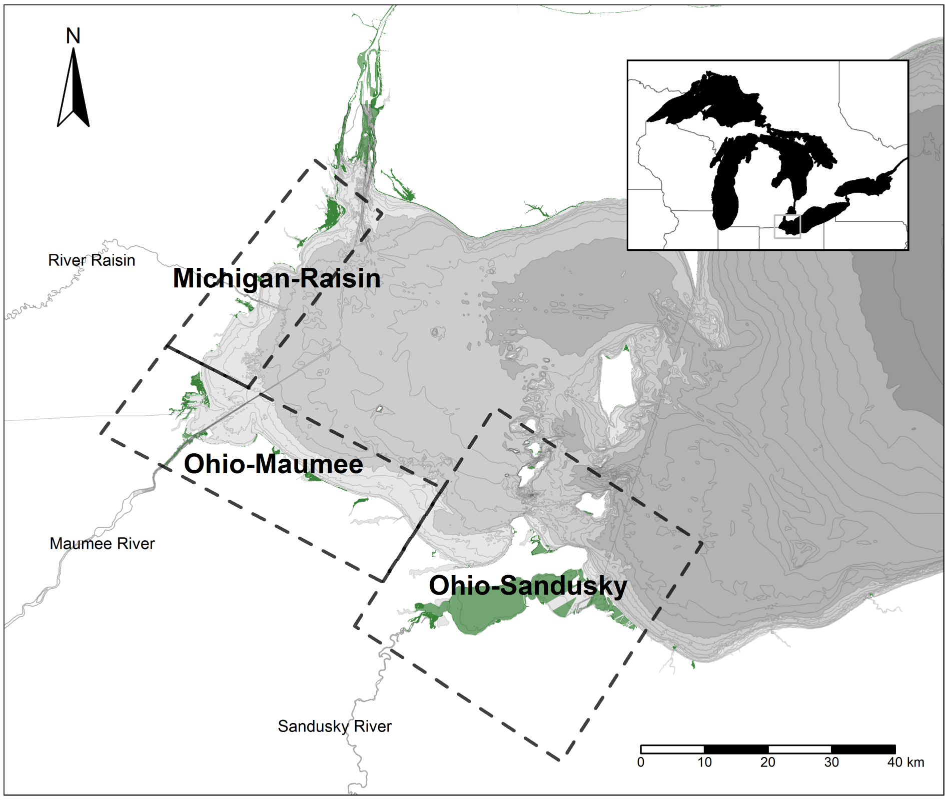

Figure 1: Lake Erie's western basin including 1 m contours (light gray lines) and estimated low-marsh habitat (light and dark green areas along coastal margins; Gertzen et al. (2017)). The boxes represent three defined areas in the matrix model structure (Michigan-Raisin, Ohio-Maumee, and Ohio-Sandusky), including open lake and riverine habitats.

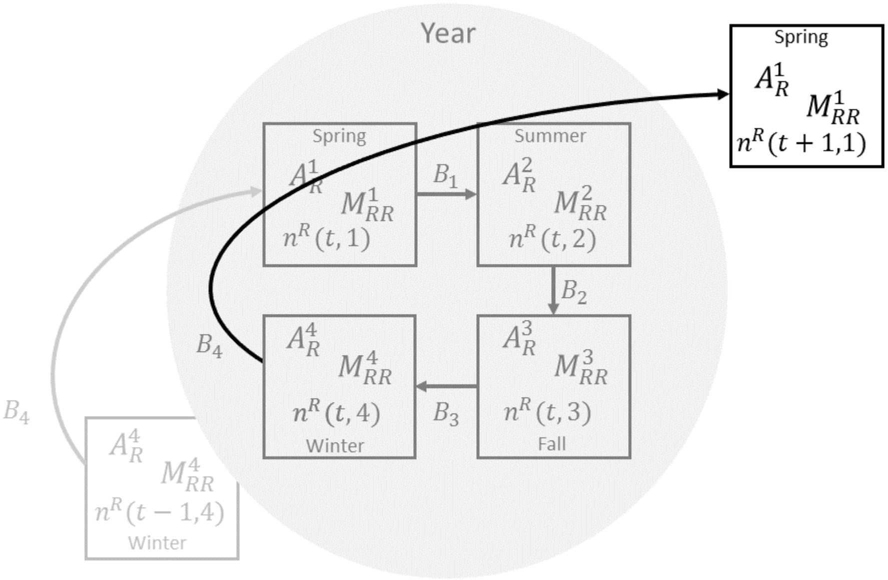

Figure 2: Conceptual diagram including season and region specific population ($n^R(t,S)$), population projection (A_R^S), and movement (M_{RR}^S) matrices, seasonal block projection matrices (B_S), and flow of within and across year projections (arrows)

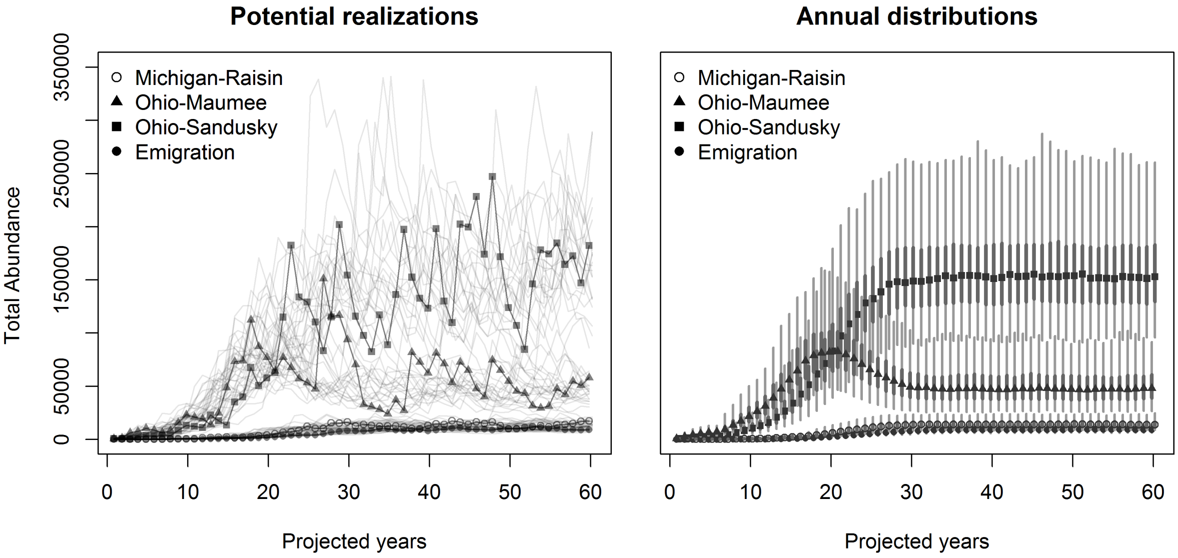

Figure 3: Total abundance projections (Scenario 1 - no response), including individual realizations (left - each line) and annual distributions (right), for Michigan-Raisin, Ohio-Maumee, and Ohio-Sandusky areas and a proposed emigration region. Black symbols represent means while dark and light gray bars are 50% and 95% credible intervals, respectively.

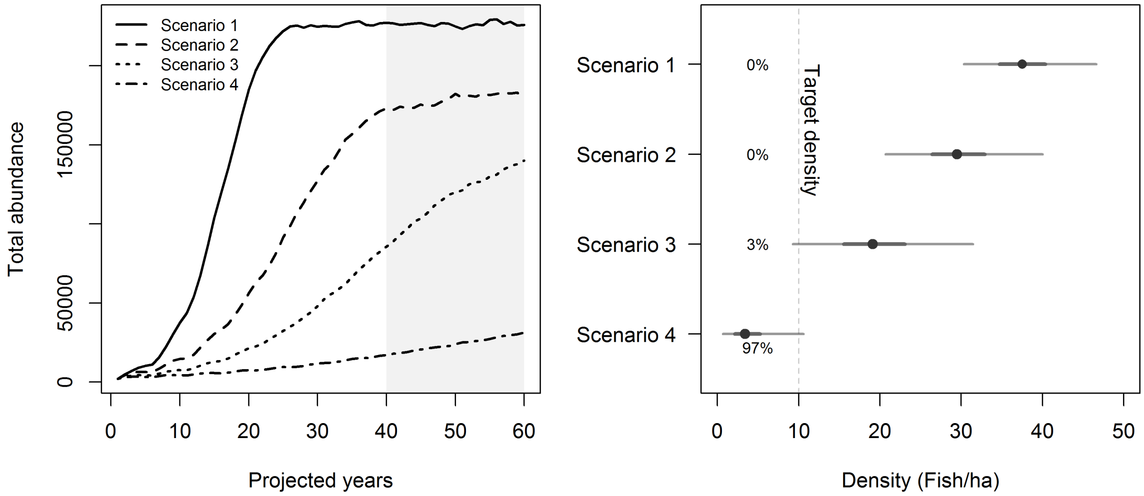

Figure 4: Projected mean total population abundance under four potential grass carp response scenarios (left, see text for scenario descriptions). Gray box represents the range over which we averaged abundances for comparison with target density. The mean, including uncertainty (50 and 95% credible intervals), over years 40 through 60 (gray box; left) compared to a management target of 10 fish per hectare of low marsh (right). Percentages represent the probability that each of the scenarios will meet the target density.

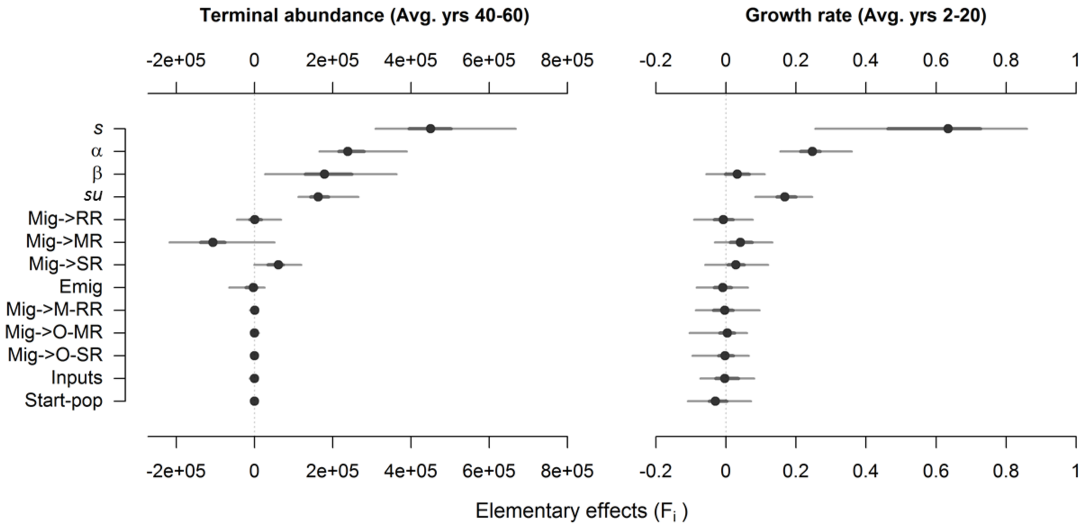

Figure 5: Sensitivity analysis results (i.e., elementary effects) for parameters of interest relative to terminal abundance (left) and population growth rate (right). Black dots represent means while dark and light gray bars are 50% and 95% credible intervals, respectively.

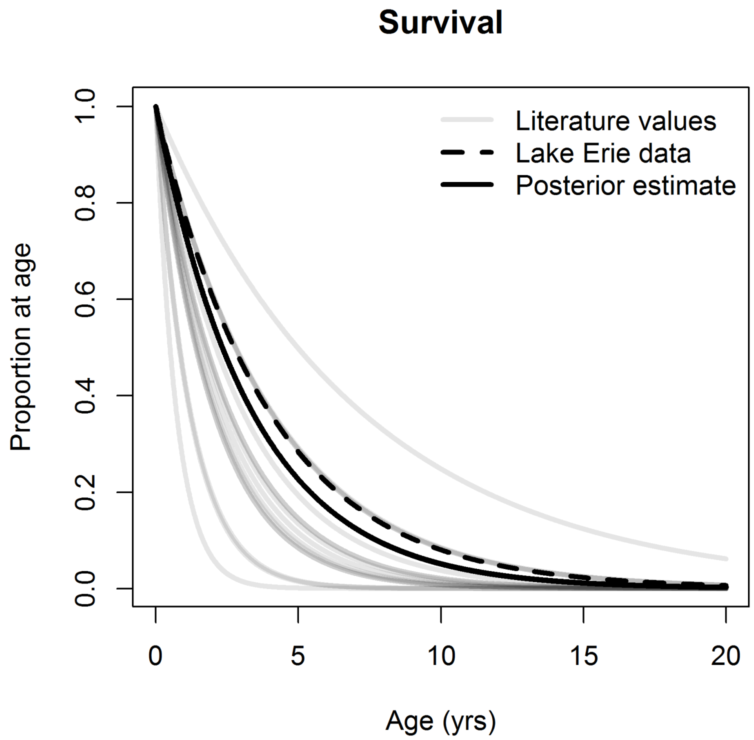

Figure 6: Estimated proportion of grass carp surviving at age for prior literature values (light gray lines), Lake Erie data (*likelihood*; dashed black line), and posterior estimate (solid black line).

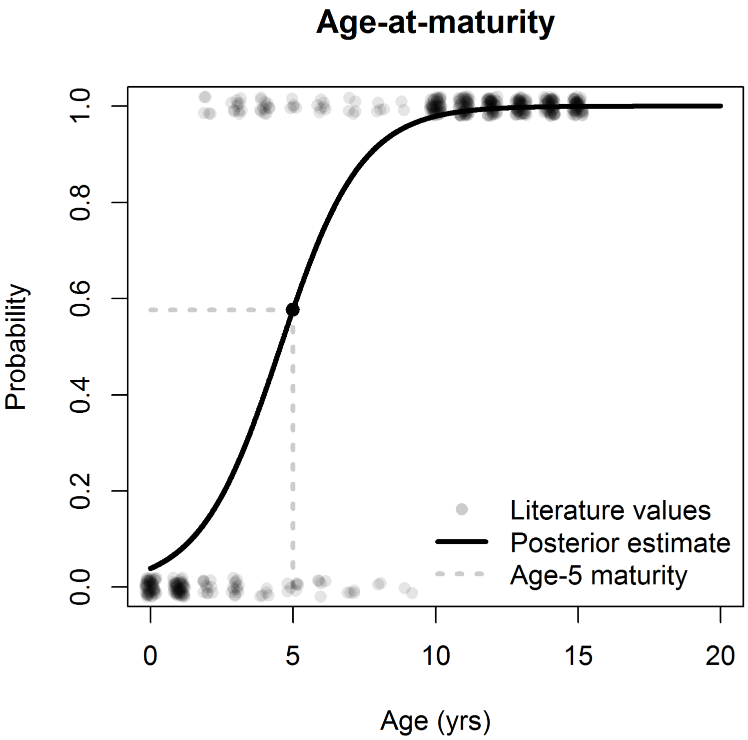

Figure 7: Estimated age at maturity (solid black line) based on literature reported data (light gray dots). Proportion of mature age-5 fish denoted by dashed gray line.

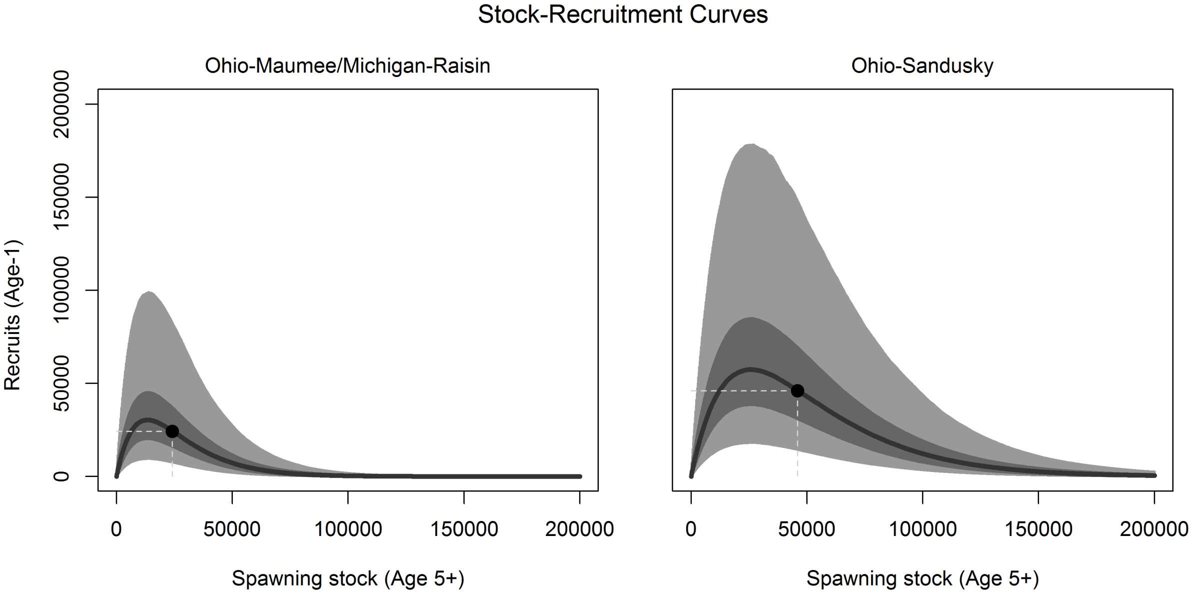

Figure 8: Stock-recruitment curves for Ohio-Maumee/Michigan-Raisin areas (left) and Ohio-Sandusky area (right), including mean recruitment(solid dark gray line) and 50% and 95% credible intervals (dark and light gray areas respectively). Equilibrium abundance (EA) is designated by light gray dashed lines.