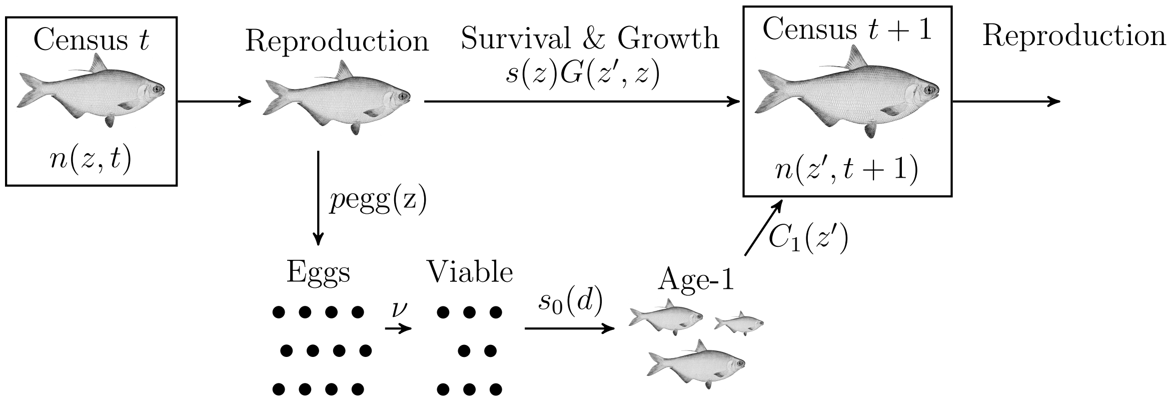

Life cycle diagram and census points for pre-reproduction census of gizzard shad used in a density-dependent integral projection model.

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4 U.S. Geological Survey, Upper Mississippi Environmental Sciences Center

Graphical Abstract

An integral projection model for gizzard shad (*Dorosoma cepedianum*) utilizing density-dependent age-0 survival

J. Peirce[1,3], G. Sandland[2,3], B. Bennie[1], R.A. Erickson[4]

Highlights

An integral projection model for gizzard shad (*Dorosoma cepedianum*) utilizing density-dependent age-0 survival

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- We introduce an integral projection model that incorporates data from studies on 1) egg production in different size classes of adult gizzard shad, 2) density-dependent survival of age-0 shad, and 3) length distributions of gizzard shad in the Upper Mississippi River system that span nearly thirty years.
- We establish survival parameters using gizzard shad data collected from the 5 sites along the Mississippi River and validate our model using empirical information collected from the La Grange Reach of the Illinois River.

An integral projection model for gizzard shad (*Dorosoma cepedianum*) utilizing density-dependent age-0 survival

J. Peirce[1,3], G. Sandland[2,3], B. Bennie[1], R.A. Erickson[4]

1 *University of Wisconsin - La Crosse, Mathematics & Statistics Department*
2 *University of Wisconsin - La Crosse, Biology Department*
3 *River Studies Center*

Abstract

Gizzard shad (*Dorosoma cepedianum*) is a common freshwater fish species found throughout the central and eastern portions of North America. Within these regions, gizzard shad play a number of critical roles in the freshwater community such as serving as prey for other fish species and translocating nutrients from substrates into the water column. Because of this, it is important that we understand how gizzard shad populations respond to environmental changes and what these changes may mean for aquatic communities in general and fish assemblages in particular. Here, we introduce an integral projection model (IPM) for gizzard shad that incorporates empirical information from a number of sources including Long Term Resource Monitoring (LTRM) data. IPMs are a generalization of stage-based, matrix population models that have been used to describe a wide range of organisms and, as such are a natural choice for gizzard shad since many aspects of their life cycle have been studied. We tested model outputs against empirical patterns reported for gizzard shad from a different location along the Illinois River (La Grange Reach). Results of our work suggest that our model could serve as an important tool for predicting gizzard shad population responses to changing environmental conditions, including those mediated through species invasions.

Keywords: population dynamics, fisheries, Mississippi River basin, population ecology, invasive species impact

1. Introduction

Gizzard shad (*Dorosoma cepedianum*) is a laterally compressed, deep-bodied fish species that occupies numerous aquatic systems throughout central, southern and eastern regions of the United States (Pierce et al., 1981; Vanni et al., 2005). They have the potential to reach high abundances in more eutrophic habitats, such as reservoirs, leading to its dominance within fish assemblages. Because of this, gizzard shad have the potential to influence freshwater systems in a number of ways. First, young shad often serve as a critical food source for many fish species, including those of commercial and recreational importance (such as walleye and largemouth bass)(Jester et al., 1972). Thus, gizzard shad can serve as an important trophic link within aquatic food webs. Second, because detritus can serve as a primary food source throughout much of gizzard shad development (i.e., from the age-0 stage onward), these fish can transport nutrients from benthic regions into pelagic habitats (Mather et al., 1995; Schaus and Vanni, 2000; Vanni et al., 2005). This process can result in an increase in the nutrients available to organisms within the water column leading to increases in phytoplankton biomass, algal blooms, and, due to these conditions, shifts in freshwater community structure (Aday et al., 2003; Schaus and Vanni, 2000). Finally, the fact that detritus can comprise a substantial portion of gizzard shad diet also makes this species an important connection between terrestrial inputs and aquatic processes (Schaus and Vanni, 2000). Given its potentially important role in aquatic ecosystems, interest has intensified in understanding how gizzard shad populations respond to environmental changes (both natural and anthropogenic) and what these changes may mean for freshwater communities in general and fish assemblages in particular.

Interactions within and between species throughout interconnected environments can have important consequences for fish populations across space and time (Thorp et al., 2006). For gizzard shad, previous work has suggested that fish densities can play an important role in both the growth and survival patterns observed in populations of these fish. For example, (Buynak et al., 1992) reported an inverse relationship between densities and the lengths of age-0 gizzard shad. Similarly (Welker et al., 1994) found that high densities of age-0 shad were negatively associated with both fish length and survival under both field and semi-natural conditions. Finally, (Michaletz, 2010) reported that the densities of age-0 gizzard shad were negatively correlated with survival in two Missouri lakes. These patterns were attributed to intraspecific competition among young shad for prey (zooplankton) resources. Although intraspecific competition may be influencing life-history traits in subsequent stages of gizzard shad development, little work has actually been conducted to address this (DiCenzo et al., 1996). There is also evidence that the densities of other co-occurring fish species (such as invasive carps) may negatively influence aspects of gizzard shad biology, such as body condition (Irons et al., 2007; Love et al., 2018).

Although substantial empirical work on gizzard shad biology has accumulated over the decades, few if any studies have attempted to use these data to model population dynamics in this species. Work by Catalano and Allen (2010, 2011) used empirically-based simulations of gizzard shad to assess population-level responses in this species. As part of this process, the authors investigated population-structure using fish lengths but did not consider the impacts of gizzard-shad densities on population patterns. Here, we introduce an integral projection model (IPM) for gizzard shad based on empirical data with density-dependent survival in age-0 fish. We then compare model outcomes to the dynamics reported for this fish species in a well-studied pool of the Illinois River (specifically, the La Grange Reach). Results from this work suggest that our model could be an important tool for predicting gizzard shad population responses to changing environmental conditions, including those mediated through species invasions (i.e., silver and bighead carp).

2. Model development

2.1. Gizzard shad life history

Mature gizzard shad tend to mate between May and June, although this can vary based on water temperatures (Bodola, 1955). Males and females aggregate and then broadcast gametes into the surrounding water; fertilized eggs then settle and adhere to the bottom substrates. After a period of days, eggs hatch and fish develop from the larval stage to juveniles and eventually to adults. In many habitats, individuals can reach sexual maturity within a year (Bodola, 1955). As gizzard shad mature, their diet preferences typically shift from phytoplankton and zooplankton early in development to detritus and zooplankton as adults. Given the large number of eggs produced by shad females (often $>$ ~~300~~100,000/year) (Jons and Miranda, 1997), there is evidence that intraspecific competition can be intense during early developmental stages in this species leading to density-dependent mortality

Table 1: A summary of parameters, their biological meaning, and source for mean values.

Parameter	Meaning (units)	Mean	Source
Logistic survival probability function, $s(z)$			
$s_{\min}$	minimum survival	0.002	(Bodola, 1955)
$s_{\max}$	maximum survival	$1 - 8.871K^{0.73}L_{\infty}^{-0.33}$	(Then et al., 2015)
α_s	inflection point	80.01	Estimated from LTRM dataset
β_s	slope	-139.93	Estimated from LTRM dataset
Growth function, $G(z, z')$			
L_{∞}	maximum length (in mm)	394.30	(Catalano and Allen, 2010)
K_g	individual growth rate	0.26	(Michaletz, 2017)
σ_g	growth standard deviation	25	(Michaletz, 2017)
Normal distribution of length of age-1, $C_1(z')$			
μ_r	mean length of recruitment (in mm)	105	(Michaletz, 2017)
σ_r	standard deviation of length	25	(Michaletz, 2017)
Eggs produced, egg(z)			
$\text{egg}_{\max}$	maximum number of eggs produced	737512.1	Estimated from (Jons and Miranda, 1997)
α_e	inflection point	314.44	Estimated from (Jons and Miranda, 1997)
β_e	slope	-7.18	Estimated from (Jons and Miranda, 1997)
Survival of age-0, $s_0(d(t))$			
a_0	intercept	0.27	Estimated from (Michaletz, 2010)
b_0	decay rate	0.003	Estimated from (Michaletz, 2010)
Spawning			
ν	probability that egg becomes viable	0.002	(Bodola, 1955)
p	probability that female spawns	0.90	

(Michaletz, 2010). The strength of competition may then subside as fish transition to feeding on different food types during later stages of development.

2.2. Equations

We used an IPM to describe the life history of female gizzard shad in the Upper Mississippi River system (UMRS). IPMs were first introduced by Easterling (Easterling et al., 2000), as a generalization of stage-based, matrix population models. Since that time, IPMs have been used to describe a wide range of organisms ~~(Ellner et al., 2016; Merow et al., 2014; Rees et al., 2014)~~ (Briggs et al., 2010; Ellner et al., 2016; Merow et al., 2014; Rees et al., 2014), but have only recently ~~be~~ been used to model fish populations, such as (Erickson et al., 2017; Liao et al., 2019; White et al., 2016; Pollesch et al., 2022). Fish are an ideal group to investigate using this approach as many species have been well studied and are therefore associated with robust information about life-history traits (i.e., growth and reproduction). Gizzard shad are one such species and have been the subject of numerous laboratory and field studies over the decades making it a logical choice for IPMs. In our model specifically, we incorporate data from studies on 1) egg production in different size classes of adults, 2) density-dependent survival of age-0 shad, and 3) length distributions of gizzard shad in the UMRS that span nearly thirty years (Table 1).

~~We assumed that variations among individual~~ In a traditional matrix population model (Caswell, 2000), the annual abundance of gizzard shad can be ~~summarized by its length z (in mm) ranging from the minimum possible length L to the maximum value U. The~~ separated by factors such as age, length, developmental stage, etc. into a finite number of disjoint subgroups. Within each subgroup, individual fish can be assumed to exhibit the same survival, growth, and fecundity. These parameters are used to build a transition matrix that updates the current state of the population at time t ~~(in years)~~ to the future state at $t+1$ through matrix multiplication. Increasing the number of subgroups also increases the number of parameters that require estimation when generating the transition matrix. Conversely, the annual update in gizzard shad abundance for an IPM is described by the ~~length distribution $n(z,t)$. Specifically, for each time t,~~ integral kernel. This kernel can be created from continuous functions for survival, growth, and fecundity and therefore IPMS

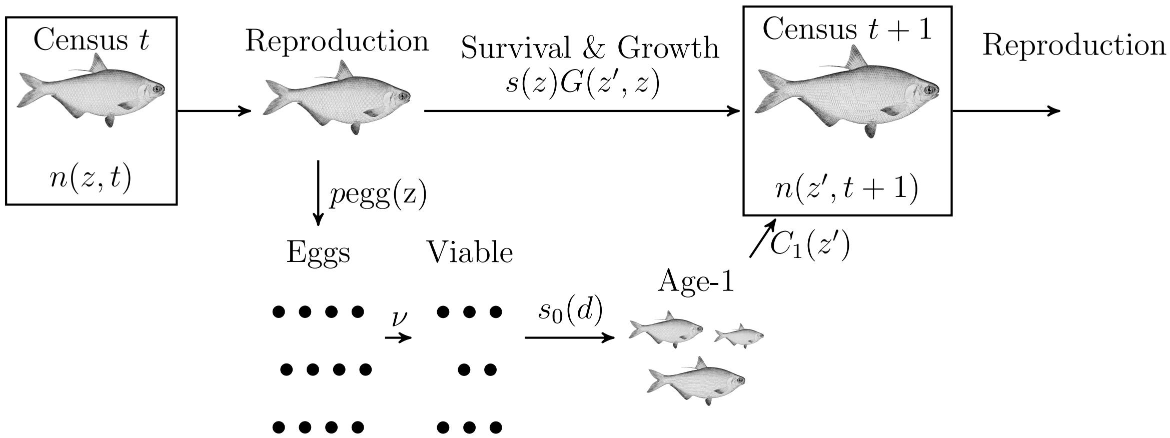


Figure 1: Life cycle diagram and census points for pre-reproduction census of gizzard shad.

almost always require fewer estimated parameters (?). When the integral kernel is applied to the current length distribution $n(z,t)$ ~~is a smooth function of z such that the~~ and integrated over the length $[L,U]$, the result is the next length distribution $n(z',t+1)$. $n(z',t+1)$ describes the number of individuals of length ~~z~~ z' in the interval ~~$[a,b]$ at time t is $\int_a^b n(z,t)\,dz$. Between times t and~~ $[a',b']$ at time $t+1$~~, individual gizzard shad may grow, die, and produce offspring that vary in length depending on the individual's current length (Figure 1).~~. For the numerical simulations in Section 4, the length vector will be discretized. As a result, $n(z,t)$ becomes a vector and the integral kernel acts on $n(z,t)$ like a large approximating transition matrix. In the following sections, we detail the functions used to create the integral kernel for the gizzard shad IPM

2.2.1. Growth and survival

For an individual of length z at time t, $P(z',z)\Delta z$ is the probability that the individual is alive at time $t+1$, and its size is in the interval $[z', z'+\Delta z]$ (as with $n(z,t)$ this is an approximation that is valid for small Δz, and the exact probability is given by an integral like the one above). We define $P(z',z) = s(z)G(z',z)$ where $s(z)$ is the annual adult survival probability and the growth $G(z',z)$ describes the annual length transitions. The survival function is a logistic function,

$$s(z) = s_{\min} + \frac{s_{\max} - s_{\min}}{1 + e^{\beta_s(\ln(z) - \ln(\alpha_s))}}, \tag{1}$$

with four parameters: the minimum survival rate $s_{\min}$; a maximum survival rate, $s_{\max}$; an intercept parameter, α_s; and a slope parameter, β_s (Bolker, 2008). The growth function is a two-variable normal distribution centered around a modified von Bertalanffy function of the length at time t (Erickson et al., 2017). Consequently if L_∞ is maximum asymptotic length and K_g is the individual growth rate of gizzard shad, then the growth kernel

$$G(z', z) = \mathrm{Prob}(z' \mid z, L_\infty, K_g) = \mathrm{NormalPDF}(\mu_g, \sigma_g)$$

where $\mu_g = L_\infty \left(1 - e^{-K_g}\right) + z(t)e^{-K_g}$ and σ_g is the standard deviation.

2.3. ~~Fecundity~~

2.2.1. Fecundity

$F(z', z)\Delta z$ is the number of new offspring in the length interval $[z', z' + \Delta z]$ present at time $t+1$, per length-z individual at time t. The fecundity kernel is

$$F(z', z) = p_b \, \mathrm{egg}(z) \, \nu \, s_0(d(t)) \, C_1(z') \tag{2}$$

where ~~p_b~~ p is the probability of reproducing, $\mathrm{egg}(z)$ is the mean number of eggs produced by a fish of length z, ν is the probability that an egg is viable, $s_0(d(t))$ is the density-dependent probability of surviving to age-1, and $C_1(z')$ is the length distribution of new recruits at age-1 (when they are first censused in the model).

The mean number of eggs produced by females of a certain length is a three-parameter logistic function,

$$\mathrm{egg}(z) = \frac{\mathrm{egg}_{\max}}{1 + e^{\beta_e(\ln(z) - \ln(\alpha_e))}}. \tag{3}$$

The probability of gizzard shad survival during their first year can depend on many factors (Michaletz, 2010) including predation, temperature, the mean total length of fish, and the density of age-0 fish. In this study, we focused only on the density factor and assumed the probability of survival of age-0 fish is the exponential function,

$$s_0(d(t)) = a_0 \, e^{-b_0 d(t)}, \tag{4}$$

where a_0 is the intercept, b_0 the decay rate, and $d(t)$ is the density at time t of age-0 gizzard shad per 1000 m^3,

$$d(t) = 10^{-3} \int_L^U p_b \, \mathrm{egg}(z) \, \nu n(z, t) \, dz.$$

Finally, Equation 2 is constructed from mulitplying the total number of eggs that survive to be an age-1 fish ~~is multiplied~~ with a normal distribution of length, $C_1(z') = \text{NormalPDF}(\mu_r, \sigma_r)$ where μ_r is the mean length of age-1 gizzard shad and σ_r is the standard deviation.

2.3. Dynamical model

The population at time $t + 1$ is the sum of the contributions from each individual alive at time t,

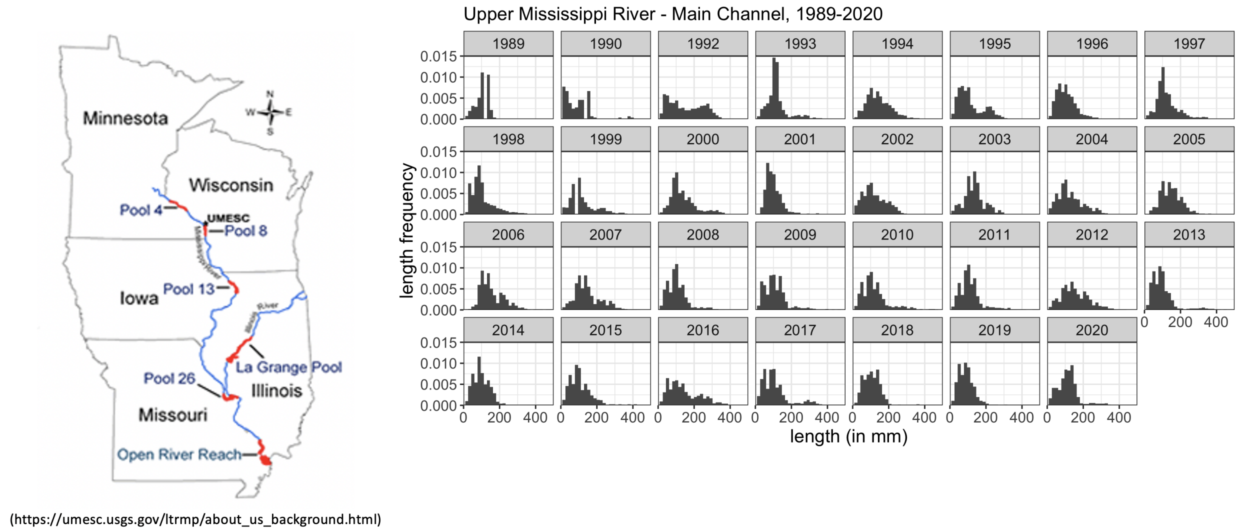
$$n(z', t+1) = \int_L^U K(z', z) n(z, t)\, dz, \tag{5}$$

where the integral kernel $K(z', z) = s(z)G(z', z) + F(z', z)$ and $[L, U]$ is the range of all possible lengths.

3. Methods

3.1. Long Term Resource Monitoring (LTRM) data and model parameterization

The LTRM element of the Upper Mississippi River Restoration monitors the UMRS to provide an understanding of the system's ecology, resource changes, and inform management (Bouska et al., 2018; Maher et al., 2015). In order to achieve this goal, numerous features of the UMRS, such as aquatic vegetation, bathymetry, fish, land use/land cover, and water quality are continually surveyed from Navigation Pool 1 (at Minneapolis, Minnesota) south to the confluence of the Mississippi and Ohio Rivers at Cairo, Illinois. LTRM fish surveys are conducted at five locations along the main channel of the Upper Mississippi River (Pools 4, 8, 13, 26, and the Open River Reach) and at one location along the Illinois River (La Grange Reach) (Figure 2a). Fish are captured using a multiple gear approach (which includes netting and electrofishing) in order to monitor the responses and health of fish communities along these two very important waterways over time (Gutreuter et al., 1995). Specific capture methodologies, protocols and modifications to the LTRM can be found in Gutreuter et al. (1995), and Ickes and Burkhardt (2002). In terms of gizzard shad, fish traits (such as total length) have been recorded since 1989 with approximately 3000 collections occurring per year along the Mississippi River (Figure 2b). For the La Grange Reach of the Illinois River, gizzard shad have been sampled and measured since 1990 with approximately 500 collections occurring per year.



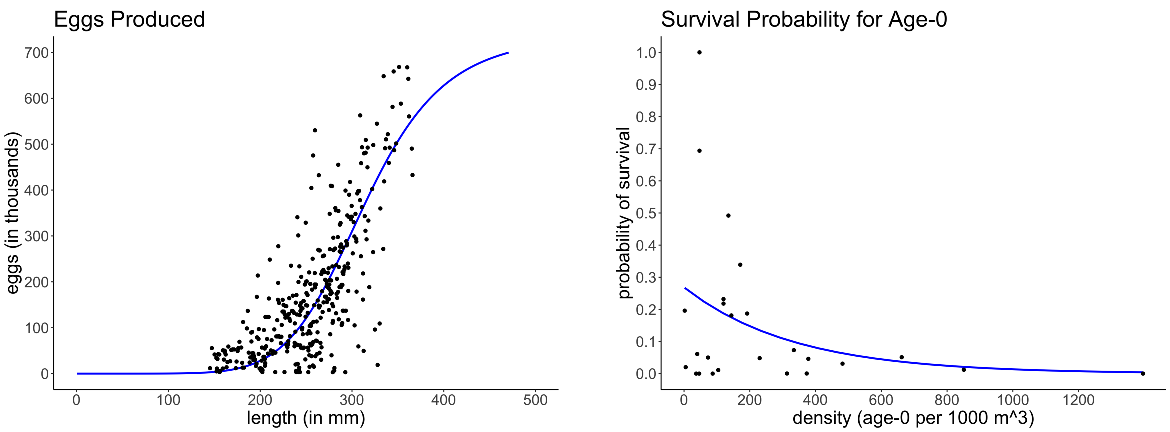
(a) (b)

Figure 2: (a) The LTRM fish survey sites in the Upper Mississippi River system. (b) Length frequency of sampled gizzard shad in the main channel of the Upper Mississippi River system.

To parameterize our model, we used gizzard shad data collected from the 5 sites (Pools 4, 8, 13, 26, and Open River Reach) along the Mississippi River (Figure 2a). We then validated our model using empirical information collected from the La Grange Reach of the Illinois River. We undertook this approach as the La Grange Reach is upstream of the Mississippi River making it a more distinct location compared to the other sites.

3.1.1. Fecundity and recruitment

Female gizzard shad begin reproducing at approximately 140 mm in length and egg numbers tend to increase with fish size (Jons and Miranda, 1997). The logistic parameters for the mean number of eggs produced by females of a certain length were obtained by fitting the three-parameter logistic function (Equation 3) to the data for batch fecundity versus length (Jons and Miranda, 1997) (Figure 3a). Fish survival to age-1 was assumed to be dependent on the density of age-0 gizzard shad (Figure 3b). Parameters for the exponentially decaying age-0 survival function (Equation 4) were determined by fitting equation 4 to the survival means for 2003-2007 cohorts of gizzard ~~shard~~ shad in five Missouri reservoirs (Michaletz, 2010). To complete the recruitment process we assign a length to the recruited individuals



(a) (b)

Figure 3: (a) Mean number of eggs produced by female gizzard shad egg(z). Data from (Jons and Miranda, 1997). (b) Age-0 density-dependent survival function $s_0(d)$. Data from (Michaletz, 2010).

by simulating a Gaussian random variable with mean $\cancel{\mu_c}$ μ_r and standard deviation $\cancel{\sigma_c}$ σ_r. The parameters for the size distribution of age-1 fish were gleaned from a study of gizzard shad located in large impoundments (Michaletz, 2017) and the historic 1990-2020 LTRM dataset from the main channel of the UMRS (discussed in Section 3.1).

3.1.2. Growth and survival of adults

The parameters for the growth function were chosen as the mean values published on a study of gizzard shad located in large impoundments in Missouri U.S.A. (Michaletz, 2017). The association between adult lengths and survival have not been well-resolved in gizzard shad leading us to make a number of assumptions. First, we assume that the probability of adult survival is related to the length by a four-parameter logistic function (Equation 1). An investigation of gizzard shad in Lake ~~Eerie~~ Erie (Bodola, 1955) provided the minimum and maximum survival rate of adults. Based on the observed length distributions of gizzard shad sampled from the main channel of the Mississippi River (Figure 2b), we assumed that solutions of our model will exhibit periodic behavior every 8-9 years. We used a least squares method to estimate the α_s and β_s parameters that minimized the total square-distance between the (observed) pre-carp LTRM length distribution in the main channel of the UMRS and (predicted) model equilibrium, $n(z, t)$ during ~~a~~ an 8-year period occurring 100 years after initialization. The slope parameter β_s was found to be large in magnitude resulting in a primarily two-valued survival probability. Gizzard shad less than α_s mm in length have a very low survival rate ($s_{\min}$) while lengths larger than α_s mm approach the maximum survival rate $s_{\max}$. This survival pattern has been reported for a number of fish species and can arise due to a number of biotic (i.e. predation) and/or abiotic (i.e. temperature) factors (Pepin et al., 1992; Nowlin et al., 2006).

4. Analysis and results

We numerically solved the integral model using the Midpoint Rule with large approximating matrices (Burden and Faires, 2005). The Midpoint Rule has been commonly used for integral projection models because of its simplicity and effectiveness (Ellner and Rees, 2006; Ramula et al., 2009; Merow et al., 2014). During the course of model development, we explored different step sizes for the Midpoint Rule and found that about 50 points provided numerically stable results. We integrated over lengths from 0 mm to 500 mm. The upper limit was chosen based upon numerical stability and consistency of the system (e.g., avoiding eviction or the loss of individuals due to numerical errors (Williams et al., 2012)).

4.1. Initial conditions

We assumed that the initial density of gizzard shad was $d_0 = 964.7$, the ~~annual average~~ average annual density of gizzard shad ~~observed in~~ caught with all gear types represented in the LTRM fish program in La Grange Reach from 1993-2020. The probability of an individual being length z at time $t = 0$ was assumed to be normally distributed with mean $0.5L_\infty$ and standard deviation $\sigma_0 = 30$. As a result, we initialized our model with length distribution

$$n(z, 0) = d_0\mathrm{Norm}(0.5L_\infty, \sigma_0) = 964.7\mathrm{Norm}(197.15, 30). \tag{6}$$

The model was coded in R (R Core Team, 2017) and the scripts are published on JP's GitHub page `https://github.com/jppeirce`.

4.1.1. Effect of density-dependence on the survival probability of the age-0 cohort

In the simulated solutions to the IPM, the density of age-0 ~~Fish strongly influenced~~ fish are strongly influenced by the density of gizzard shad at subsequent developmental stages.

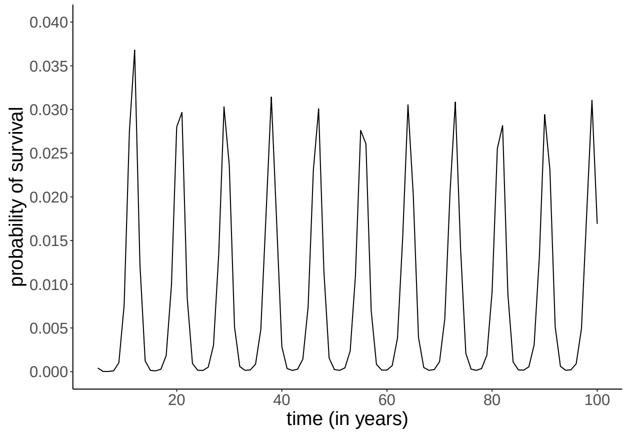


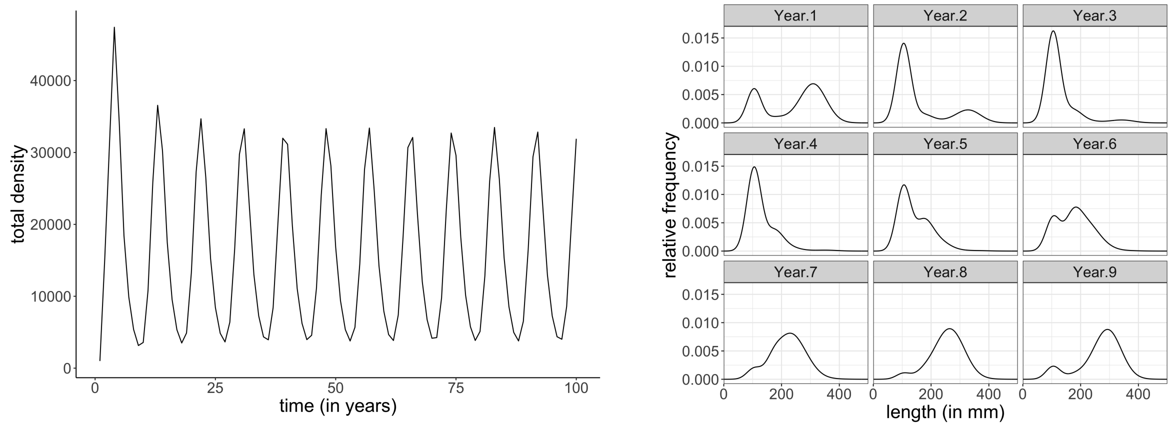
Figure 4

Figure 5: Survival probability of age-0 gizzard shad.

When adult densities are large, there may be more fish of longer lengths that can produce a greater number of eggs. More eggs leads to a higher density of age-0 fish and reflectively a reduction in the survival to age-1. If reduced survival continues over subsequent years, the overall density of fish within the population may decline and result in a smaller number of longer length fish that are reproducing. Fewer fish spawning could result in a smaller age-0 class which, in turn, could enhance survival probability in this cohort (through reduced competition). We would then expect the overall density of fish to increase over the following years, until large numbers of eggs are again produced by larger, adult fish. This oscillatory pattern is reflected in our model by the time-dependent survival probability of age-0 recruits (Figure 4).

4.1.2. Periodic orbit and validation with external dataset

The total number of gizzard shad in our simulation reached a stable periodic orbit (Figure 6a) within 50 years. After simulating an additional 50 years, we fit a periodic function to the annual density of gizzard shad and determined the period of approximately 8.74 years. Figure 6b illustrates the periodic length dynamics within the gizzard shad population during a 9-year window of the periodic orbit. As a validation of the model, the simulated length distributions during a periodic orbit (Figure 6b) have similarities to fish lengths observed from the La Grange Reach (Figure **??**). In addition, the ebb and flow of the frequency of the



(a) (b)

Figure 6: (a) The total density of gizzard shad in La Grange Reach predicted by the IPM in the first 100 years. (b) Simulated length distributions during a 9 year interval of time (approximately 1 period of the total density function).

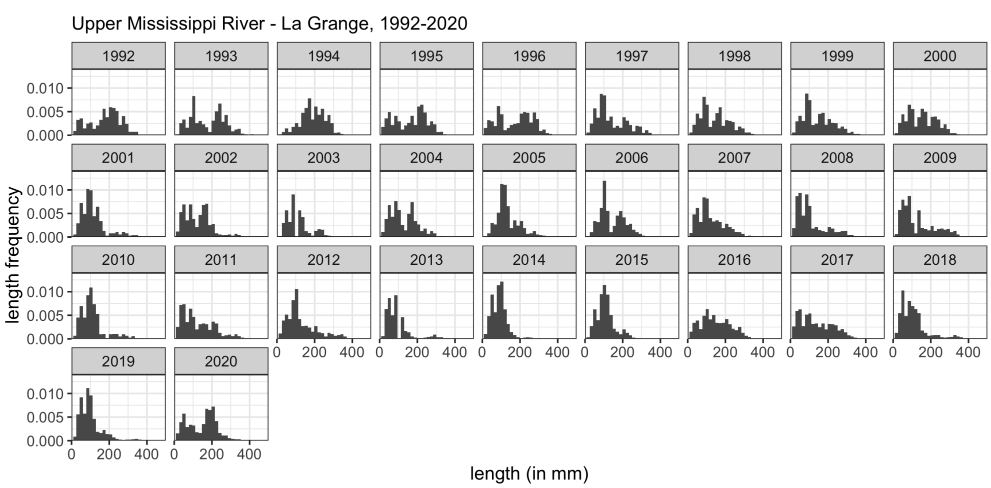


Figure 7: ~~(a)~~ Length frequencies of sampled gizzard shad in La Grange for each year, 1992-2020. ~~(b)~~

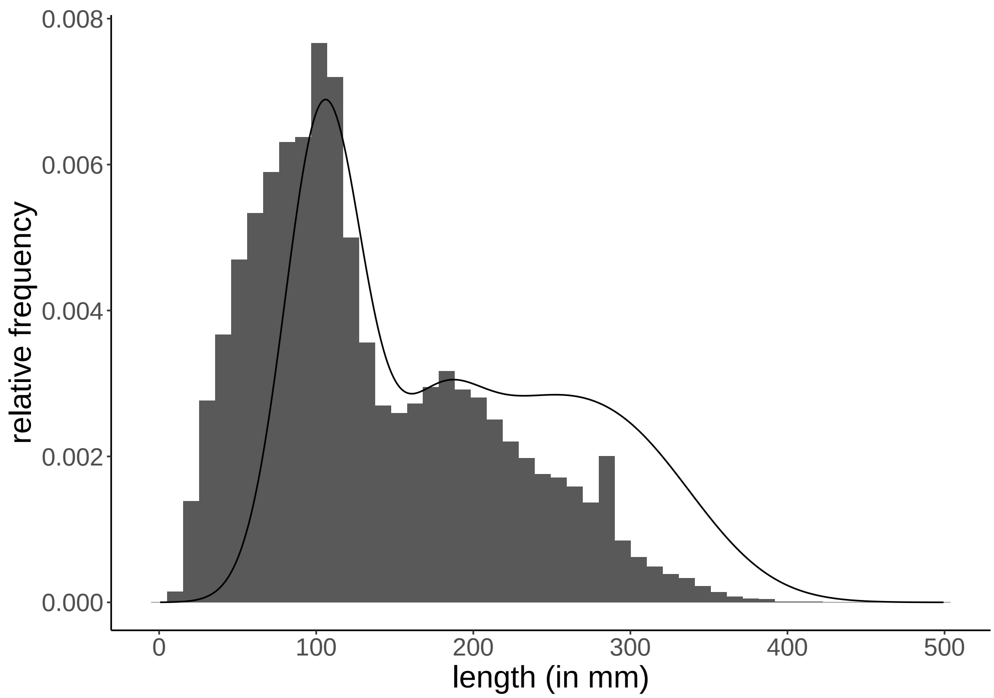


Figure 8: Overall length frequencies of gizzard shad sampled in La Grange Reach from 1992-2020 compared with the average (over 1 period) simulated length frequency.

age-1 cohort can be observed and is associated with the density-dependent survival function for age-0 fish (explained in Section 4.1.1).

5. Discussion

Gizzard shad are common in freshwater systems of North America where they contribute to the integrity of aquatic communities. Given this, it is important to understand how populations of this species vary with changing environmental circumstances, such as the occurrence of invasive species. Herein, we use both LTRM data and parameters gleaned from other empirical studies to develop an integral projection model for gizzard shad and test model outputs against patterns reported from a well-studied population of this species from the La Grange Reach of the Illinois River.

After fitting two adult survival parameters using LTRM data from the main channel of the Mississippi River, we compared a simulated length distribution with empirical data collected from the La Grange Reach of the Illinois River from 1992 to 2020. The resulting simulated length distributions (Figure 6b) reflected a number of the patterns observed in gizzard shad captured from the La Grange Reach over the same timeframe (Figure **??**). For example, the predicted transition from bimodal length distributions to a single peak in smaller gizzard shad in our simulations was reflected in the empirical data from 1996 to 2000. This trend was also observed from 2004-2008. It should be noted, that there were also discrepancies between model simulations and the empirical data. In particular, we did not notice a distinct, single peak in intermediate sized fish from field collections even though this was predicted by our model. Temporal and spatial variations in the La Grange Reach environment and their subsequent impacts on growth within the shad population may help explain why certain trends in our IPM outputs were not well represented in the field collections.

The average (over 1 period) simulated length frequency compared well with the overall length frequencies of gizzard shad sampled in La Grange Reach from 1992-2020 (Figure **??**). Our simulated size frequencies of gizzard shad captured the general trends seen in fish collected from the study site; however the model did predict a slightly higher density of adult lengths and fewer juvenile (smaller) lengths than in the empirical data. This may be explained by gear type and capture method which vary from site to site potentially introducing bias in the observed length distributions year to year. In addition, studies also suggest that environmental stochasticity and food variability may alter recruitment densities which are difficult to measure accurately ~~(Rose, 2000; Okamoto et al., 2016)~~ ~~.~~ (Michaletz, 2010; Okamoto et al., 2016; Rose, 2000). Future investigations may use spring water temperature measurements from the LTRM Water Quality component to modify the adult survival function (Equation 1) to be temperature dependent.

While our model uses the density of age-0 gizzard shad to affect the survival probability in their first year, we assumed constant viability at subsequent developmental stages, which may also be sensitive to density-related factors. That being said, there is little information available on the role that density plays in the life-history responses of adult gizzard shad. The location of the maximum length and the variation in the ~~of~~ length of new recruits recorded in the LTRM data suggests that there may be smaller age-0 fish in La Grange Reach than in the study location (Michaletz, 2017) used to parameterize the model.

Gaining an understanding of how length distributions of gizzard shad emerge under density-dependent survival in the age-0 class will serve as a foundation for investigating density effects at subsequent stages in the life cycle. In addition, this single-species model could also be expanded to incorporate interspecific interactions between gizzard shad and species such as invasive carp, which appear to negatively impact gizzard shad life-histories through competition for food resources.

6. Acknowledgments

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References

R. J. Pierce, T. E. Wissing, B. A. Megrey, Aspects of the feeding ecology of gizzard shad in acton lake, ohio, Transactions of the American Fisheries Society 110 (1981) 391–395.

M. J. Vanni, K. K. Arend, M. T. Bremigan, D. B. Bunnell, J. E. Garvey, M. J. Gonzalez, W. H. Renwick, P. A. Soranno, R. A. Stein, Linking landscapes and food webs: effects of omnivorous fish and watersheds on reservoir ecosystems, BioScience 55 (2005) 155–167.

D. B. Jester, B. L. Jensen, et al., Life history and ecology of the gizzard shad, *Dorosoma cepedianum* (le sueur) with reference to Elephant Butte Lake (1972).

M. E. Mather, M. J. Vanni, T. E. Wissing, S. A. Davis, M. H. Schaus, Regeneration of nitrogen and phosphorus by bluegill and gizzard shad: effect of feeding history, Canadian Journal of Fisheries and Aquatic Sciences 52 (1995) 2327–2338.

M. H. Schaus, M. J. Vanni, Effects of gizzard shad on phytoplankton and nutrient dynamics: role of sediment feeding and fish size, Ecology 81 (2000) 1701–1719.

D. D. Aday, R. J. H. Hoxmeier, D. H. Wahl, Direct and indirect effects of gizzard shad on bluegill growth and population size structure, Transactions of the American Fisheries Society 132 (2003) 47–56.

J. H. Thorp, M. C. Thoms, M. D. Delong, The riverine ecosystem synthesis: biocomplexity in river networks across space and time, River Research and Applications 22 (2006) 123–147.

G. L. Buynak, R. S. Hale, B. Mitchell, Differential growth of young-of-year gizzard shad in several kentucky reservoirs, North American Journal of Fisheries Management 12 (1992) 656–662.

M. T. Welker, C. L. Pierce, D. H. Wahl, Growth and survival of larval fishes: roles of competition and zooplankton abundance, Transactions of the American Fisheries Society 123 (1994) 703–717.

P. H. Michaletz, Overwinter survival of age-0 gizzard shad in missouri reservoirs spanning a productivity gradient: roles of body size and winter severity, Transactions of the American Fisheries Society 139 (2010) 241–256.

V. J. DiCenzo, M. J. Maceina, M. R. Stimpert, Relations between reservoir trophic state and gizzard shad population characteristics in alabama reservoirs, North American Journal of Fisheries Management 16 (1996) 888–895.

K. S. Irons, G. Sass, M. McClelland, J. Stafford, Reduced condition factor of two native fish species coincident with invasion of non-native asian carps in the illinois river, usa is this evidence for competition and reduced fitness?, Journal of Fish Biology 71 (2007) 258–273.

S. A. Love, N. J. Lederman, R. L. Anderson, J. A. DeBoer, A. F. Casper, Does aquatic invasive species removal benefit native fish? the response of gizzard shad (dorosoma cepedianum) to commercial harvest of bighead carp (hypophthalmichthys nobilis) and silver carp (h. molitrix), Hydrobiologia 817 (2018) 403–412.

M. J. Catalano, M. S. Allen, A size-and age-structured model to estimate fish recruitment, growth, mortality, and gear selectivity, Fisheries Research 105 (2010) 38–45.

M. J. Catalano, M. S. Allen, A whole-lake density reduction to assess compensatory responses of gizzard shad *Dorosoma cepedianum*, Canadian Journal of Fisheries and Aquatic Sciences 68 (2011) 955–968.

A. Bodola, The life history of the gizzard shad, *Dorosoma cepedianum*, in western Lake Erie, Ph.D. thesis, Doctoral dissertation. Ohio State University, Columbus, 1955.

A. Y. Then, J. M. Hoenig, N. G. Hall, D. A. Hewitt, H. editor: Ernesto Jardim, Evaluating the predictive performance of empirical estimators of natural mortality rate using information on over 200 fish species, ICES Journal of Marine Science 72 (2015) 82–92.

P. Michaletz, Variation in characteristics among gizzard shad populations: The role of impoundment size and productivity, Fisheries Management and Ecology 24 (2017) 361–371.

G. Jons, L. Miranda, Ovarian weight as an index of fecundity, maturity, and spawning periodicity, Journal of Fish Biology 50 (1997) 150–156.

M. R. Easterling, S. P. Ellner, P. M. Dixon, Size-specific sensitivity: applying a new structured population model, Ecology 81 (2000) 694–708.

S. P. Ellner, D. Z. Childs, M. Rees, et al., Data-driven modelling of structured populations: A practical guide to the Integral Projection Model., Springer International Publishing, Switzerland, 2016.

C. Merow, J. P. Dahlgren, C. J. E. Metcalf, D. Z. Childs, M. E. Evans, E. Jongejans, S. Record, M. Rees, R. Salguero-Gómez, S. M. McMahon, Advancing population ecology with integral projection models: a practical guide, Methods in Ecology and Evolution 5 (2014) 99–110.

M. Rees, D. Z. Childs, S. P. Ellner, Building integral projection models: a user's guide, Journal of Animal Ecology 83 (2014) 528–545.

J. Briggs, K. Dabbs, M. Holm, J. Lubben, R. Rebarber, B. Tenhumberg, D. Riser-Espinoza, Structured population dynamics: An introduction to integral modeling, Mathematics Magazine 83 (2010) 243–257.

R. A. Erickson, E. A. Eager, M. K. Brey, M. J. Hansen, P. M. Kocovsky, An integral projection model with yy-males and application to evaluating grass carp control, Ecological Modelling 361 (2017) 14–25.

B. Liao, X. Shan, C. Zhou, Y. Han, Y. Chen, Q. Liu, A dynamic energy budget–integral projection model (deb-ipm) to predict population-level dynamics based on individual data: a case study using the small and rapidly reproducing species *Engraulis japonicus*, Marine and Freshwater Research 71 (2019) 461–468.

J. W. White, K. J. Nickols, D. Malone, M. H. Carr, R. M. Starr, F. Cordoleani, M. L. Baskett, A. Hastings, L. W. Botsford, Fitting state-space integral projection models to size-structured time series data to estimate unknown parameters, Ecological Applications 26 (2016) 2677–2694.

N. Pollesch, K. Flynn, S. Kadlec, J. Swintek, S. Raimondo, M. Etterson, Developing integral projection models for ecotoxicology, Ecological Modelling 464 (2022) 109813.

H. Caswell, Matrix population models, volume 1, 2000.

B. M. Bolker, Ecological models and data in R, Princeton University Press, 2008.

K. L. Bouska, J. N. Houser, N. R. De Jager, J. Hendrickson, Developing a shared understanding of the upper mississippi river, Ecology and Society 23 (2018).

R. Maher, M. Griffin, K. Stauffer, J. Sternburg, J. Fischer, K. Hagerty, M. Hubbell, B. Johnson, K. McCain, K. Mitvalsky, T. Novak, K. Westlake, B. Clevenstine, J. Duyvejonck, J. Hauser, M. Jawson, B. Johnson, J. Stoner, G. Benjamin, D. Buntin, K. Mickelsen, Enhancing Restoration and Advancing Knowledge of the Upper Mississippi River, A Strategic Plan for the Upper Mississippi River Restoration Program 2015-2025, Technical Report, U.S. Army Corps of Engineers, 2015.

S. Gutreuter, R. Burkhardt, K. S. Lubinski, Long term resource monitoring program procedures [microform] (1995).

B. S. Ickes, R. W. Burkhardt, Evaluation and proposed refinement of the sampling design for the Long Term Resource Monitoring Program's fish component, Technical Report, Geological Survey La Crosse WI Upper Midwest Environmental Sciences Center, 2002.

P. Pepin, T. Shears, Y. De Lafontaine, Significance of body size to the interaction between a larval fish (*Mallotus villosus*) and a vertebrate predator (*Gasterosteus aculeatus*), Marine Ecology Progress Series (1992) 1–12.

W. H. Nowlin, R. W. Drenner, K. R. Guckenberger, M. A. Lauden, G. T. Alonso, J. E. Fennell, J. L. Smith, Gape limitation, prey size refuges and the top–down impacts of piscivorous largemouth bass in shallow pond ecosystems, Hydrobiologia 563 (2006) 357–369.

R. Burden, J. D. Faires, Numerical analysis 8th ed, Thomson Brooks/Cole (2005).

S. P. Ellner, M. Rees, Integral projection models for species with complex demography, The American Naturalist 167 (2006) 410–428.

S. Ramula, M. Rees, Y. M. Buckley, Integral projection models perform better for small demographic data sets than matrix population models: a case study of two perennial herbs, Journal of Applied Ecology 46 (2009) 1048–1053.

J. L. Williams, T. E. Miller, S. P. Ellner, Avoiding unintentional eviction from integral projection models, Ecology 93 (2012) 2008–2014.

R Core Team, R: A Language and Environment for Statistical Computing, R Foundation for Statistical Computing, Vienna, Austria, 2017. URL: `https://www.R-project.org/`.

K. A. Rose, Why are quantitative relationships between environmental quality and fish populations so elusive?, Ecological Applications 10 (2000) 367–385.

D. K. Okamoto, R. J. Schmitt, S. J. Holbrook, Stochastic density effects on adult fish survival and implications for population fluctuations, Ecology letters 19 (2016) 153–162.