Figure 1: Life cycle diagram and census points for pre-reproduction census of gizzard shad used in a density-dependent integral projection model.

1 # Graphical Abstract

2 **An integral projection model for gizzard shad (*Dorosoma cepedianum*) utilizing**

3 **density-dependent age-0 survival**

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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 established survival parameters using gizzard shad data collected from the 5 sites along the Mississippi River and validated 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

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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 collected from the Mississippi River. 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 test 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). In more eutrophic habitats, such as reservoirs, gizzard shad can reach high abunadances 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 (Di-Cenzo 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 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 (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. 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. 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 ($> 300,000$/year), there is evidence that intraspecific competition

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 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_b	probability that female spawns	0.90	

86 can be intense during early developmental stages in this species leading to density-dependent

87 mortality. The strength of competition may then subside as fish transition to feeding on

88 different food types during latter stages of development.

89 *2.2. Equations*

90 We used an integral projection model (IPM) to describe the life history of gizzard shad

91 in the Upper Mississippi River system (UMRS). IPMs were first introduced by Easterling

92 (Easterling et al., 2000), as a generalization of stage-based, matrix population models. Since

93 that time, IPMs have been used to describe a wide range of organisms (Ellner et al., 2016;

94 Merow et al., 2014; Rees et al., 2014), but have only recently be used to model fish populations

95 (Erickson et al., 2017; Liao et al., 2019; White et al., 2016; Pollesch et al., 2022). Fish are an

96 ideal group to investigate using this approach as many species have been well studied and

97 are therefore associated with robust information about life-history traits (i.e. growth and

98 reproduction). Gizzard shad are one such species and have been the subject of numerous

99 laboratory and field studies over the decades making it a logical choice for IPMs. In our

100 model specifically, we incorporate data from studies on 1) egg production in different size

101 classes of adults, 2) density-dependent survival of age-0 shad, and 3) length distributions of

102 gizzard shad in the UMRS that span nearly thirty years.

103 We assumed that variations among individual gizzard shad can be summarized by its

104 length z (in mm) ranging from the minimum possible length L to the maximum value U.

105 The state of the population at time t (in years) is described by the length distribution

106 $n(z,t)$. Specifically, for each time t, $n(z,t)$ is a smooth function of z such that the number

107 of individuals of length z in the interval $[a,b]$ at time t is $\int_a^b n(z,t)\,dz$. Between times t

108 and $t+1$, individual gizzard shad may grow, die, and produce offspring that vary in length

109 depending on the individuals current length (Figure 2).

110 *2.2.1. Growth and survival*

111 For an individual of length z at time t, $P(z',z)\Delta z$ is the probability that the individual

112 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

113 approximation that is valid for small Δz, and the exact probability is given by an integral

114 like the one above). We define $P(z',z) = s(z)G(z',z)$ where $s(z)$ is the annual adult survival

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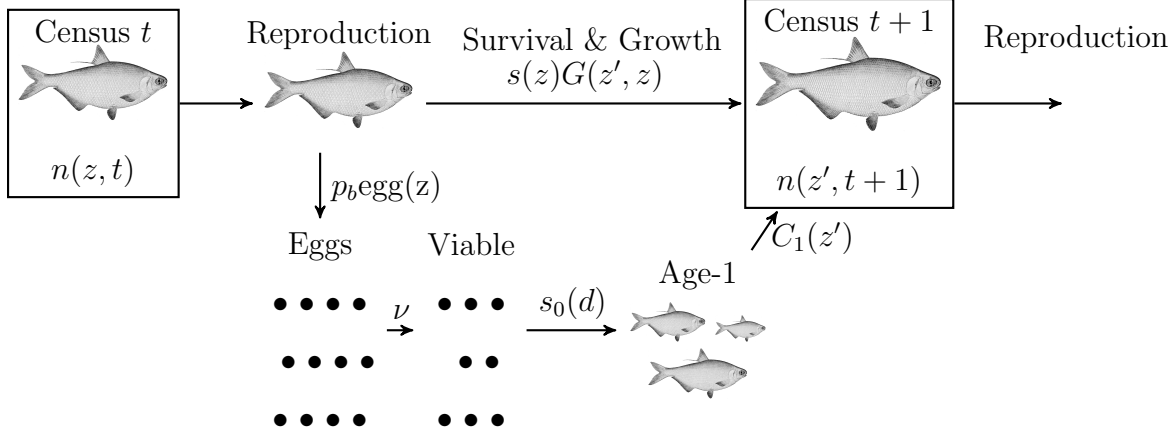
Figure 2: Life cycle diagram and census points for pre-reproduction census of gizzard shad.

probability and the growth $G(z', z)$ describes the annual length transitions. We assumed that 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).

We assumed that the growth function is a two-variable normal distribution centered around a modified von Bertalanffy function of the length at time t. The von Bertalanffy equation, commonly used to describe the length of a fish over time, is given by $z(t) = L_\infty \left(1 - e^{-K(t-t_0)}\right)$ where L_∞ is maximum asymptotic length, K is the growth rate, and t_0 is the initial time. The expected fish length the following year is:

$$z' = z(t+1) = L_\infty \left(1 - e^{-K(t+1-t_0)}\right) = L_\infty - L_\infty e^{-K(t-t_0)} e^{-K}$$
$$= L_\infty - (z(t) - L_\infty) e^{-K} = L_\infty \left(1 - e^{-K}\right) + z(t)e^{-K}.$$

Consequently, the growth kernel $G(z', z) = \text{Prob}(z' \mid z, L_\infty, K_g) = \text{NormalPDF}(\mu_g, \sigma_g)$ where $\mu_g = L_\infty \left(1 - e^{-K_g}\right) + z(t)e^{-K_g}$, K_g is the individual growth rate of gizzard shad, and σ_g is the standard deviation.

2.3. 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

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

where p_b is the probability of reproducing, $\text{egg}(z)$ is the mean number of eggs produced, 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).

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

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

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,

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

Finally, 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.

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

3. Methods

3.1. LTRM data and model parameterization

The integrity and health of the UMRS is assessed through Long Term Resource Monitoring (LTRM) which is overseen by a number of agencies including the U.S. Army Corp of Engineers, the United States Geological Survey, and the United States Fish and Wildlife Service. The goal of the LTRM is to track changes in the condition and/or stability of the UMRS ecosystem and participate in restoration activities throughout the region. 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 3a). 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 3b). 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.

To parameterize our model, we used gizzard shad data collected from the 5 sites along the Mississippi River. 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 increases with fish size (Jons and Miranda, 1997). The logistic parameters

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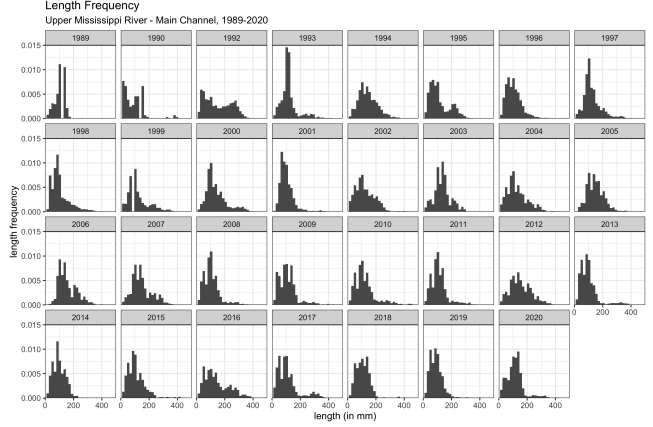
Figure 3: (a) The LTRM fish survey sites in the Upper Mississippi River system. (b) Length frequency of sampled gizzard shad in the main channel of the Upper Mississippi River system.

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 4a). Fish survival to age-1 was assumed to be dependent on the density of age-0 gizzard shad (Figure 4b). 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 in five Missouri reservoirs (Michaletz, 2010). To complete the recruitment process we assign a length to the recruited individuals by simulating a Gaussian random variable with mean μ_c and standard deviation σ_c. 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 (Bodola, 1955) provided the minimum
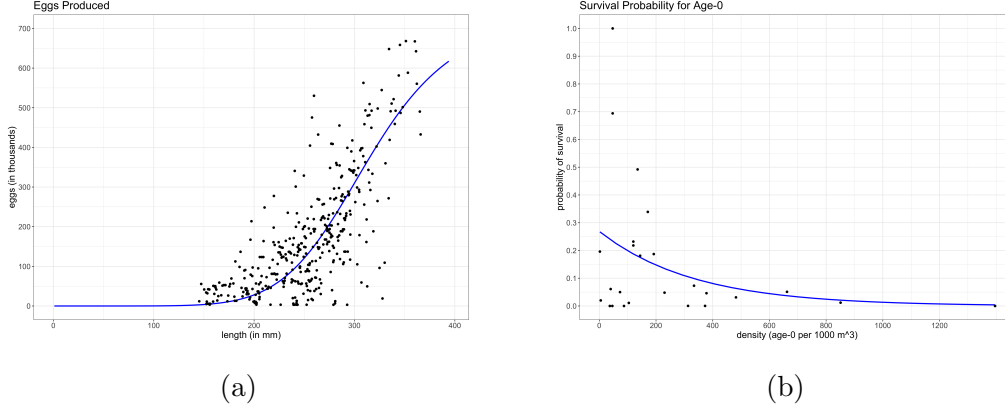
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Figure 4: (a) Mean number of eggs produced by female gizzard shad egg(z). Data from (Jons and Miranda, 1997). (b) Age-0 density-dependent survival function $s_0(d)$. Data from (Michaletz, 2010).

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 3b), 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 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

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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 density of gizzard shad observed 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

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

The model was coded in R (R Core Team, 2017) and the scripts are published on JP 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 the density of gizzard shad at subsequent developmental stages. 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 5).

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 7a) 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 7b illustrates the periodic length dynamics within the gizzard shad population during
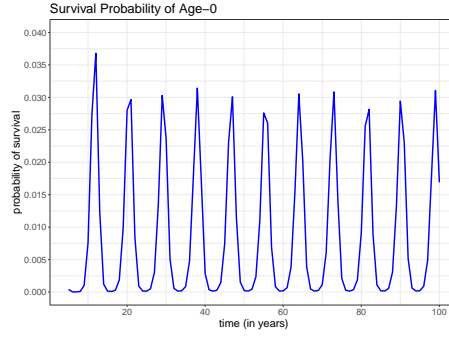
Figure 5

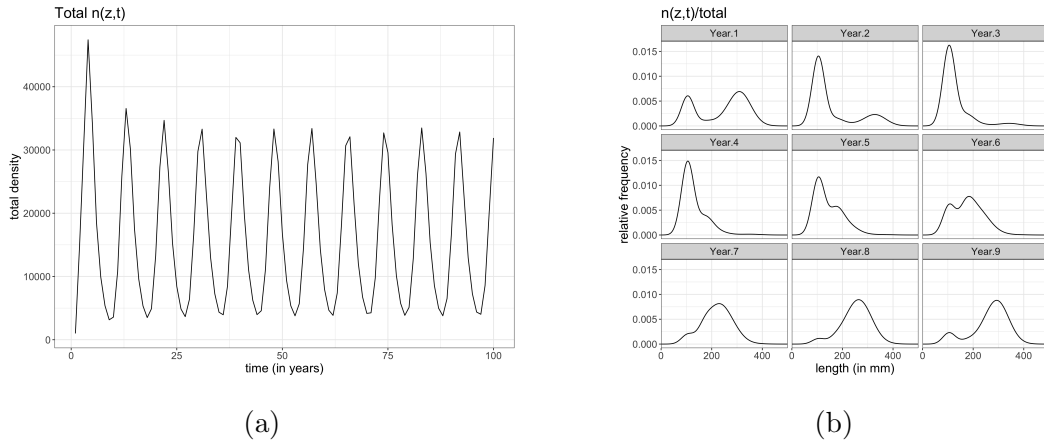Figure 6: Survival probability of age-0 gizzard shad.

(a)

(b)

Figure 7: (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).
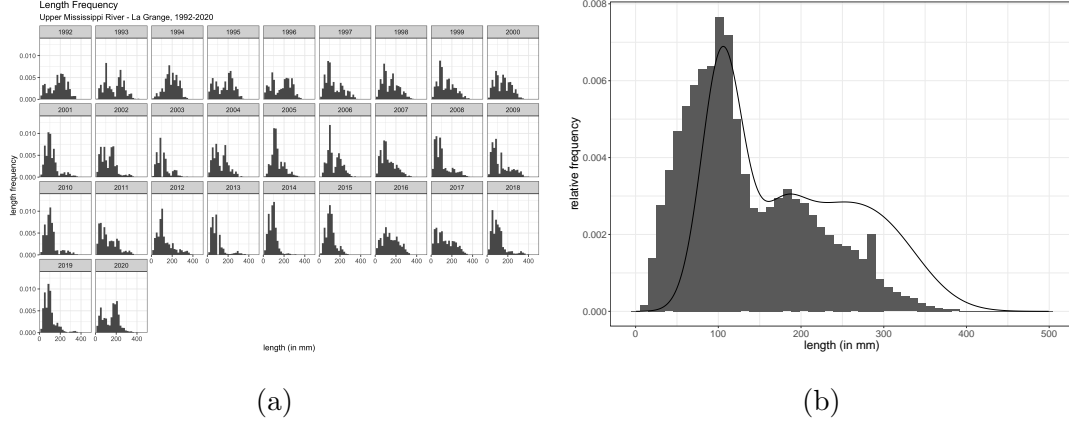
Figure 8: (a) Length frequencies of sampled gizzard shad in La Grange for each year, 1992-2020. (b) Overall length frequencies of gizzard shad sampled in La Grange Reach from 1992-2020 compared with the average (over 1 period) simulated length frequency.

a 9-year window of the periodic orbit. As a validation of the model, the simulated length distributions during a periodic orbit (Figure 7b) have similarities to fish lengths observed from the La Grange Reach (Figure 8a). In addition, the ebb and flow of the frequency of the 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 are important components of the 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 7b) reflected a number of the patterns observed in gizzard shad captured from the La Grange Reach over the same timeframe (Figure 8a).

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The average (over 1 period) simulated length frequency compares well with the overall length frequencies of gizzard shad sampled in La Grange Reach from 1992-2020 (Figure 8b). Peak frequencies are near the same lengths with the model predicting slightly more adults lengths and fewer juvenile lengths than the observations. 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 be difficult to measure accurately (Rose, 2000; Okamoto et al., 2016).

While our model uses the density of age-0 gizzard shad to effect the survival probability in their first year, we assumed constant viability which may be sensitive to the external factors mentioned above. In addition, 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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