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 30 years.

- We establish survival parameters using gizzard shad data collected from the Mississippi River and validate our model using empirical information collected from the La Grange Reach of the Illinois River.

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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 several 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 to 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 sources including Long Term Resource Monitoring (LTRM) upper Mississippi River restoration 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 because 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 indicate 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, population ecology, invasive species impact

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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 several 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 (*Sander vitreus*) and largemouth bass (*Micropterus salmoides*))(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 indicated 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 been conducted to address (DiCenzo et al., 1996) 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 effects 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 navigational pool of the Illinois River (specifically, the La Grange Reach). Results from this work indicate 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 (*Hypophthalmichthys molitrix*) and bighead carp (*Hypophthalmichthys nobilis*)).

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

Table 1: A summary of parameters, their biological meaning, and source for mean values. Adult survival parameters estimated from the Long Term Resource Monitoring (LTRM) dataset (LTRM, 2022) as indicated below.

Parameter	Meaning (units)	Mean	Source
Logistic survival probability function, $s(z)$			
$s_{\min}$	minimum survival	0.002	(Bodola, 1955)
$s_{\max}$	maximum survival	$1 - 8.871 K_g^{0.73} L_\infty^{-0.33}$	(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 (in 1/year)	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	

adults. Given the large number of eggs produced by shad females (often $> 100{,}000$/year) (Jons and Miranda, 1997), intraspecific competition can be intense during early developmental stages in this species leading to density-dependent mortality (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) (33 U.S. Code Section 652, 1986). 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 (Briggs et al., 2010; Ellner et al., 2016; Merow et al., 2014; Rees et al., 2014), but have only recently 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).

In a traditional matrix population model (Caswell, 2001), the annual abundance of gizzard shad can be separated by into a finite number of disjoint subgroups factors such as age, length, and developmental stage. 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 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 integral kernel. This kernel can be created from continuous functions for survival, growth,
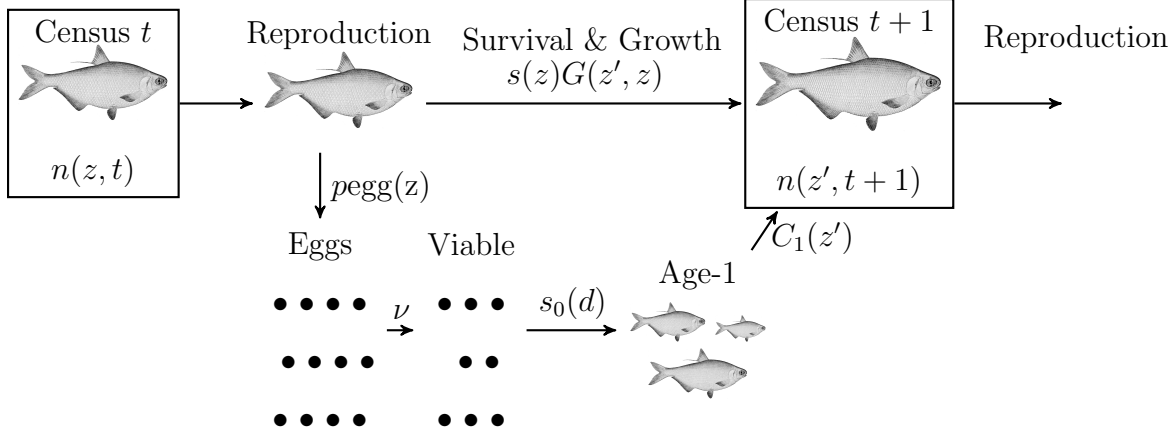
Figure 1: Life cycle diagram and census points for pre-reproduction census of gizzard shad.

and fecundity and therefore IPMs almost always require fewer estimated parameters (Briggs et al., 2010). When the integral kernel is applied to the current length distribution $n(z, t)$ 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' in the interval $[a', b']$ at time $t + 1$. 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

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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

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

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

131 *2.2.2. Fecundity*

132 $F(z', z)\Delta z$ is the number of new offspring in the length interval $[z', z' + \Delta z]$ present at
133 time $t + 1$, per length-z individual at time t. The fecundity kernel is

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

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

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

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

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

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

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

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

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

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2.3. Dynamical model

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

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

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

3. Methods

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

156 The LTRM element of the Upper Mississippi River Restoration monitors the UMRS to
157 provide an understanding of the system's ecology, resource changes, and inform management
158 (Bouska et al., 2018; Maher et al., 2015). In order to achieve this goal, numerous features
159 of the UMRS, such as aquatic vegetation, bathymetry, fish, land use/land cover, and water
160 quality are surveyed in particular reaches along the upper Mississippi River. LTRM fish
161 surveys are conducted at five locations along the main channel of the upper Mississippi
162 River (Pools 4, 8, 13, 26, and the Open River Reach) and at one location along the Illinois
163 River (La Grange Reach) (Figure 2a). Fish are captured using a multiple gear approach
164 (which includes netting and electrofishing) in order to monitor the responses and status
165 of fish communities along these two waterways over time (Gutreuter et al., 1995). Specific
166 capture methodologies, protocols, and modifications to the LTRM can be found in Gutreuter
167 et al. (1995), and Ickes and Burkhardt (2002) and the dataset can be access online(LTRM,
168 2022). In terms of gizzard shad, fish traits (such as total length) have been recorded since
169 1989 with approximately 3000 collections occurring per year along the Mississippi River
170 (Figure 2b). For the La Grange Reach of the Illinois River, gizzard shad have been sampled
171 and measured since 1990 with approximately 500 collections occurring per year.

172 To parameterize our model, we used gizzard shad data collected from the 5 sites (Pools 4,
173 8, 13, 26, and Open River Reach) along the Mississippi River (Figure 2a). We then validated
174 our model using empirical information collected from the La Grange Reach of the Illinois
175 River. We undertook this approach as the La Grange Reach is upstream from the Mississippi
176 River making it a more distinct location compared to the other sites.
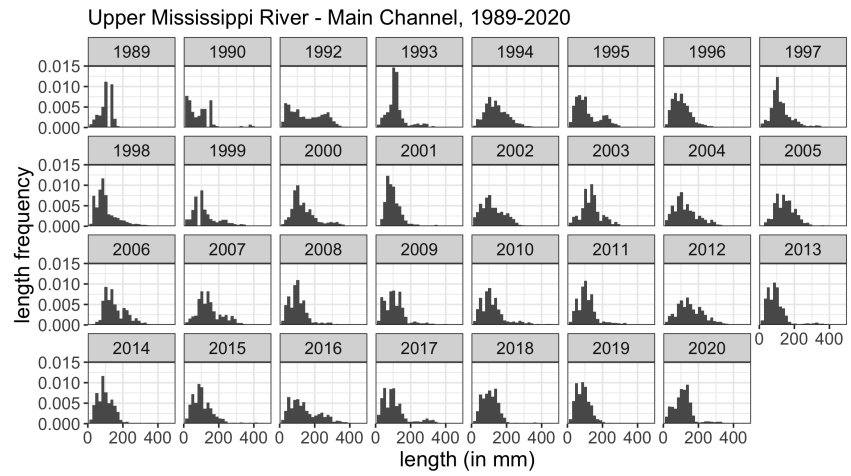
(a) (b)

Figure 2: (a) The LTRM fish survey sites in the UMRS. (b) Length frequency of sampled gizzard shad from all sites in the main channel of the UMRS (Pools 4, 8, 13, 26, and the Open River Reach).
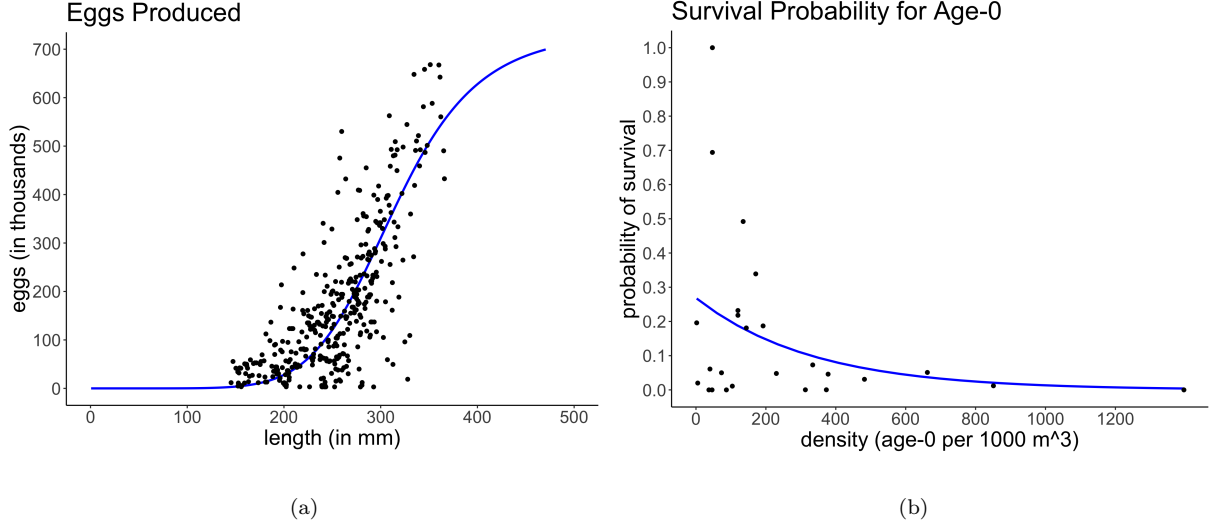
Figure 3: (a) Mean number of eggs produced by female gizzard shad egg(z). Data from (Jons and Miranda, 1997). (b) Age-0 density-dependent survival function $s_0(d)$. Data from (Michaletz, 2010).

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 shad 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_r and standard deviation 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 historical 1990-2020 LTRM dataset(LTRM, 2022) 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).

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The association between adult lengths and survival have not been well-resolved in gizzard shad leading us to make a few 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 Erie (Bodola, 1955) provided the minimum and maximum survival rate of adults.

We used a least squares method to estimate the α_s and β_s parameters that minimize the total square-distance between the pre-carp LTRM length distribution in the main channel of the UMRS (observed) and the predicted model distribution, $n(z,t)$, during an 8-year period occurring 100 years after initialization. Observed length distributions of gizzard shad sampled from the main channel of the Mississippi River (Figure 2b) have similar profiles, however some variation does exist. This may be attributed to changes in factors such as hydrology, water quality, and the occurrence of submersed, aquatic vegetation. We averaged the simulated length distributions over an 8-year period in order to reduce contributions from these environmental factors. 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 ($s_{\min}$) and lengths larger than α_s mm approach the maximum survival rate $s_{\max}$. This survival pattern has been reported for several 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)).

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4.1. Initial conditions

²²³   We assumed that the initial density of gizzard shad was $d_0 = 1487.93$ fish, the average
²²⁴ annual density of gizzard shad caught with all gear types represented in the LTRM fish
²²⁵ program in La Grange Reach from 1993-2020. The probability of an individual being length
²²⁶ z at time $t = 0$ was assumed to be normally distributed with mean $0.5L_\infty$ and standard
²²⁷ deviation σ_g. As a result, we initialized our model with length distribution

$$n(z, 0) = d_0 \text{Norm}(0.5L_\infty, \sigma_g) = 1487.93 \text{Norm}(197.15, 25). \tag{6}$$

²²⁸   The model was coded in R (R Core Team, 2017), and the scripts are published on JP's
²²⁹ GitHub page `https://github.com/jppeirce`.

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

²³¹   In the simulated solutions to the IPM, the density of age-0 fish are strongly influenced by
²³² the density of gizzard shad at subsequent developmental stages. When adult densities are
²³³ large, there may be more fish of longer lengths that can produce a greater number of eggs.
²³⁴ Assuming that there are not additional food resources and egg/larval predators present, a
²³⁵ greater number of eggs leads to a higher density of age-0 fish and reflectively a reduction in
²³⁶ the survival to age-1. If reduced survival continues over subsequent years, the overall density
²³⁷ of fish within the population may decline and result in a smaller number of longer length
²³⁸ fish that are reproducing. Fewer fish spawning could result in a smaller age-0 class which, in
²³⁹ turn, could enhance survival probability in this cohort (through reduced competition). We
²⁴⁰ would then expect the overall density of fish to increase over the following years, until large
²⁴¹ numbers of eggs are again produced by larger, adult fish. This oscillatory pattern is reflected
²⁴² 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

²⁴⁴   The total number of gizzard shad in our simulation reached a stable periodic orbit (Figure
²⁴⁵ 6a) within 50 years. After simulating an additional 50 years, we fit a periodic function to
²⁴⁶ the annual density of gizzard shad and determined the period of approximately 8.74 years.
²⁴⁷ Figure 6b illustrates the periodic length dynamics within the gizzard shad population during
²⁴⁸ a 9-year window of the periodic orbit. As a validation of the model, the simulated length
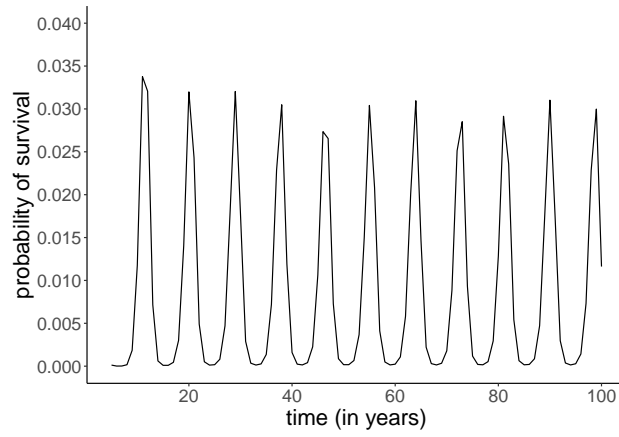
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Figure 4

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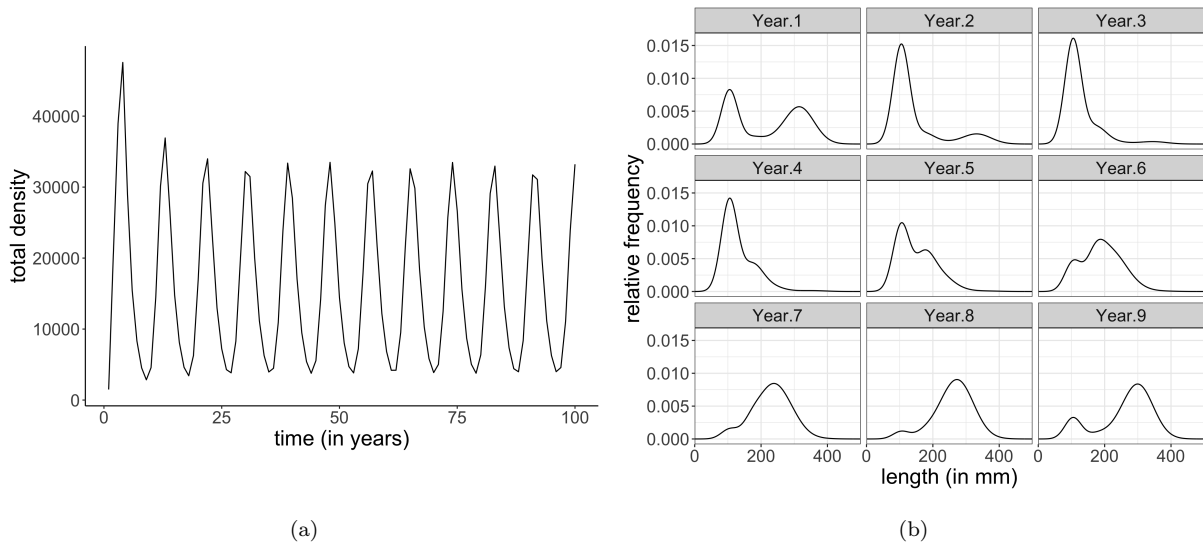

(a)

(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 an interval of time (approximately 1 period of the total density function).
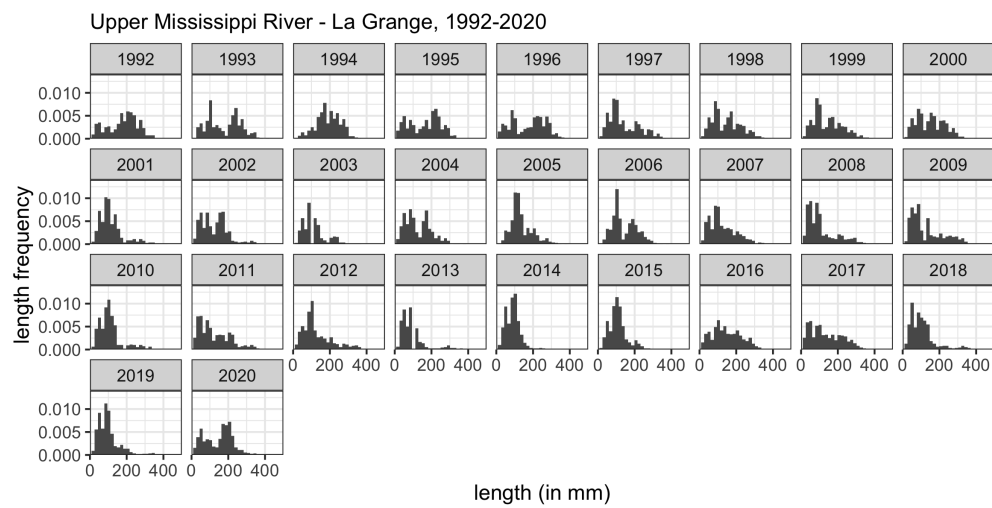
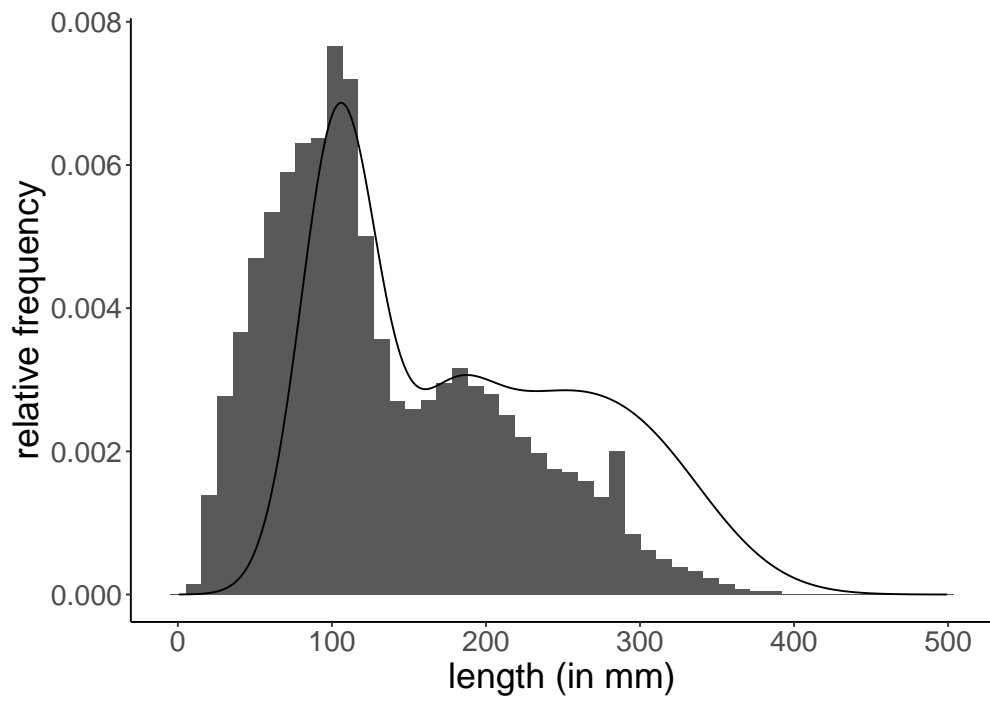Figure 7: Length frequencies of sampled gizzard shad in La Grange for each year, 1992-2020.

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.

distributions during a periodic orbit (Figure 6b) have similarities to fish lengths observed from the La Grange Reach (Figure 7). 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 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 many of the patterns observed in gizzard shad captured from the La Grange Reach over the same timeframe (Figure 7). 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 the subsequent effect 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 8). 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

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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 indicate that environmental stochasticity and food variability may alter recruitment densities, which are difficult to measure accurately (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.

Although 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. However, currently 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 length of new recruits recorded in the LTRM data indicates 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 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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