

Graphical Abstract

An integral projection model for Gizzard Shad utilizing density-dependent age-0 survival

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Highlights

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- Research highlight 1

- Research highlight 2

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Abstract

Keywords:

1. Introduction

Gizzard shad are a common freshwater fish throughout the central and eastern portions of North America, occupying both lotic and lentic habitats (Pierce et al., 1981; Vanni et al., 2005). Within these areas, gizzard shad play a number of important roles in the freshwater community. 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). Second, because detritus serves as an important food source throughout much of gizzard shad development (i.e. from the age-0 stage onward), these fish translocate 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 comprises gizzard shad diets makes this species an important link between aquatic and terrestrial ecosystems through nutrient inputs (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.

[NEED] Paragraph about density effect on fish species in Upper Mississippi River. While present density of gizzard shad may influence the growth and survival of adults, we emphasize our present investigation the role density has in age-0 survival.

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 the population dynamics of the particular species. 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 dynamics reported for this fish species in the La Grange Station along the Illinois River. The model itself could be an important tool for predicting gizzard shad popula-

tion responses to changing environmental conditions, including those mediated through species invasions (i.e. silver and big-head carp).

2. Model Development

2.1. Gizzard shad life history

The American gizzard shad (*Dorosoma cepedianum*) is a laterally compressed, deep-bodied fish that inhabits numerous fresh and brackish waterbodies across North American. This species tends to reach its highest abundance in eutrophic systems (such as reservoirs) where it often comes to dominate fish assemblages. In these habitats, gizzard shad serve as an important trophic link between primary producers and consumers. Mating within this species can be temperature-dependent, but tends to occur between May and June. 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 can be intense during early developmental stages in this species. However, the strength of competition can subside as fish transition to different food types during latter stages of development.

2.2. Equations

We use an integral projection model to describe the life history of gizzard shad in the Upper Mississippi River (UMR) system. Integral projection model (IPM) were introduced by Easterling (Easterling et al., 2000), as a generalization of stage-based, matrix population models. IPMs have been used to describe a wide range of organisms (Ellner et al., 2016; Merow

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	0.10	(Kirk and Socha, 2003)
s_{\max}	maximum survival	0.70	(Kirk and Socha, 2003)
α_s	inflection point	modeled	(Soballe et al., 1995)
β_s	slope	-5	
Growth function, $G(z, z')$			
L_{∞}	maximum length (in mm)	394.30	(Catalano and Allen, 2010)
K_g	growth rate	0.60	(Catalano and Allen, 2010)
σ_g	growth standard deviation	10	(Erickson et al., 2017)
Normal distribution of length of age-1, $C_1(z')$			
μ_r	mean length of recruitment (in mm)	112	(Bodola, 1955)
σ_r	standard deviation of length	40	(Bodola, 1955)
Eggs produced, $\text{egg}(z)$			
egg_{\max}	maximum number of eggs produced	742,094	Estimated from (Jons and Miranda, 1997)
α_e	inflection point	314.44	Estimated from (Jons and Miranda, 1997)
β_e	slope	-7.12	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	

et al., 2014; Rees et al., 2014) and are a natural choice for gizzard shad since many aspects of their life cycle have been studied. Specifically, functions used in our model incorporate data from studies on egg production and adult size as well as the survival of the age-0 stage and density.

We assume that variations among individual gizzard shad can be summarized by its length z (in mm) ranging from the minimum possible length L to the maximum value U . The state of the population at time t (in years) is described by the length distribution $n(z, t)$. Specifically, for each time t , $n(z, t)$ is a smooth function of z such that the number of individuals of length z in the interval $[a, b]$ at time t is $\int_a^b n(z, t) dz$.

Between times t and $t + 1$, individual gizzard shad may grow, die, and produce offspring that vary in length all depending on the individuals current length (Figure ??). At time $t + 1$ the population will have a length distribution defined by $n(z, t + 1)$. For our model, we partition the life cycle of gizzard shad into two stages: 1) survival and growth, and 2) reproduction. 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). Similarly, $F(z', z)\Delta z$ is the number of new offspring in the interval $[z', z' + \Delta z]$ present at time $t + 1$, per length- z individual at time t .

2.2.1. Growth and survival

We define $P(z'z) = s(z, T)G(z', z)$ where $s(z)$ is the adult annual survival probability and $G(z', z)$ describes the annual length transitions. We assume that the survival function is a

logistic function,

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

with four parameters: the minimum survival rate s_{\min} ; a maximum survival rate, s_{\max} ; and intercept parameter, α_s ; and a slope parameter, β_s (Bolker, 2008).

We assume 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 $z(t) = L_{\infty}(1 - e^{-K(t-t_0)})$ where L_{∞} is maximum asymptotic length, K is the growth rate, and t_0 is the initial time. The expected length in the next year

$$\begin{aligned} z' = z(t + 1) &= L_{\infty}(1 - e^{-K(t+1-t_0)}) = L_{\infty} - L_{\infty}e^{-K(t-t_0)}e^{-K} \\ &= L_{\infty} - (z(t) - L_{\infty})e^{-K} = L_{\infty}(1 - e^{-K}) + z(t)e^{-K}. \end{aligned}$$

Consequently, we assume that $G(z', z) = \text{Prob}(z' | z, L_{\infty}, K_g) = \text{NormalPDF}(\mu_g, \sigma_g)$ where K_g is the individual growth rate, $\mu_g = L_{\infty}(1 - e^{-K_g}) + z(t)e^{-K_g}$, and σ_g is the standard deviation.

2.3. Fecundity

We define the fecundity kernel,

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

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, $s_0(n(z, t))$ 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).

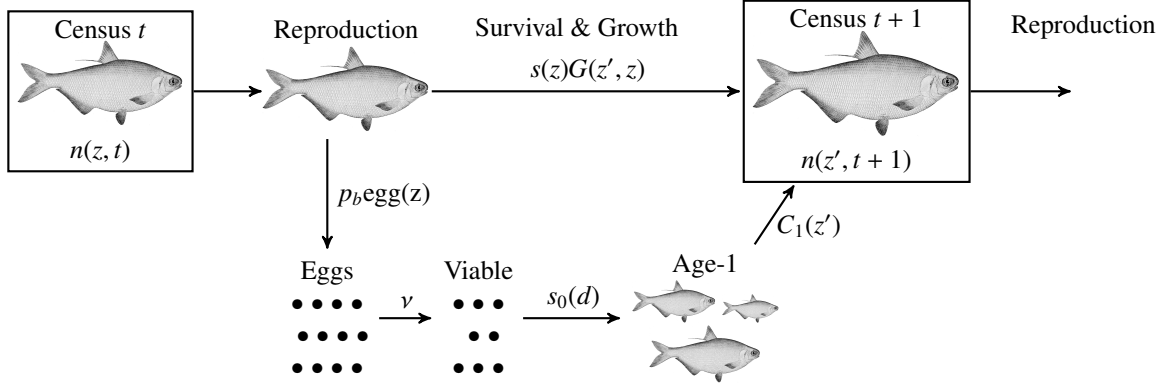


Figure 1: Life cycle diagram and census points for pre-reproduction census of gizzard shad.

We assume that the mean number of eggs produced by females of a certain length is a three-parameter logistic function,

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

The probability of survival of gizzard shad during their first year may depend on many factors (Michaletz, 2010) such as mean temperature, mean total length, the present density of age-0 fish. In this study, we focus only on the density factor and define the probability of survival of age-0 fish as the exponential function

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

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 ,

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

Finally, after computing the total number of viable eggs produced and survive to age-1 fish, we multiply this number 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 ,

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

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. Study Area and LTRM Data Collection

The 129 km long La Grange Reach is located between La Grange Lock and Dam (L&D) and Peoria L&D on the Illinois River, U.S., and is about midway between the Mississippi

River and Lake Michigan. The Illinois River is a major tributary of the Mississippi River, draining nearly two-thirds of the state of Illinois. Along with the main channel of the UMR, the fish community of La Grange Reach has been monitored by the Long-term Resource Monitoring Program (LTRMP) from 1990 to the present, with approximately 500 random collections each year from 15 June to 31 October. The LTRMP fish collection methodology included a multiple gear approach (netting and electrofishing) to monitor the general fish community of the UMR system through time (Gutreuter et al., 1995). The total lengths were recorded for all fishes captured. Methodology, protocols and modifications to the LTRMP can be found in Gutreuter et al. (1995), and Ickes and Burkhardt (2002).

The location of La Grange Reach was the primary reason it was chosen for the methods part of our study. Its location has two important features. We parameterized the IPM using data from the main channel of the UMR. As a part of Illinois River and UMR, La Grange Reach is upstream from the main channel (should we include figure/map?). The proximity to, but relative independence from, the main channel, made it a good choice. Secondly, La Grange Reach is a large pool between the main channel of the Mississippi River and Lake Michigan. In recent years, there have been concerns with the threatening introduction of invasive carp to the Great Lakes. Consequently, the impact of invasive carp on the native fish populations in the pools leading to the Great Lakes have received an elevated level of attention. Understanding the population dynamics of gizzard shad, may in the future make it easier to assess the impacts carp has on native fish populations.

3.2. Parameterization

The parameters for the growth function were chosen as the mean values published on a study of gizzard shad located in large impoundments (Michaletz, 2017). The survival rate of adults gizzard shad dependent on their length is not well documented and required us to make some additional modeling assumptions. An investigation of gizzard shad in Lake Erie (Bodola (1955)) provided the minimum and maximum survival rate of adults. In many of the river domains included in our analysis, invasive carp are also present (CITE LTRM FISH

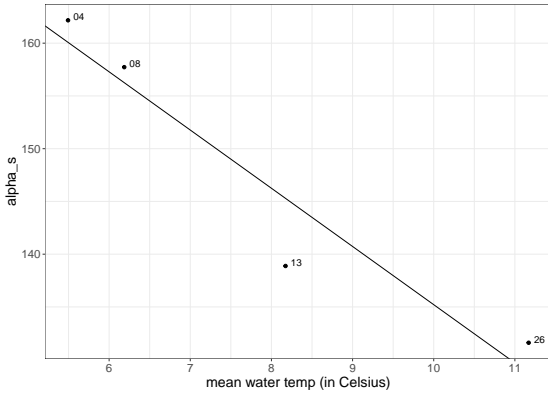


Figure 2: Inflection point parameter for adult survival as a function of the mean water temperature (March 15 - April 15). Points are identified by Pool number within the UMR. Linear regression model is also shown.

DATA). Invasive carp is a well-studied invasive species along the Mississippi and Illinois Rivers. Assuming the resources that effect survival are similar, we use the published (Erickson et al., 2017) slope parameter, β_s , for the gizzard shad population. As good practice, we attempted to reduce the number of non-observable parameter estimates and we elected to determine the inflection point of the adult survival function from mean Spring-time water temperature.

3.2.1. Inflection Point of the Adult Survival Function

We used a least squares method to find the inflection parameter, α_s , that minimizes the distance between the model equilibrium length frequency distribution (at $t = 300$ years) and the observed frequency from the LTRM fish dataset for each of the four pools within the main channel of the UMR. Using the LTRM water quality dataset, we associated each pool with the average water temperature T (in $^{\circ}\text{C}$) during the early Spring period March 15 - April 15. The relationship between inflection parameter and temperature is illustrated in Figure 2 and is modeled using the linear regression line $\alpha_s = -5.518T + 190.391$ ($R^2 = 0.871$). Finally, we applied the linear model to the average early spring water temperature in La Grange, $T = 10.19^{\circ}\text{C}$, to find $\alpha_s(10.19) = 135.55$.

3.2.2. Fecundity and recruitment

Maturity of female gizzard shad corresponds with lengths of approximately 140 mm and the number of eggs produced increase as the females increase in size (Jons and Miranda, 1997). The mean eggs produced per female is described by a three-parameter logistic function (see Figure 1) whose parameters are estimated from data provided in Figure 1a. of (Jons and Miranda, 1997).

The survival to age-0 is assumed to be dependent on the density of age-0 gizzard shad (Figure 3b). We estimated the exponential parameters using data provided in Table 2 of (Michaletz, 2010). The parameters for the size distribution of age-1 fish were gleaned from a study of gizzard shad located in large

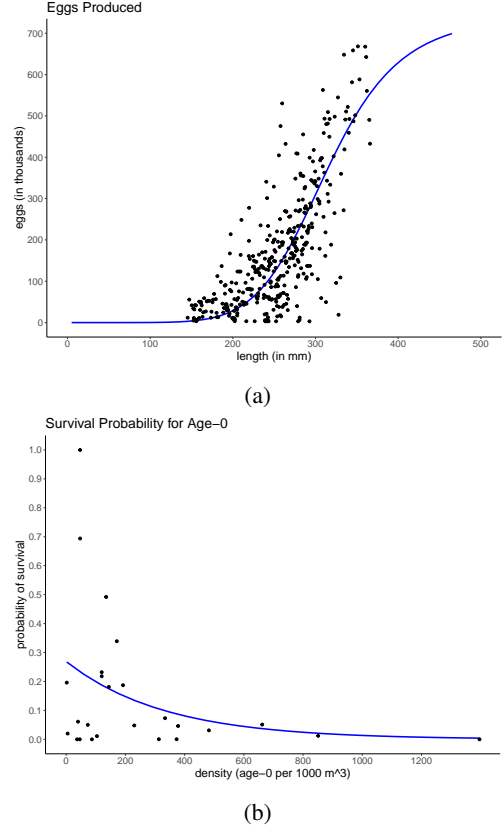


Figure 3: (a) Graph of $\text{egg}(z)$. Data from (Jons and Miranda, 1997). (b) Graph of $s_0(d)$. Data from (Michaletz, 2010).

impoundments (Michaletz, 2017) and the historic 1990-2020 LTRMP dataset of gizzard shad in La Grange Reach.

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 400 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 $d_0 = 964.7$, the annual average density of gizzard shad observed in La Grange Reach from 1993-2019. 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 $\sigma_0 = 30$, similar to observations (1990-2020) in LTRMP dataset. As a

result, we initialized our model with

$$n(z, 0) = d_0 \text{Norm}(0.5L_\infty, \sigma_0) = 964.7 \text{Norm}(166, 30). \quad (6)$$

The model is coded in R (R Core Team, 2017) and the scripts are published on JP github page <https://github.com/jppeirce>.

4.1.1. Comparison with the LTRM La Grange dataset

The only data used in the model from La Grange Reach was the average water temperature during the early Spring period March 15 - April 15 (used to determined the adult survival inflection point). The total number of gizzard shad in our simulation reached a stable equilibrium (Figure 4a) within 200 years and, more relevantly, the length distribution at that equilibrium compares favorably with the observations from La Grange found in the LTRMP fish dataset (Figure 4b). We notice that the peak frequencies are near the same length with the model predicting slightly more adults lengths and fewer juvenile lengths than the observations. The location of the maximum in the LTRM data, corresponding to new recruits, suggests that there may be smaller age-0 fish than in study from (Michaletz, 2017) that was used in the model psrameterization.

4.1.2. Survival and Relative Growth

The dependence on survival of next generation of age-0 fish on the present density of age-0 fish strongly influences the density, at all ages, of gizzard shad within the population. When the fish density is large, there may be more fish at longer lengths and consequently a greater number of eggs produced. More eggs leads to a higher density of age-0 fish and reflectively a reduction in the survival to age-1. If this reduced survival continues for a few years, the overall density of fish may decline and there may not be as many larger fish reproducing. If fewer eggs are spawned, there are less age-0 fish and the reduced density leads to a better survival probability. For these years we would expect the overall density to increase. This cycle of oscillation continues, reflected in our model by the time-dependent survival probability of age-0 (Figure 5a) and the relative growth rate

$$\lambda(t) = \int_L^U n(z, t+1) dz \Bigg/ \int_L^U n(z, t) dz$$

(Figure 5b).

4.2. Time Evolution of Initial State

Starting with $n(z, 0)$ defined by Equation 6, we computed the length distribution for 3 years. In year 1, there are two relative maximum frequencies corresponding to the recruitment of age-1 fish and the survival of the adults.

4.2.1. Dynamics of the Age-1 Over Time - Fixed Frame

The greatest value of $n(z, 1)$ during year one is centered at the mean length of recruitment. In the following years, the decrease in the maximum value is a result of the two factors: the reduction in the density of adults and the density-dependent survival function for age-0 fish. Starting in year 1, there is a reduction

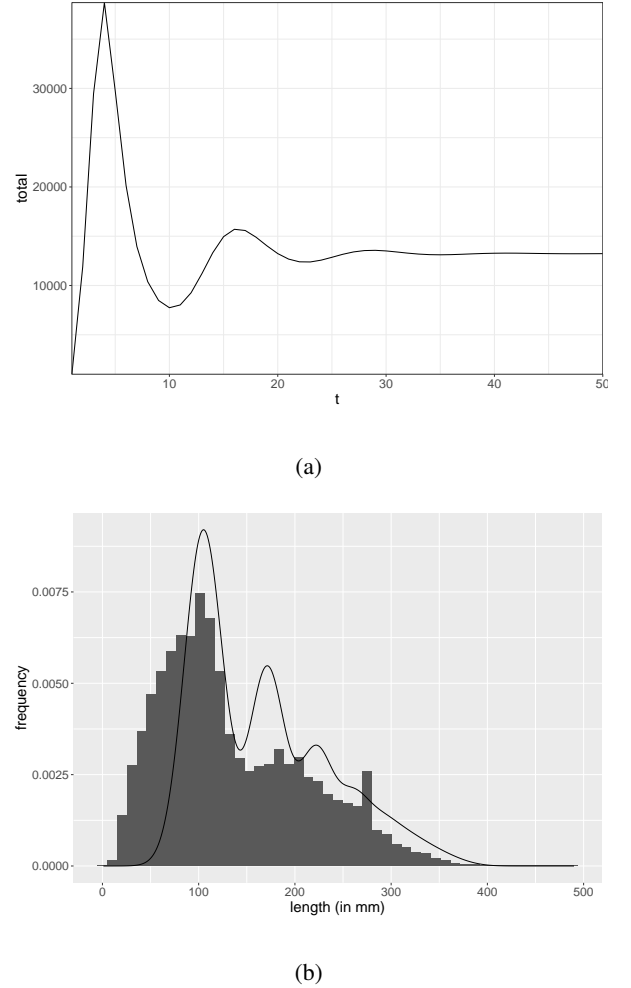
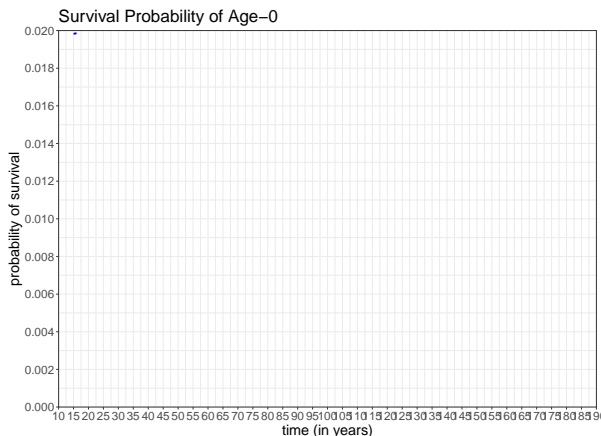
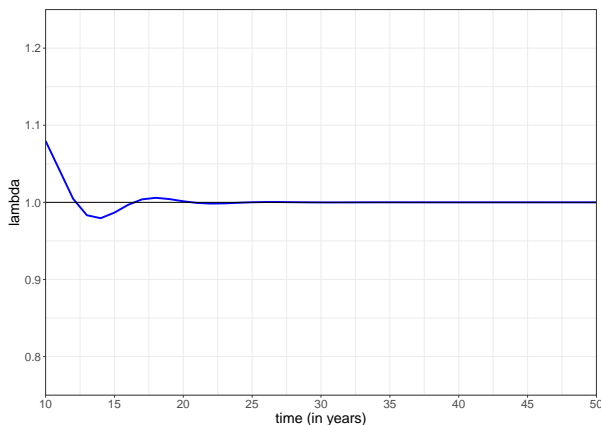


Figure 4: (a) The total number of gizzard shad in La Grange Reach predicted by IPM for first 50 year. (b) LTRMP observations of gizzard shad in La Grange Reach (histogram with 50 len) compared with the IPM length frequency at equilibrium ($t = 50$ years)



(a)



(b)

Figure 5: (a) Survival of age-0. (b) Relative growth rate of gizzard shad density

in the number of egg-producing adults (lengths above 140 mm) compared with the initial population. From Figure 3a, fewer longer adults implies fewer eggs produced. The eggs that are produced, however, may have a greater chance of survival to the age-1 census (Figure ??). This is evident in the increase in density of recruits (NEED TO SHOW?) but is illustrated in lower frequency of recruits (Figure 6b)

[Theme: Dynamics of a cohort - moving frame] Figure XXX also demonstrates the growth in gizzard shad population. The peak length frequency of age-1 fish in $n(z, 1)$ near $z = 105$ mm is seen as a peak in $n(z, 2)$ near 160 mm, and again as a peak in $n(z, 3)$ at about 210 mm. MORE DISCUSSION NEEDED

5. Discussion

We compare a simulated length distribution with U.S. Geological Survey (USGS) Long-Term Resource Monitoring (LTRM) data from the La Grange Reach of the Illinois River from 1992-2019. The La Grange Reach of the Illinois River is a 125 km segment of the lower Illinois River between the La Grange Lock and Dam at RKM 129 and the Peoria Lock and Dam at RKM 254. It is characterized by a wide floodplain surrounding the main channel and a mosaic of side channels, fully connected backwaters, and semi-connected backwaters.

[Comparison of Frequency plots vs Simulation - Similarities] In these data, we see similar patterns as displayed in Figure XXX. Specifically, from years 2010-2012...

[Comparison of Frequency plots vs Simulation - Differences]

[Possible explanation of differences and future direction]

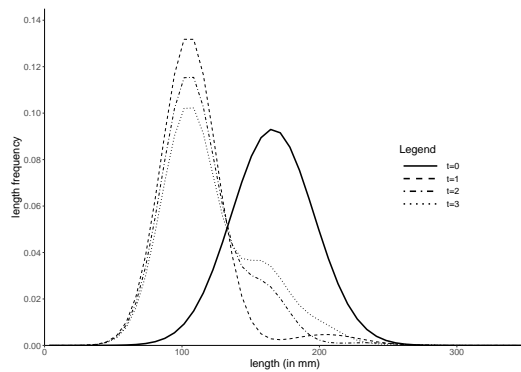
[More future direction - two species model]

6. Acknowledgements

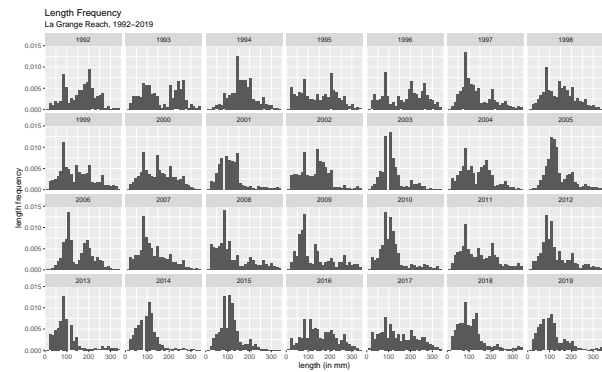
These data are a product of the U.S. Army Corps of Engineer's Upper Mississippi River Restoration Program (UMRR) Long Term Resource Monitoring (LTRM) element implemented by the U.S. Geological Survey in collaboration with the five Upper Mississippi River System (UMRS) states of Illinois, Iowa, Minnesota, Missouri, and Wisconsin. The U.S. Army Corps of Engineers (Corps) provides guidance and has overall program responsibility. In addition, research was supported by NSF-DMS Grant #1852224, ?REU Site: Ecological Modeling of the Mississippi River Basin?.

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.



(a) Simulated frequency of lengths of Gizzard Shad. Initial density and $N=xxx$



(b) Simulated frequency of lengths of Gizzard Shad. Initial density and $N=xxx$

Figure 6: (a) Survival of age-0. (b) LTRM Data from La Grange Reach 1992-2020

- 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. P. Kirk, R. C. Socha, Longevity and persistence of triploid grass carp stocked into the santee cooper reservoirs of south carolina, *Journal of Aquatic Plant Management* 41 (2003) 90–92.
- D. M. Soballe, R. Burkhardt, K. Lubinski, R. Burdis, T. Clemment, J. Fischer, L. Hodge-Richardson, L. Conaway, J. Frazier, D. Gould, M. Steuck, E. Ratcliff, M. Sitzes, S. Stenzel, R. Wright, Long term resource monitoring program procedures: Water quality monitoring, U.S. Geological Survey, Biological Resources Division, Upper Midwest Environmental Sciences Center, La Crosse, Wisconsin (1995).
- 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.
- 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.
- 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.
- G. Jons, L. Miranda, Ovarian weight as an index of fecundity, maturity, and spawning periodicity, *Journal of Fish Biology* 50 (1997) 150–156.
- 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.
- 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*. Cham: Springer (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.
- B. M. Bolker, *Ecological models and data in R*, Princeton University Press, 2008.
- 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. Michaletz, Variation in characteristics among gizzard shad populations: The role of impoundment size and productivity, *Fisheries Management and Ecology* 24 (2017) 361–371.
- 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/>.