**Contract #SI40613**

**FINAL REPORT**

# Compensatory changes in gizzard shad growth, maturity, and juvenile survival following experimental removal at Lake Dora, Florida, and implications for future biomanipulation

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**Period of Study:** 1 November 2007 to 30 September 2009

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**Project Title:**    **Assessing Effects of Gizzard Shad Removal on Gizzard Shad Population**

**Dynamics in Florida Lakes**

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## EXECUTIVE SUMMARY

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Gizzard shad (Dorosoma cepedianum) have been harvested from the Harris Chain of Lakes since the mid-1990s as a lake restoration technique to reduce internal nutrient cycling and ultimately improve water clarity.  Compensatory density-dependent responses (e.g., increased growth and juvenile survival, decreased length at maturity) by gizzard shad in response to harvesting could reduce the effectiveness of removals.  Catalano et al. (2007) conducted an analysis of compensatory gizzard shad responses following the 2005-2006 Lake Dora harvest and evaluated the potential effectiveness of the removals for reducing population biomass. Catalano et al.'s (2007) analysis was based on three years (2005-2007) of gizzard shad population data.  The short time series made it difficult to estimate compensatory responses because post-removal cohorts could not be followed for more than two years and age-1 fish were not fully vulnerable to sampling gear.  Additional gizzard shad population data were collected at Lake Dora in 2008 and 2009, and we used those data along with the original data set to conduct a new set of analyses.  These new analyses revisited Catalano et al.'s (2007) report and also used the data in a stock assessment framework to obtain maximum likelihood estimates of the strength of compensation for gizzard shad at Lake Dora.  Specifically, we evaluated changes in growth, maturity, and juvenile survival as mechanisms for compensation following the experimental removal at Lake Dora.

Growth and length at maturity did not differ at Lake Dora following gizzard shad removal and were not related to population density across Lakes Dora, Eustis, and Harris.  The 2005-2006 Lake Dora gizzard shad removal reduced spawner biomass (biomass of mature gizzard shad) by 72% of the unfished level in 2006 However, age-1 recruitment in 2007 (2006

cohort) <u>was near the long-term average for Lake Dora.  This suggest that juvenile ($<$ age 1)</u> <u>survival increased in 2006 in response to the removal</u> because no similar <u>increases in survival</u> <u>were observed in 2006 at unharvested control Lakes Eustis and Harris</u>. We conducted a spawner-recruit analysis using spawner biomass and recruitment estimates from the three lakes and found that juvenile survival could increase up to seven-fold at low spawner abundance relative to an unfished condition.  This could be an important mechanism for gizzard shad compensation following harvesting in Florida lakes.  For example, a harvest rate of 75% applied to the Lake Dora gizzard shad population over 15 years *in the absence of compensation* should result in an 85% reduction in the total population biomass.  However, at the *observed level of compensation* (7-fold increase in juvenile survival), that same harvest rate applied for 15 years would result in only a 25 % decline in biomass.

We used these estimates (and their associated uncertainty) for the strength of compensation to evaluate the efficacy of gill net harvesting for gizzard shad biomass reduction at the Harris Chain of Lakes.  The analysis was carried out using a population model that simulated the total gizzard shad biomass reduction under different harvest intervals (frequency of harvesting in years), exploitation rates, and gill net mesh sizes.  We then used these simulations to calculate the probability of attaining a target reduction in total population biomass of 75% across the range of scenarios.  The 75% target was chosen from the literature to represent the population level at which we could expect changes in lake water quality as a result of fish biomanipulation.  We found that the current harvesting regime (50-80% annual exploitation rate, 102-mm gill net mesh) is highly unlikely to reduce gizzard shad population biomass by more than 40%, and thus would not achieve the 75% reduction target.  Fishers would need to use a 51-mm mesh at an exploitation rate exceeding 50% to achieve substantial biomass reductions. All other harvest scenarios resulted in weak ($<$50%) biomass reductions and low probabilities of attaining a 75% biomass reduction.

Our simulation analyses rested on two key assumptions.  The first assumption was that the 75% biomass reduction target is applicable to the Harris Chain of Lakes.  The actual biomass reduction target for the Harris Chain could be higher or lower than 75%, but we have no information from the lakes that would indicate an alternative target.  We recommend that quantitative peer-reviewed analyses are conducted to determine the biomass reduction level that would be required to induce long-term changes in water quality at the Harris Chain of Lakes.

However, choosing a smaller biomass reduction target may not change our findings qualitatively because the probability of attaining even a 50% biomass reduction was relatively low for all scenarios except at unrealistically high harvest rates or when using the smallest gill net mesh size (51-mm). However, if the target were found to be less than 40% then our conclusions could change. The other assumption was that when simulating harvest with a given mesh size, our model accounted for the process of fishers "fishing down" the population by starting the year with large mesh sizes then using progressively smaller meshes as catches of large fish drop-off. For example, the 51-mm mesh size scenario actually models the use of 51-102-mm meshes by fishers. Thus, our results could be viewed as a "best case" scenario with respect to biomass reduction because reductions would be less if fishers either used only the minimum mesh size or preferred to use larger meshes then the minimum.

We recommend that our simulation model be coupled with models describing temperature- and mass-specific nutrient excretion rates of gizzard shad. This approach would allow forecasting of nutrient reductions (attributable to gizzard shad) under various removal scenarios (e.g., mesh size, exploitation rate). These forecast estimates could then be viewed against data on whole-lake nutrient budgets to determine whether the reductions are large relative to other nutrient sources. Conducting these analyses before removal begins is critical to identify situations in which biomanipulation could be successful, or conversely, to prevent spending large amounts of money on gizzard shad removal subsidies and monitoring for situations that have a low probability of success.

# SUMMARY AND RECOMMENDATIONS

- Gizzard shad at Lake Dora did not exhibit compensatory increases in growth or maturity following commercial harvest in 2005 and 2006, and growth and maturity were not density-dependent at control lakes.

- Total population biomass reduction was relatively weak (30% reduction), which may not have been a strong enough manipulation to induce compensatory changes in growth and maturity that have been observed for gizzard shad in other systems.

- Juvenile survival increased following density reduction at Lake Dora and was negatively related to spawner biomass across lakes. We found that juvenile survival at Lake Dora could increase up to seven-fold at low population density relative to an unfished population, which could substantially reduce the effectiveness of gizzard shad removal efforts by SJRWMD.

- Because total biomass reductions were relatively weak, these estimates of the strength of density dependence should be viewed as conservative. We cannot rule out that compensation could increase via changes in growth and maturity (in addition to juvenile survival) if total biomass were reduced to a greater extent through a less size selective fishery and higher harvest rate.

- Previous research has shown that ~75% reduction in total biomass of rough fish is required to expect improvements in water quality. Our simulations show that gill net fishery configurations used to date at the Harris Chain of Lakes are unlikely to cause >40% reductions in total gizzard shad biomass, and thus would not achieve a 75% biomass reduction target. Resource managers should consider either smaller mesh sizes for gill nets or different fishing gears that are less size selective for future biomanipulation projects.

- The simulation model presented here (Chapter 2) should be linked with mass- and temperature-specific nutrient excretion rate estimates for gizzard shad. These models could be used to forecast reductions in nutrient loading from gizzard shad under various removal scenarios (e.g., gear type, mesh size, exploitation rate). These forecasted

reductions could then be compared with lake nutrient budgets to assess whether gizzard shad removal has potential to improve water quality. This is a need for future study and could be used to determine the applicability of the 75% biomass reduction target to the Harris Chain of Lakes.

# COOPERATORS AND ACKNOWLEDGMENTS

This study was a collaborative effort that included substantial contributions from personnel in many agencies and academic units. St. Johns River Water Management District (SJRWMD) staff including Larry Battoe, Mike Coveney, and Walt Godwin aided all phases of the project. The Florida Fish and Wildlife Conservation Commission (FWC) staff including John Benton, Steve Crawford, Marty Hale, Bill Johnson, and Brandon Thompson helped with field data collection, laboratory sample processing, and project logistics. University of Florida students and staff who made significant contributions to the field and lab portions of this study were Christian Barrientos, Greg Binion, David Buck, Aaron Bunch, Meredith Bunch, Troy Davis, Drew Dutterer, Porter Hall, Kevin Johnson, Galen Kaufman, Patrick O'Rouke, Nick Seipker, Erika Thompson, and Allison Watts. Carl Walters provided insights on the assessment model and stock-recruitment analysis.

# PROJECT INTRODUCTION

Biomanipulation via removal of planktivorous and detritivorous fishes is a strategy that has potential for improving water clarity in lakes. In Florida, gizzard shad removal projects using gill nets and/or haul seines have been conducted in an attempt to improve lake water clarity and reduce algal blooms. The St. Johns River Water Management District (SJRWMD) has conducted gizzard shad reductions on four hypereutrophic lakes (Lakes Apopka, Denham, Dora, and Griffin) from the late 1980's to the present using subsidized commercial fisheries.

Compensatory responses (increases in growth, juvenile survival, or decreases in age/size at maturity) following removal of gizzard shad due to density-dependent processes should be considered because they could reduce the effectiveness of the SJRWMD programs. Catalano et al. (2007) conducted preliminary analyses to assess the amount of compensation in the gizzard shad population following the 2005-2006 Lake Dora removal. They found a decrease in length at maturity and an increase in recruitment after gizzard shad removal. However, the data collected for their analysis was not of adequate duration to conclusively assess the strength of compensation. Consequently, their conclusions were tentative and would have benefitted from more years of data to track post-manipulation cohorts through the age structure to better assess compensatory responses. In the absence of such information, Catalano et al. (2007) conducted a preliminary simulation of the efficacy of different removal scenarios (mesh size, harvest interval, exploitation rate) to reduce gizzard shad biomass. These analyses suggested that SJRWMD removals were unlikely to reduce gizzard shad population density enough to conclusively evaluate the potential for biomanipulation to improve water clarity. However, these simulations were based on "best guess" values for the strength of gizzard shad compensation, since better estimates were not available at that time. Obtaining more reliable estimates of gizzard shad compensation would benefit the SJRWMD removal program by better informing this simulation model.

Assessing recruitment trends over time is critical to evaluating compensatory responses following biomanipulation. Catalano et al. (2007) used catch rates of age-1 gizzard shad in January as an index of recruitment because not enough years of data were available to directly estimate recruitment trends. A critical assumption of this approach was that age-1 catch rates

were proportional to age-1 abundance. This is often not the case for catch rate indices due to interannual changes in environmental factors affecting catch rates (moon phase, wind, temperature). Moreover, experimental gillnets used by Catalano et al. (2007) were highly size selective and therefore did not capture representative samples of the population age structure and recruitment because age-1 shad in January were not fully vulnerable to the gear. This was particularly evident at Lakes Eustis and Harris where abundance and/or catchability of age-1 shad may have been lower. Consequently, catches of age-1 shad at Lakes Eustis and Harris were extremely low (<0.5 fish/net). This prohibited a reasonable assessment of changes in recruitment after gizzard shad removal because the first two post-harvest cohorts (2006 and 2007) were not fully vulnerable to the gear until they turned age-2 in January of 2008 and 2009. A longer time series of age/length catch data would allow the use of a stock assessment model to obtain model-based estimates of recruitment (numbers of age-1 fish) rather than use age-1 catch rates as an index of recruitment.

Here we present new analyses that include two additional years of gizzard shad age, growth, and maturity information from the Lake Dora removal. In particular, we use a stock assessment model to estimate recruitment trends over time from before and after the removal at Lake Dora. These estimates were used to assess the strength of compensation in juvenile survival of gizzard shad. The strength of compensation and uncertainty in these estimates were used to revisit Catalano et al.'s (2007) simulation model to evaluate the efficacy of gizzard shad removal using gillnets.

The purpose of this project was to experimentally assess impacts of a commercial gizzard shad removal (i.e., biomanipulation) on their population dynamics (i.e., juvenile survival, growth, maturity). Our objectives were to:

1. assess gizzard shad population dynamics (juvenile survival, growth, maturity) before and after an experimental removal project and compare to two reference lakes (Chapter 1),

2. develop a population model for gizzard shad and forecast effects of varying levels of commercial fishing on gizzard shad population dynamics while explicitly accounting for uncertainty in the strength of gizzard shad compensation (Chapter 2),

# CHAPTER 1:  COMPENSATORY RESPONSES OF GIZZARD SHAD FOLLOWING EXPERIMENTAL DENSITY REDUCTION AT LAKE DORA

## Introduction

Compensatory responses of gizzard shad following biomanipulation could reduce the effectiveness of SJRWMD removal efforts at hypereutrophic Florida lakes.  Compensatory density-dependence is a negative feedback on population growth rate via functional relationships between population density and vital rates such as growth, survival and maturation. Understanding the strength and mechanisms of compensation of fish populations is critical because these factors determine the ability of populations to withstand harvesting.  Knowing the life stage where density dependence occurs for a particular population can provide insight into how populations might respond to different methods of harvesting that target different ages or sizes of fish.  Recent meta-analyses of spawner-recruit data have confirmed that fish populations are subject to strong compensatory density-dependence via changes in per-capita reproduction (Myers et al. 1999).  Compensation results in high reproductive rates in fishes at low spawner abundance and relatively low reproductive rates at high abundance (Myers et al. 1999).

When considering biomanipulation as a lake restoration tool at Florida lakes, understanding how fish life history metrics respond to commercial fishing is critical to understanding the potential impact of biomanipulation on gizzard shad populations and lake food webs.  Catalano et al. (2007) conducted preliminary analyses on gizzard shad compensation following the 2005-2006 Lake Dora removal, but those analyses were based on only three years of data.  A longer time series would allow post-manipulation cohorts to be observed over a longer time period, which would improve estimates of compensation.  In this chapter, we tested the hypothesis that gizzard shad removal at Lake Dora would result in compensatory changes in reproductive rates of the gizzard shad population. We sought to understand the mechanisms for these compensatory responses by evaluating changes in growth, maturation schedules, and juvenile survival. Essentially, we updated the analyses of gizzard shad growth and maturation conducted by Catalano et al. (2007) with two additional years of data.  We also used two additional years of data on gizzard shad age and length composition as inputs in a stock

assessment model to estimate recruitment trends following removal, which elucidates changes in juvenile gizzard shad survival. We defined juvenile survival as survival from egg to age-1.

## Biomanipulation Timeline and Study Sites

This study was conducted at Lakes Dora, Eustis, and Harris in Lake County, Florida (Figure 1-1). The lakes are part of the Harris Chain of Lakes, which constitutes the upper reaches of the Ocklawaha River system. Commercial fishers harvested gizzard shad at Lake Dora in March-April 2005 and January-March 2006. Data contained in this report span a time period that includes pre-harvest (November – February 2005), two years during the harvest period (March 2005 through March 2006), and three years of post-harvest (2007-2009). Lakes Eustis and Harris represented reference sites and were sampled using the same methods and sample times as Lake Dora.

Lake Dora is the smallest of the three lakes with a surface area of 2,320 ha and a mean depth of 2.2 m. The lake has long-term chlorophyll *a* concentrations > 100 *u*g/L (Florida LAKEWATCH 2001) and is considered eutrophic. Lakes Eustis and Harris were used as reference lakes, where gizzard shad sampling was conducted throughout the same time period as Lake Dora for comparison to the fished-population (Lake Dora). Lake Harris is the largest of the lakes at 5,580 ha followed by Lake Eustis at 3,159 ha. Mean depth is 3.3 m at Lake Harris and 3.0 m at Lake Eustis. Lakes Eustis and Harris are also considered eutrophic. Macrophytes are confined to the shallow riparian zones of all three lakes and their abundance is generally low, filling < 3% of the lake volume (Florida LAKEWATCH, 2005). The lakes are connected by a series of narrow (width < 30 m) canals. The degree to which fish move among the lakes via the canals is unknown. However, due to the small size of the canals relative to the lakes, we suspected that fish movement among the lakes was not a significant factor affecting gizzard shad populations.

Biomanipulation at Lake Dora was achieved with a commercial gill net fishery funded by the SJRWMD. Prior to fish removal, gizzard shad populations in all lakes were unfished. Commercial fishers removed gizzard shad from Lake Dora during March-April 2005 and again during January-April 2006. Gizzard shad were removed using gill nets with a minimum mesh size restriction of 102 mm, which selected for gizzard shad larger than approximately 300-mm total length. Removal was carried out by commercial fishers, with an average of five boats

setting 3-5 sinking gill nets per day, each net ranging in length from 75 to 600 m. The total harvest was 125,000 kg in 2005 and 135,000 kg in 2006. Catalano et al. (*in review*) estimated exploitation rates (*u*; annual proportion of vulnerable sized fish removed) of 0.71 in 2005 and 0.65 in 2006. The total biomass reduction was estimated at 30% through the two years of fishing (Catalano et al. *in review*). This estimate is slightly lower than reported by Catalano et al. (2007; 40%). These new estimates are the best current values because they incorporate recruitment estimates from Chapter 1, below, whereas Catalano et al. (2007) assumed constant recruitment in their analysis.

## Methods

We evaluated density-dependence in growth, maturity, and juvenile survival using data from the density reduction at Lake Dora and two control lakes (Lakes Eustis and Harris). There are two ways to analyze this type of control-impact design. One approach would be to conduct a before-after-control-impacts analysis. In such cases, controls are treated strictly as a reference system for comparison to the impact system. However, we were interested in density effects on demographic rates, and density varied at the control lakes as well, although not as much as at Lake Dora. A second approach would be to include data from the control lakes as well to take advantage of natural changes in density in those lakes due to recruitment variability. We chose this second approach and thus used all lake years of data as replicates in the analyses, such that the density reduction at Lake Dora served to increase contrast in the data set, but data from control lakes were also included in the assessment of density dependent processes. This approach improved the scope of inference for the study by including naturally fluctuating populations as observations, along with the observations from the density reduction at Lake Dora.

*Field Data Collection*

Gizzard shad demographic information (growth, maturity, juvenile survival) was collected via annual fishery-independent gill net surveys conducted by UF and SJRWMD at each lake. The UF survey set multi-panel floating gill nets at 20 fixed randomly-selected sites at each lake (Figure 1-1, Appendix A) in January/February (all lakes: 2005 - 2009) and November (all lakes: 2004 - 2006; Lake Dora: 2009). The SJRWMD survey set multi-panel gill nets at 10 fixed

sites at Lakes Eustis and Harris and 20 sites at Lake Dora during January (Lake Dora: 2003, 2005 – 2009; Lake Eustis: 2003, 2006-2009; Lake Harris: 2003).  Survey gill nets were 2.4-m deep and contained six, 15.3-m long panels of 64, 76, 89, 102, 114, and 127-mm stretch monofilament mesh and nets were set for 2 hours each.  The UF gill nets had three additional panels of 38, 51, and 64-mm mesh to target age-1 fish.

We collected information on size, age, and maturity for gizzard shad.  Captured gizzard shad from both surveys were counted and measured for total length (mm).  Gizzard shad from the UF survey were aged by analyzing otoliths from a subsample of 10 fish per 10-mm length interval; fish from SJRWMD surveys were not aged.  At the lab, fish were measured, weighed, and otoliths were sectioned using a South Bay Tech$^{©}$ Model 650 low-speed saw and aged by three independent readers using a dissecting microscope.  The length and age composition of the UF survey data were estimated from the length distribution by multiplying the number of fish captured in each length interval by the proportion of fish at each age within that interval (i.e., age-length key method).  Gender was determined on aged fish and the ovaries removed, weighed (g), and preserved in 10% buffered formalin solution to assess age/size at maturity.  To verify that the January/February survey was carried out when female gizzard shad were at or near peak spawning condition, additional gill nets (one to three nets) were set twice per month from January to May 2005-2007 at each lake.  At least 30 adult females were collected per trip to assess temporal trends in the gonadosomatic index (GSI; GSI = ovary weight/ovary free fish weight), which indicated the duration and peak of the spawning period.

*Recruitment*

Recruitment and other critical demographic parameters were estimated using the data collected above input into an age- and length-structured population assessment model (Appendix B; Figures B-1 and B-2).  The model was fitted to gizzard shad data from Lake Dora and the two control lakes (Lakes Eustis and Harris) to estimate time-specific annual recruitment to age 1 for lake $i$ ($R_{t,i}$), age and time-invariant instantaneous natural mortality ($M_i$), von Bertalanffy growth parameters (asymptotic length, $L_{\infty i}$; metabolic parameter, $K_i$, and time-at-zero length, $t_{0i}$), and gear selectivity parameters (fishery and survey) using a multinomial maximum likelihood function.  Data inputs were (1) length- and age-specific gill net catches from the November and January/February UF fishery-independent surveys, (2) annual length distributions from the

January SJRWMD fishery-independent gill net surveys, (3) gizzard shad length distributions from the 2005 and 2006 Lake Dora fishery from the onboard observers program, and (4) total harvested biomass at Lake Dora in 2005 and 2006. The model was conditioned on total harvested biomass (observed harvest was subtracted from predicted biomass in the model) and likelihood terms for each of the other three data sources were summed to calculate the total likelihood. Parameter uncertainty was evaluated by sampling from the posterior distribution of parameters with Markov Chain Monte Carlo simulation using the Metropolis-Hastings algorithm (Hastings 1970). We simulated 250,000 iterations with a burn-in period of 25,000 and thinning interval of 250. The tuning parameter was set to obtain an acceptance rate of 0.25. Convergence of the chains was evaluated by inspecting trace plots. Sampling from the posterior distribution of the length-age model parameters was used to assess uncertainty in density-dependent parameters of gizzard shad (see *Juvenile Survival*, below).

The model scaled recruitment estimates (i.e., age-1 abundance) at Lake Dora such that they were large enough to explain the observed harvested biomass in 2005 and 2006. Therefore, annual recruitments at Lake Dora could be freely estimated as parameters in the model. However, recruitments at Lakes Eustis and Harris had no scaling information because those lakes were unharvested. Thus, recruitments at Lakes Eustis and Harris were estimated as lognormally distributed residuals ($\omega_{t,i}$) around an average annual recruitment value of 1.0:

$$R_{t,i} = \overline{R}e^{\omega_{t,i} - 0.5\sigma_{R,i}^2} \tag{1-1}$$

and the variance was constrained using a penalty function that was added to the total likelihood value:

$$-\ln P(\omega_{t,i} \mid \sigma_{R,i}) = \sum_t \ln(\sigma_{R,i}) + \frac{\omega_{t,i}^R}{2\sigma_{R,i}^2}, \tag{1-2}$$

where $\sigma_{R,i}$ is the standard deviation of the recruitment residuals (Maunder and Deriso 2003). This approach maintained an average recruitment of 1.0 and constrained the standard deviation of the recruitment anomalies to realistic values for Lakes Eustis and Harris.

*Growth*

We tested for compensation in growth rates by modeling associations between annual growth increments and population density across the three lakes. Length and age data from the

UF January gill net survey were used to calculate mean length-at-age using methods of Devries and Frie (1996) for age-length keys. This approach produced unbiased means when aged fish are subsampled on fixed length intervals for an age-length key (i.e., 10 fish per 10-mm length interval). Growth increments were calculated as the difference in mean length from one year to the next for a given cohort and were $\log_e$ transformed. Growth increments were obtained for the 2003 – 2007 cohorts and were limited to age-5 or younger fish because of low sample sizes of older age classes. Analysis of covariance was used to test for effects of population density on logged growth increments using age as the concomitant variable and lake as a block factor in the model. Population density was the annual total population biomass at the beginning of the year over which the growth increment was calculated. It was calculated as the predicted numbers of fish in each 10-mm length interval multiplied by the mean weight of fish of that interval using a lake and time invariant length-weight relationship. Density values were obtained as outputs from the length age model and were rescaled to a mean of zero. Model selection was carried out using Akaike's information criterion (AIC).

*Maturity*

We developed a relationship between GSI and maturity using a subset of female gizzard shad. This allowed the use of GSI as a proxy for maturity, which could be applied to individual fish whose ovaries were not examined with histology. Preparing histology on ovaries of all females would have been cost-prohibitive. Histological sections were prepared from formalin-preserved ovaries from Lakes Dora and Eustis in late January to early March 2007 when fish were in peak spawning condition. Gizzard shad are batch spawners and reproduce over a 2-3 month period in central Florida (personal observation). Preliminary analyses of temporal trends in GSI from January to May indicated that fish were in peak spawning condition from late-January to early March, and this pattern was relatively consistent across years. Thus, only females collected during January-March were used in the analysis to minimize bias due to the timing of sampling relative to spawning. We sampled at least five females per 25-mm length interval. Histological sections were stained with hematoxylin and eosin, embedded in paraffin, sectioned, and mounted on a glass slide at the University of Florida College of Veterinary Medicine, Department of Tissue Pathology. Females were considered mature if histology showed the presence of vitellogenic (yolked) oocytes. Maturity was modeled as a function of

GSI using logistic regression and testing for lake and lake × length effects. Probability of maturity was estimated as a function of GSI for females from lakes and/or years with no histological information. This model was then applied to all other females whose ovaries were not examined with histology. Individuals with a model-predicted probability of maturity (based on their GSI value) exceeding 0.5 were classified as mature and all others were classified as immature.

We modeled maturation as a cohort-specific process, with each cohort potentially maturing according to its own cohort-specific ogive. We evaluated two types of density effects on cohort maturity: intercohort and intracohort. Intercohort effects were modeled by including a term for the total biomass ($B_{2+}$) of all other age-classes when a given cohort recruited to age 1. Intracohort effects were modeled by including a term for cohort size, or the year class strength for a given cohort. Population density values were obtained from the length-age model and were rescaled to a mean of zero as in *Growth*, above. Cohort size was the annual recruitment estimate for each cohort from the length-age model and was also rescaled to a mean of zero. Maturity ogives (proportion of fish mature) were modeled as a function of length, cohort size, $B_{2+}$, lake, and lake × length interactions with logistic regression. The lake × length interaction tested whether the shape of the maturity schedule varied among lakes. Preliminary analyses indicated that length was a better predictor of maturity than age, but the two factors were highly collinear. Thus age was excluded from the models describing the maturity ogives. Model selection was carried out using AIC. Statistically significant associations between cohort size or population density and maturity would indicate density dependence in maturation.

*Juvenile Survival*

Lake- and time-specific juvenile survival ($S_{t,i}$) was estimated from the length-age assessment model by dividing annual estimates of recruitment ($R_{t,i}$) by the model-predicted total spawner biomass ($B_{t-1,i}$) from the previous year. Spawner biomass was calculated for lake *i* and time *t* as:

$$B_{t-1,i} = \sum_l \sum_a N_{l,a,t-1,i} m_{l,a,t-1,i} w_l - H_{t-1}, \tag{1-3}$$

where $N_{l,a,t-1,i}$ is the model-predicted number of age-*a* gizzard shad of length *l* in the population at time *t*, $m_{l,a,t-1,i}$ is the length- age- and time-specific proportion of mature fish at lake *i*, $w_l$ is the

weight of a length-$l$ fish, and $H_{t-1}$ represents the spawner biomass that was removed by the fishery just prior to the spawn in the previous year. Population numbers ($N_{l,a,t-1,i}$) were predicted from the model as a function of estimated parameters. Maturity was predicted from the logistic regression model relating maturity to length, age, cohort size, population density, and lake (see *Maturity*, above). Weight is commonly used as a proxy for fish fecundity (Quinn and Deriso 1999) and was estimated from gizzard shad length data from the lakes using the lake- and time-invariant allometric relationship $w_l = 6.97\text{e-7 } l^{3.49}$. Harvest in 2006 began before gizzard shad spawned and this needed to be incorporated into the spawner biomass estimates. Examination of densities of yolked larval gizzard shad from biweekly larval fish tows suggested that approximately half of the catch had been taken before the gizzard shad spawned. Thus we subtracted from the $B_t$ an estimate of the spawner biomass that was removed just prior to the spawn in the previous year:

$$H_{t-1,i} = 0.5 \sum_l \sum_a N_{l,a,t-1,i} m_{l,a,t-1,i} w_l v_l u_{t-1}, \tag{1-4}$$

where $v_l$ is the length based selectivity of the fishery and $u_{t-1}$ is the proportion of vulnerable sized fish harvested the previous year (exploitation rate).

Annual recruitments were scaled differently at Lake Dora (scaled to the observed harvest) than at Lakes Eustis and Harris (scaled to mean of 1.0 fish). Juvenile survival was a quotient and was thus dimensionless and comparable among lakes, but spawner biomass was scaled to the annual recruitments and thus was not comparable. Consequently, spawner biomass was rescaled to a mean unfished value of 1.0 kg at each lake prior to use in estimating density dependence in juvenile survival. The mean unfished spawner biomass at Lake Dora was the average of the 2003 to 2005 pre- density reduction estimates.

The strength of density-dependent recruitment at the lakes was evaluated by modeling juvenile survival as a function of spawner biomass and environmental factors using the linear form of the Ricker stock-recruit function:

$$\ln(S_{t,i}) = \ln(\alpha) - b_i B_{t,i} + w_t t + \varepsilon_{t,i}, \tag{1-5}$$

where α is the maximum juvenile survival at very low population density (initial slope of recruitment vs. spawner biomass relationship) and was the parameter of primary interest in this model, $b$ describes the strength of density dependence at high spawner biomass, the $w_t$ terms represent annual environmental effects on juvenile survival that act on all of the lakes. Including

these shared environmental affects in the model helped ameliorate bias due to serial autocorrelation in juvenile survival and spawner biomass (Walters and Martell 2004). The mechanism for these environmental effects was not of interest but visual examination of temporal trends in survival suggested that the lakes were affected by a shared environmental influence on year class strength, which is not uncommon for geographically proximate fish populations (Maceina and Stimpert 1998).

Myers et al. (1999) concluded that the Ricker model was appropriate for evaluating density-dependent recruitment for a range of species when the primary parameter of interest is α. However, the magnitude of α is not comparable among populations unless it is compared to juvenile survival in an equilibrium unharvested population. Thus, the more valuable measure of density-dependence of juvenile survival is the maximum lifetime reproductive rate ($\hat{\alpha}$; Myers et al. 1999), which is also referred to as the Goodyear compensation ratio (Goodyear 1980). This value represents the ratio of juvenile survival at low population density to survival in the unfished condition and is a standardized measure of density dependence that is comparable across populations (Myers et al. 1999). We calculated $\hat{\alpha}$ for each lake as:

$$\hat{\alpha}_i = \alpha \phi_{0,i},$$ (1-6)

where $\phi_{0,i}$ is the equilibrium lifetime spawner biomass per recruit for gizzard shad at lake $i$:

$$\phi_{0,i} = \sum_a s_{a,i} w_a M_{a,i},$$ (1-7)

where $s_{a,i}$ is the survivorship to age $a$, $w_a$ is the average weight, and $m_{a,i}$ is the proportion mature to age $a$. Uncertainty in the maximum lifetime reproductive rate was assessed by repeatedly fitting the stock-recruitment model to survival and spawner biomass estimates taken from posterior samples of the parameter distributions obtained via the MCMC? simulation of the length-age model.

## Results

*Recruitment*

Estimated recruitment time series showed some degree of temporal synchrony in year class strength among lakes with relatively strong year classes generally observed in even-numbered years (Figure 1-2). Lake Dora had strong age-1 recruitment in 2000 and 2006 (1999 and 2005 year classes; Figure 1-2a). Lake Eustis had above average recruitment in 2000 as well, but also

had high recruitment in 1999 and 2009, as did Lake Harris (Figure 1-2b,c). The 2006-2008 post-manipulation year classes at Lake Dora showed no decline following density reduction but rather were near the long-term average recruitment for the time series, suggesting that the density reduction did not substantially affect recruitment (Figure 1-2a). All other model parameter estimates are listed in Table 1-1.

*Growth*

Annual growth increments differed among ages, but not among lakes or with population density (Table 1-2). The model with age only had the best AIC support (Table 1-2; intercept = 5.64±0.08; slope (age) = -0.51±0.02; $df$ = 55; $R^2$ = 0.89). Fitting additional parameters for population density and lake was not justified based on AIC (Table 1-2). The best model (age) fit the data considerably better than the single parameter (null) model (Table 1-2). Thus we concluded that growth was not density dependent and did not increase at Lake Dora following gizzard shad removal. Rather, it remained relatively constant throughout the time period at each of the lakes.


*Maturity*

Maturity was strongly related to GSI and there were no significant lake or lake×length effects. The best model had two parameters (intercept = -9.2±2.53, slope (GSI) = 4.6±1.28) on 94 residual degrees of freedom. The GSI (%) at which the model-predicted probability of maturity was 0.5, was 1.99%. Correct classification rates of mature and immature females were high. Ninety-three percent (3/48) of females classified by the model as mature were in fact mature as indicated by histology. Likewise, 93% (3/48) of females classified as immature were in fact immature. Hence, female gizzard shad were likely to be mature if their GSI exceeded 2%. Because of the high classification rates, we were comfortable extrapolating the model to other lakes and years to estimate maturity of females for which ovarian histology was not analyzed.

Length-at-maturity was weakly related to population density and the direction of the effect was opposite of our prediction (Table 1-3). The minimum AIC model was an additive model with length, lake, and population density (Table 1-3). However, there were seven other models with nearly equivalent AIC support (ΔAIC < 5), each of which included lake (Table 1-3). Thus, maturity varied among lakes (Figure 1-3); models excluding lake had ΔAIC values near 50. Including density resulted in marginal improvements in model parsimony over the model with

just length and lake (ΔAIC = 3) and including cohort size resulted in no improvement in AIC (Table 1-3).  The population density coefficient was positive in the model suggesting that gizzard shad matured earlier at higher population densities but the size of the effect was relatively small; 50% increase in population density would result in a 20-mm decrease in length at maturity.  Thus maturity was not strongly related to density under the range of variation in density that we observed in the study lakes.  Of the seven models with nearly equivalent AIC support, the simplest included the factors length and lake (intercept = -11.29; length = 0.041±0.002; lake = -1.52±0.23; $df$ = 1166), and was selected as the most parsimonious, biologically plausible model, and was used in subsequent calculations of spawner biomass (see below).  In conclusion, length at maturity did not decrease substantially following gizzard shad removal at Lake Dora.  Across lakes, there were very weak density effects on maturity that were not well supported by the data. Rather, the most parsimonious model suggested that there were much more substantial differences among lakes than with changes in population density.

*Juvenile Survival*

Spawner biomass at Lake Dora decreased to 28% of the average unharvested biomass in 2006 following the second year of harvest (Figure 1-4a).  This reduction exceeded the natural variation in spawner biomass observed at control lakes (Figure 1-4).  Spawner biomass decreased steadily from 2003-2009 at control lakes due to natural mortality of large year classes in 1999 and 2000 (Figure 1-4b,c).  Juvenile survival was greatest at Lake Dora in 2005- 2007 just after density reduction, because recruitment was near the long-term average despite substantially reduced spawner biomass (Figure 1-5).  Thus, we detected compensatory increases in juvenile survival at Lake Dora following gizzard shad removal.

Juvenile survival increased with decreasing spawner biomass across lakes and years when including data from Lake Dora as well as the control lakes (Figure 1-5).  The most parsimonious model included spawner biomass and year effects (Table 1-4).  The point estimate of maximum juvenile survival at low spawner abundance (α) was 0.07.  Lake-specific estimates of the maximum lifetime reproductive rate, $\hat{\alpha}$ , were  7.3 at Lake Dora, 7.0 at Lake Eustis, and 5.5 at Lake Harris.  Variability in $\hat{\alpha}$ among lakes was due to variation in equilibrium lifetime spawners per recruit, $\phi_0$ among lakes (Lake Dora: 153.8; Lake Eustis: 140.7; Lake Harris: 106.4).  This variation resulted primarily from differences in length at maturity, with Lake Dora having the

youngest length at 50% maturity and therefore a larger $\hat{\alpha}$ estimate. The mean $\hat{\alpha}$ value of 7.3 at Lake Dora suggests that juvenile survival could increase seven-fold at Lake Dora at low population sizes relative to an unfished population. Another way to think of the meaning of the maximum lifetime reproductive rate is that at low population sizes, each gizzard shad spawner (i.e., egg) is capable of replacing itself seven times.

A value for $\hat{\alpha}$ of 1.0 results in a linear relationship between juvenile survival and spawner biomass and signifies a lack of density dependence in juvenile survival. Examination of 95% confidence intervals indicated that a value of 1.0 was not contained in the interval for any lake, indicating that a lack of density dependence in juvenile survival was unlikely for these populations (Lake Dora 95%CI: 1.9-16.5; Lake Eustis 95%CI: 1.8-16.0; Lake Harris 95%CI: 1.4-13.3; Figure 1-6).


## Discussion

We found that juvenile survival increased at Lake Dora following density reduction, and was density-dependent across the study lakes as a whole. The gizzard shad removal at Lake Dora caused a substantial reduction in spawner biomass in 2006, yet estimates of age-1 recruitment the following year were near the long-term average recruitment for the lake. In the absence of compensation, we would have expected a reduction in recruitment, but that was not the case at Lake Dora, indicating that compensatory juvenile survival occurred following the removal. We did not detect compensation in growth and maturation, which could have been due to the relatively weak total biomass reduction (30%). Further biomass reductions could induce compensatory growth and maturation as has been observed at other systems, but we do not have the data to determine if this would occur at Lake Dora. Thus, our estimates of compensation for gizzard shad at Lake Dora should be viewed as conservative. Stronger biomass reductions with less size-selective gear would be helpful in evaluating possible additional compensatory mechanisms that were not evident due to the relatively weak biomass manipulation at Lake Dora.

We found that gizzard shad could compensate for harvest at Lake Dora via seven-fold increases in juvenile survival at low population densities. This level of compensation is relatively weak when compared to some commercially exploited species such as cod (*Gadus spp.*), but would be enough to substantially reduce the effectiveness of the SJRWMD gizzard shad harvesting program. To put this level of compensation in context, a harvest rate of 75%

applied to the Lake Dora gizzard shad population over 15 years *in the absence of compensation* should result in an 85% reduction in the total population biomass. However, at the *observed level of compensation* (7-fold increase in juvenile survival), that same harvest rate applied for 15 years would result in only a 25 % decline in biomass. Thus the strength of compensation in juvenile survival is a critical parameter of interest and has important implications for the efficacy of gizzard shad harvesting to reduce population biomass and ultimately improve water quality.

The additional two years of data collected from 2008-2009 were critical to obtaining estimates of juvenile survival. This additional age/length composition data allowed the use of a stock assessment model to estimate recruitment trends over time. In the previous report by Catalano et al. (2007), they used fishery-independent gill net CPUE of age-1 gizzard shad as a proxy for recruitment, but could not obtain formal maximum-likelihood recruitment estimates from the short time series available at that time. Their analysis suggested that recruitment increased following density reduction, which suggested a strongly dome-shaped (overcompensatory) stock recruitment function for gizzard shad. The additional two years of data presented in this report suggest that recruitment did not increase following density reduction, but rather tracked along the long-term average recruitment despite a substantial reduction in spawner biomass. This new analysis indicated weaker compensation for gizzard shad than was concluded by Catalano et al. 2007. Despite these weaker compensation estimates, gizzard shad exhibited enough compensatory reserve to sustain high annual harvest rates (>50%), particularly when applied with a highly size selective removal method such as 102-mm mesh gill nets.

We found no change in length at maturity for gizzard shad at Lake Dora. This disagrees with the findings of Catalano et al. (2007) who reported a decrease in length at maturity following density reduction. This can be explained by the fact that Catalano et al. (2007) did not have enough data to fully estimate the maturation schedules for post-manipulation cohorts. For example, the 2005 cohort turned age 2 in January 2007, yet most cohorts are not fully mature until age-3. Thus, the maturity data from this cohort (and the 2006 year class) were incomplete at the time of Catalano et al.'s (2007) analysis. With an additional two years of maturity data on these cohorts, the analysis in this report is superior to that of Catalano et al. (2007) and represents the best available knowledge as to compensation (or lack thereof) in size at maturity for gizzard shad at Lake Dora (or elsewhere).

There are many peer reviewed studies showing increased juvenile survival, increased growth and reduced size/age at maturity at low population densities in fishes, but there is debate about the relative importance of these mechanisms in fish compensation. Density-dependent changes in juvenile survival have been considered the primary mechanism for compensation in fish populations (Rose et al. 2001). For example, individual-based-model simulations by Cowan et al. (2000) indicated that density dependent feedbacks on recruitment are most likely during the late larval to early juvenile phase because of peak total cohort consumption rates during that phase. Conversely, Lorenzen and Enberg (2002) suggested that density dependence in adult growth alone could explain observed compensation in 15 exploited fish populations. They further postulated that density dependence in growth may be most important under moderate reduction in density but that increased juvenile survival would be the dominant compensatory mechanisms at very low population sizes. Our results disagree with Lorenzen and Enberg's (2002) findings and indicated that under a moderate change in population density, juvenile survival increased substantially at Lake Dora whereas growth and maturation schedules remained relatively unchanged. This suggests that changes in juvenile survival may be important under moderate as well as severe reductions in population density.

Recent meta-analyses have made major advances in our understanding of compensation in fish populations. Myers et al. (1999) and Goodwin et al. (2006) estimated the maximum lifetime reproductive rate (i.e., compensation ratio), $\hat{\alpha}$, for 237 and 54 stocks of commercially exploited fishes, respectively. We calculated an average $\hat{\alpha}$ of 47 (95%CI: 10-84) across all stocks included in both studies. Clupeids had below-average maximum reproductive rates at 19.3 (95%CI: 13.4-25) across stocks, and no gizzard shad stocks were included in their analyses. The mean estimate for clupeids was greater than the upper 95% confidence interval for the maximum lifetime reproductive rate for gizzard shad from our study. Gizzard shad may have relatively weak compensation when compared to other clupeids, or alternately, the estimates from other species could be biased. Most estimates of $\hat{\alpha}$ come from stock recruitment data generated from stock assessment models, which contain substantial uncertainty and possible biases from serial autocorrelation, error in spawner biomass estimates, and lack of contrast in the data (Walters and Martell 2004). We were able to use an experimental density reduction with control systems to measure $\hat{\alpha}$, and quantified the uncertainty in this parameter, which may provide less biased estimates than those obtained from traditional stock assessments.

Goodwin et al. (2006) identified associations between life history characteristics and the strength of compensation. They found that fishes fall along a continuum of long-lived highly-fecund species with low annual recruitment and strong compensation ('survivors', eg., sturgeon) to short-lived, early-maturing species with high annual recruitment and weak density dependence (;'highly productive' e.g., clupeids). The survivors group exhibits a bet hedging strategy to reproduce over many years whereas the 'highly productive" species are adapted to quickly invade and exploit highly variable resources (Stearns 1992). Our data suggested that gizzard shad fall toward the 'highly productive' end of the spectrum with fast growth, early maturation, and relatively weak density dependence in recruitment compensation.

Our study assessed the relative importance of density dependence of several demographic rates, but was unable to assess specific mechanisms influencing changes in those rates. We observed increased juvenile survival following density reduction but this change could have been due to several mechanisms. Walters and Juanes (1993) proposed that reduced survival at high juvenile densities results from increased risk taking at small spatial and temporal scales by individuals attempting to procure scarce resources in a competitive environment. For example, juveniles may be forced to leave food-poor refugia and spend more time in predator-dense feeding zones in order to maintain adequate growth rates when density of conspecifics is high. Density dependent growth rates of juveniles may also affect survival rates. Numerous studies have shown increased predation risk for slower growing individuals within a cohort (reviewed by Sogard 1997). The 'bigger is better' hypothesis (Shepherd and Cushing 1980) proposes that larger age-0 individuals have lower rates of mortality, because faster growth decreases the duration of exposure to stages where mortality is high (Houde 1987; Miller et al. 1988; Sogard 1997). Additional growth and survival studies on juveniles are needed within the context of experimental density reduction to evaluate mechanisms for density-dependent survival that could not be addressed by our study.

We expected adult demographic rates such as maturity and growth to respond following density reduction. Substantial research has shown changes in these rates with changing density. Age at maturity, for example, generally decreases with increased exploitation (Trippel 1995). Populations with size-dependent maturation schedules may also undergo changes in age at maturity via increases in growth rate (Trippel 1995). Somatic growth typically increases when population density decreases due to decreased intraspecific competition. Many studies have

documented increases in growth related to exploitation of fish stocks. Kim and Devries (2000) reported substantial increases in age-0 gizzard shad growth following density reduction at Walker County Lake, Alabama, and Schaus et al. (2002) found increased growth of gizzard shad at Acton Lake, Ohio, in years with low-population density. Thus, gizzard shad have clearly exhibited plasticity in growth in other systems.

The strength of manipulation should be a consideration in any whole-lake experiment and researchers should strive for large perturbations to elicit system responses (Carpenter 1989). In our study, size-selective removal of gizzard shad reduced spawner biomass by approximately 70%. This corresponds to a spawning potential ratio (SPR) of 0.3, which would put some species at risk for recruitment overfishing (Mace 1994; Clark 2002). However, changes in total population biomass were moderate (30%; Catalano et al. *in review*) due to high estimated natural mortality and gear selectivity which caused a large proportion of the population to reside in young age classes that were invulnerable to harvest. Contrast in total population biomass was less than contrast in spawner biomass, which may have dampened growth and maturation responses. The change in total population biomass may not have been enough to elicit strong responses in growth and maturation. Thus, the lack of change in growth and maturation may have been an artifact of the relatively weak total density reduction. Nevertheless, the experiment resulted in a substantial reduction in spawner biomass, which allowed estimation of density-dependent changes in juvenile survival. Future density reduction studies should achieve stronger total biomass reductions so that changes in all demographic rates can be evaluated.

Table 1-1. Parameter estimates (95% confidence intervals) from the length/age assessment model for Lakes Dora, Eustis and Harris. Note: gear selectivity parameters were not estimable for SJRWMD survey gill nets at Lake Harris because there was only one year (2003) of SJRWMD data collected at that lake.

| Lake | Parameter | | Value (95% CI) |
|---|---|---|---|
| Dora | $M$ | Instantaneous natural mortality rate | 0.94 (0.86 - 1.02) |
| | $K$ | Von Bertalanffy metabolic coefficient | 0.61 (0.60 - 0.63) |
| | $L_\infty$ | Von Bertalanffy asymptotic length | 387.89 (385.08 - 390.73) |
| | $t_0$ | Von Bertalanffy time at zero length | 0.16 (0.13 - 0.18) |
| | $\lambda_1$ | Distribution in length-at-age parameter | 30.86 (30.43 - 31.29) |
| | $\lambda_2$ | Distribution in length at age parameter | 0.06 (0.04 - 0.09) |
| | $L50_{UF}$ | Length at 50% gear selectivity for UF survey gill nets | 462.45 (445.64 - 479.89) |
| | $\gamma_{UF}$ | Shape parameter for UF survey gillnet selectivity | 0.84 (0.71 - 0.97) |
| | $\beta_{UF}$ | Steepness parameter for UF survey gillnets | 0.09 (0.04 - 0.2) |
| | $L50_{SJRWMD}$ | Length at 50% gear selectivity for SJRWMD survey gill nets | 319.46 (312.66 - 326.42) |
| | $\gamma_{SJRWMD}$ | Shape parameter for SJRWMD survey gillnet selectivity | 0.00 (0.00 – 0.00) |
| | $\beta_{SJRWMD}$ | Steepness parameter for SJRWMD survey gillnets | 0.04 (0.03 - 0.04) |
| | $\sigma_R$ | Standard deviaition in annual recruitment residuals | |
| | $L50_{05}$ | Length at 50% selectivity for 2005 commercial fishery | 357.80 (340.36 - 376.13) |
| | $\beta_{05}$ | Shape parameter for 2005 commercial fishery | 0.04 (0.03 - 0.06) |
| | $\gamma_{05}$ | Steepness parameter for 2005 commercial fishery | 0.00 (0.00 – 0.00) |
| | $L50_{06}$ | Length at 50% selectivity for 2006 commercial fishery | 300.86 (297.06 - 304.70) |
| | $\beta_{06}$ | Shape parameter for 2006 commercial fishery | 0.15 (0.11 - 0.21) |
| | $\gamma_{06}$ | Steepness parameter for 2006 commercial fishery | 0.00 (0.00 – 0.00) |
| Eustis | $M$ | Instantaneous natural mortality rate | 1.02 (0.92 - 1.13) |
| | $K$ | Von Bertalanffy metabolic coefficient | 0.70 (0.66 - 0.74) |
| | $L_\infty$ | Von Bertalanffy asymptotic length | 406.85 (401.87 - 411.89) |
| | $t_0$ | Von Bertalanffy time at zero length | 0.34 (0.29 - 0.40) |
| | $\lambda_1$ | Distribution in length-at-age parameter | 33.80 (32.86 - 34.77) |
| | $\lambda_2$ | Distribution in length at age parameter | -0.19 (-0.24 - -0.14) |
| | $L50_{UF}$ | Length at 50% gear selectivity for UF survey gill nets | 440.15 (428.78 - 451.82) |
| | $\gamma_{UF}$ | Shape parameter for UF survey gillnet selectivity | 0.65 (0.56 - 0.74) |
| | $\beta_{UF}$ | Steepness parameter for UF survey gillnets | 0.06 (0.05 - 0.08) |
| | $L50_{SJRWMD}$ | Length at 50% gear selectivity for SJRWMD survey gill nets | 395.05 (374.20 - 417.07) |
| | $\gamma_{SJRWMD}$ | Shape parameter for SJRWMD survey gillnet selectivity | 0.00 (0.00 – 0.00) |
| | $\beta_{SJRWMD}$ | Steepness parameter for SJRWMD survey gillnets | 0.03 (0.03 - 0.03) |
| | $\sigma_R$ | Standard deviaition in annual recruitment residuals | 0.61 (0.40 - 0.92) |
| Harris | $M$ | Instantaneous natural mortality rate | 1.07 (0.99 - 1.16) |
| | $K$ | Von Bertalanffy metabolic coefficient | 0.76 (0.73 - 0.79) |
| | $L_\infty$ | Von Bertalanffy asymptotic length | 389.67 (386.91 - 392.45) |
| | $t_0$ | Von Bertalanffy time at zero length | 0.39 (0.34 - 0.44) |
| | $\lambda_1$ | Distribution in length-at-age parameter | 30.39 (29.17 - 31.66) |
| | $\lambda_2$ | Distribution in length at age parameter | -0.11 (-0.16 - -0.05) |
| | $L50_{UF}$ | Length at 50% gear selectivity for UF survey gill nets | 471.28 (460.62 - 482.19) |
| | $\gamma_{UF}$ | Shape parameter for UF survey gillnet selectivity | 0.81 (0.62 – 1.00) |
| | $\beta_{UF}$ | Steepness parameter for UF survey gillnets | 0.14 (0.05 - 0.40) |
| | $L50_{SJRWMD}$ | Length at 50% gear selectivity for SJRWMD survey gill nets | |
| | $\gamma_{SJRWMD}$ | Shape parameter for SJRWMD survey gillnet selectivity | |
| | $\beta_{SJRWMD}$ | Steepness parameter for SJRWMD survey gillnets | |
| | $\sigma_R$ | Standard deviation in annual recruitment residuals | 0.77 (0.50 - 1.18) |

Table 1-2.  Delta AIC values for competing models describing associations between growth increments and age, lake, and population density (i.e., total population biomass).

| Model | AIC | ΔAIC |
|---|---|---|
| age | 5.5 | 0.0 |
| age+lake | 7.2 | 1.7 |
| age+density | 7.4 | 1.9 |
| intercept only (null) | 130.7 | 125.2 |


Table 1-3.  Delta AIC values for competing models describing associations between gizzard shad maturity and lake, population density ($B_t$), cohort size, year, and cohort.

| Model | AIC | ΔAIC |
|---|---|---|
| length+lake+density | 614.1 | 0.0 |
| length+lake+density+length×lake | 615.4 | 1.3 |
| length+lake+density+cohort size | 616.0 | 1.9 |
| length+lake | 617.1 | 3.0 |
| length+lake+cohort size+length×lake | 617.2 | 3.1 |
| length+lake+cohort size | 617.4 | 3.3 |
| length+lake+lake×length | 618.5 | 4.4 |
| length+lake+cohort size+length×lake | 618.5 | 4.4 |
| length+density | 662.9 | 48.8 |
| length | 664.1 | 50.0 |
| length+cohort size | 664.2 | 50.1 |
| intercept only (null) | 1501.5 | 887.4 |


Table 1-4.  Delta AIC values for competing models describing associations between gizzard shad juvenile survival and spawner biomass (SB) and year.

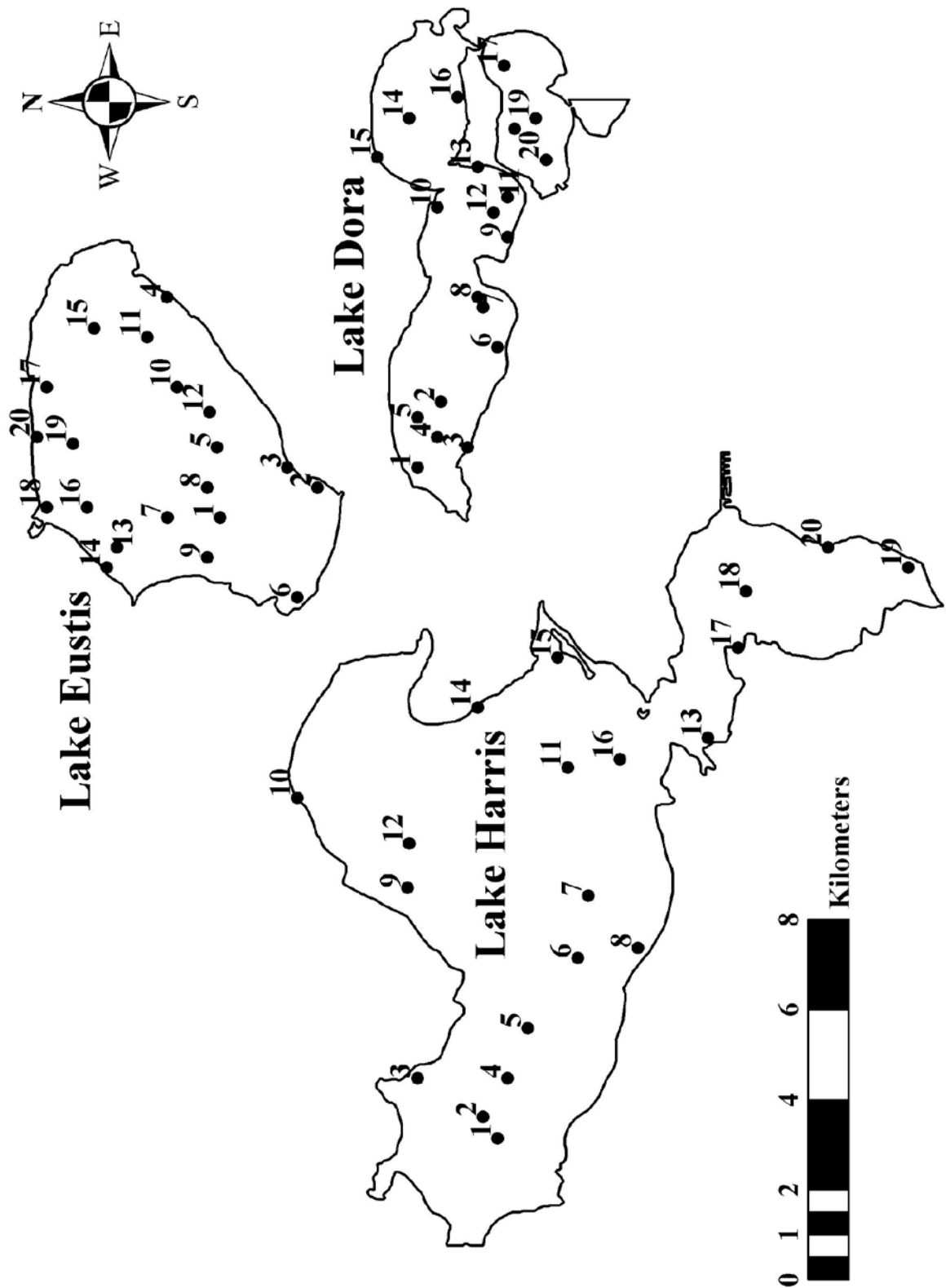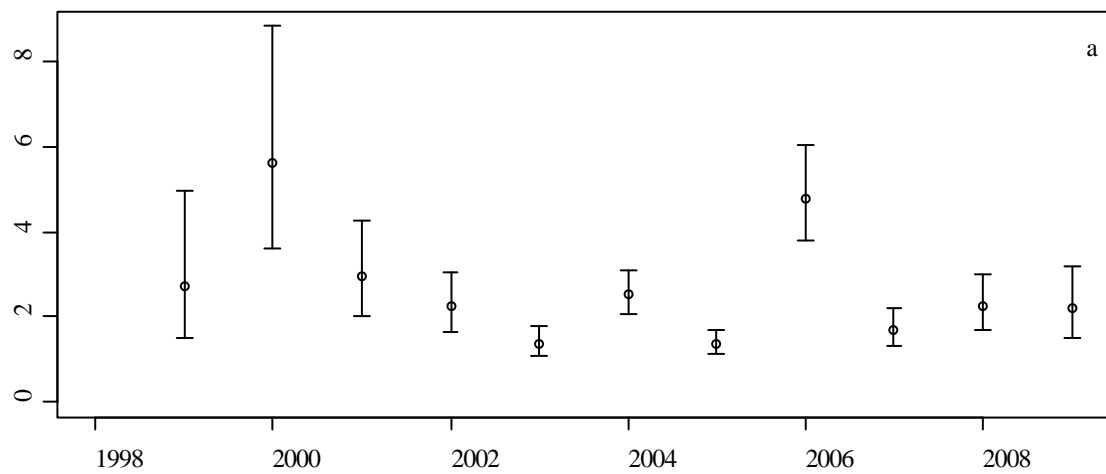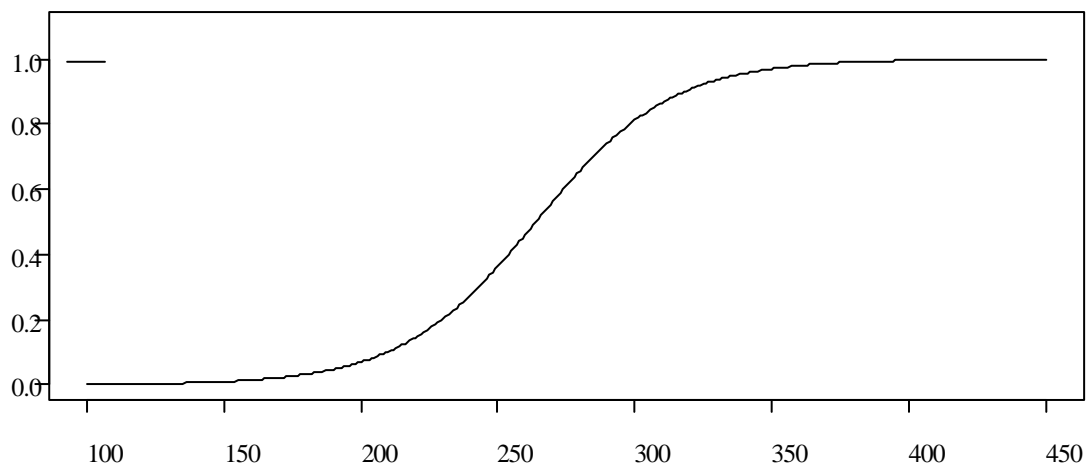| Model | AIC | ΔAIC |
|---|---|---|
| SB+year | 26.0 | 0.0 |
| SB | 31.9 | 5.9 |
| intercept only (null) | 37.6 | 11.6 |

Figure 1-1. Gill net sample sites at Lakes Dora, Eustis, and Harris. Sites are numbered from one to 20 at each lake. Sites were randomly selected from a systematic grid of latitude and longitude coordinates. Site-specific lat/long coordinates and sampling activities are shown in Appendix A.
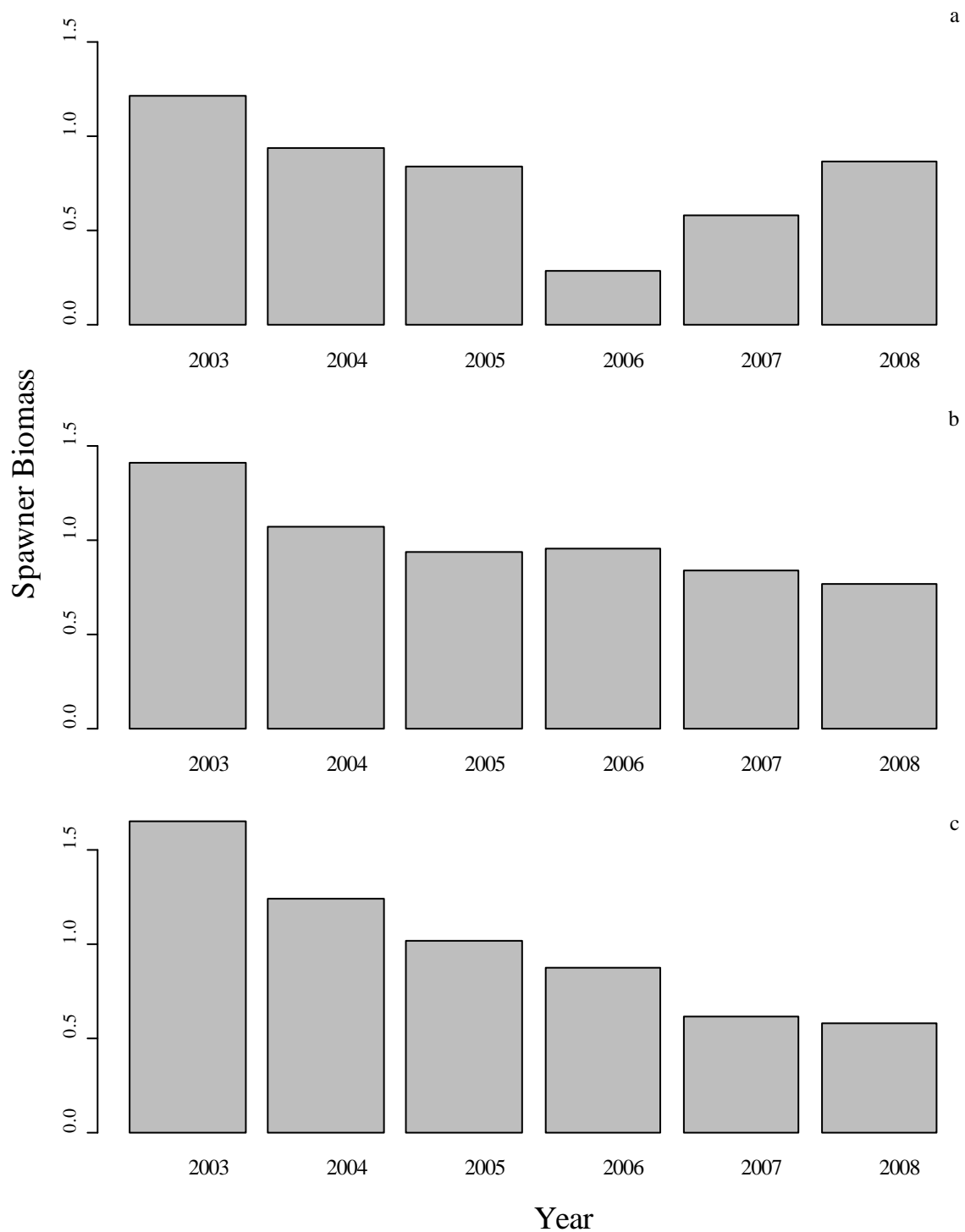
Figure 1-4.  Time series of predicted spawner biomass for 2003 – 2008 at Lakes Dora (a), Eustis (b), and Harris (c) from the length-age model.
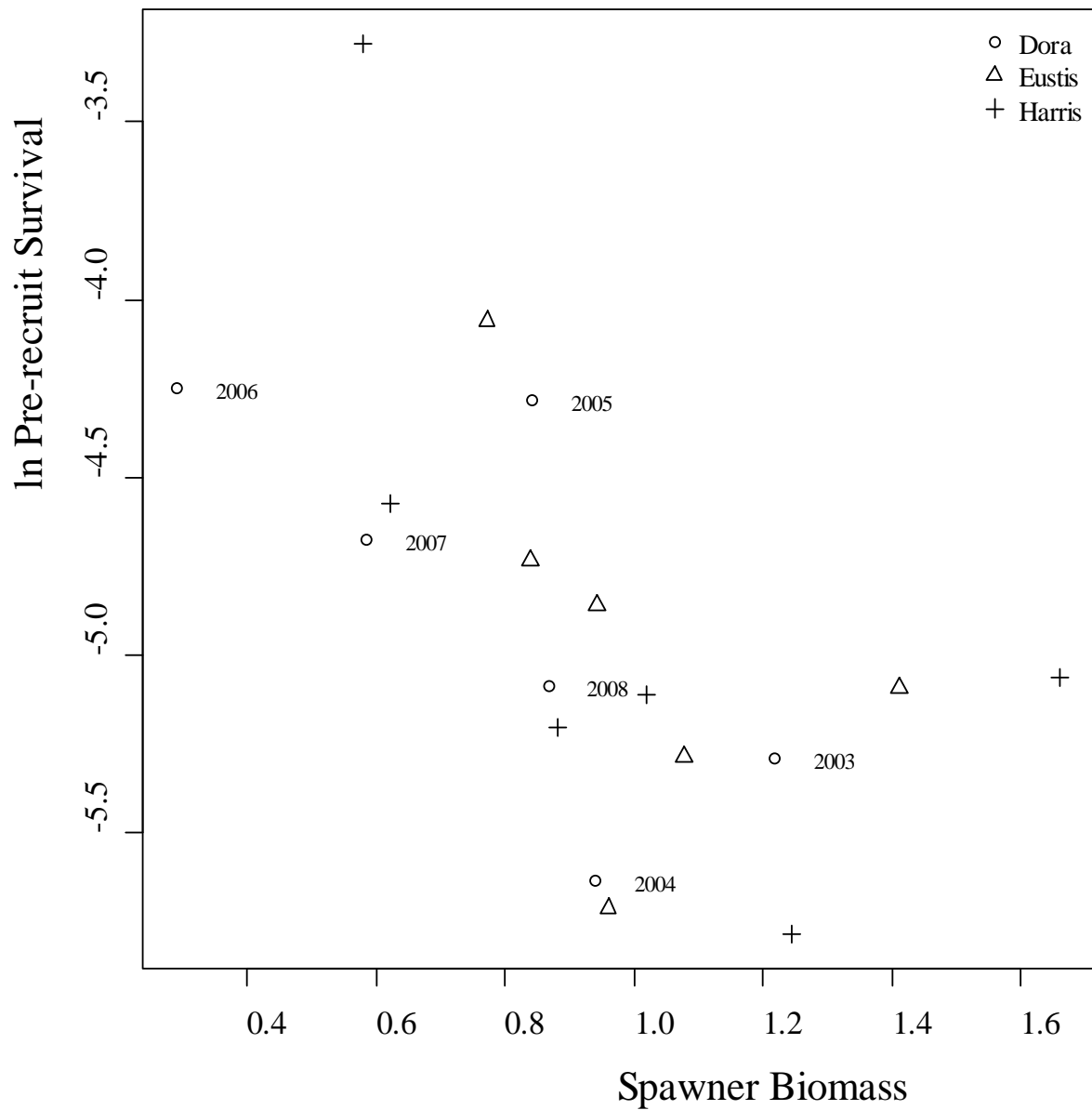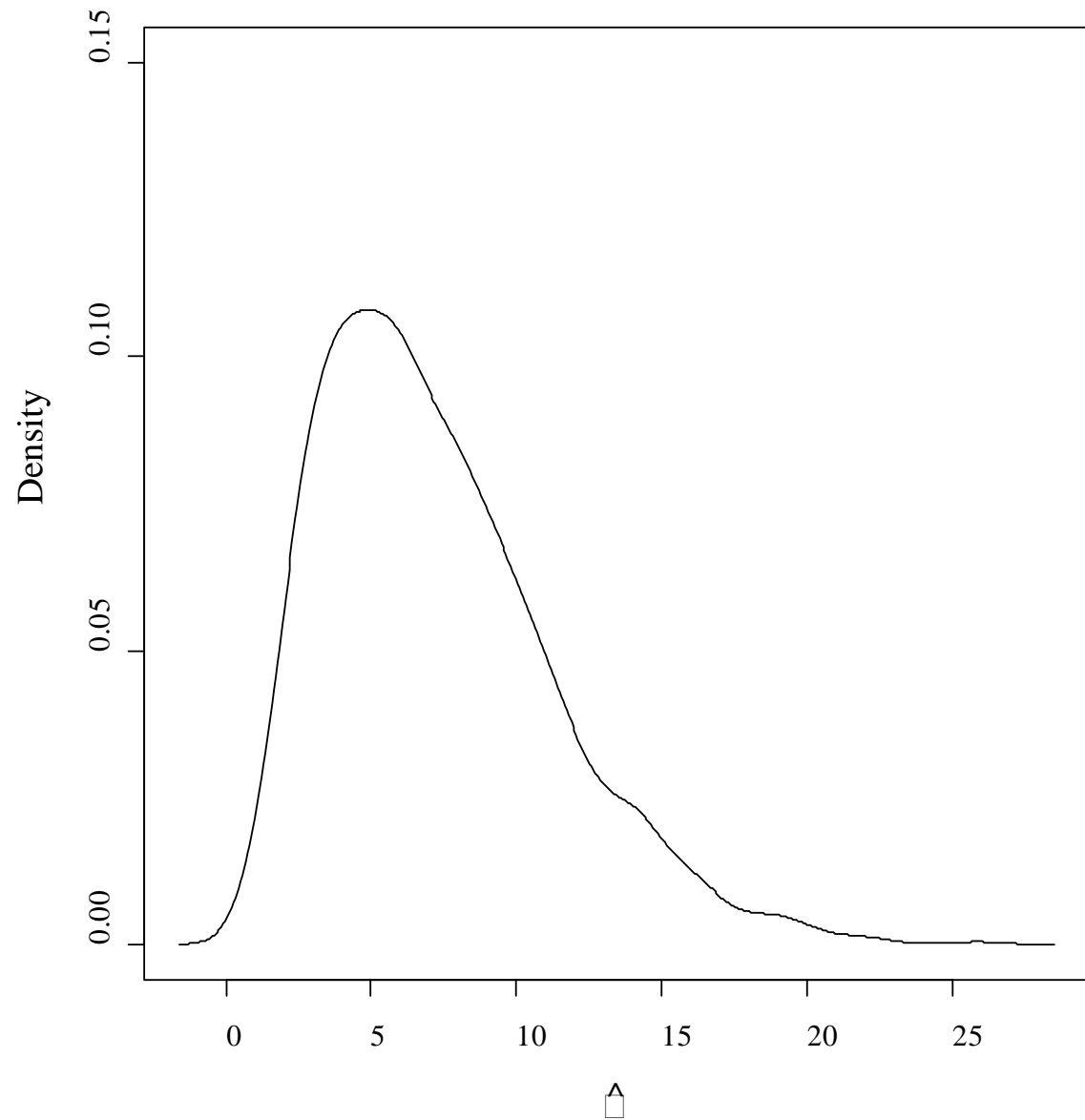
Figure 1-5.  Log$_e$ juvenile (pre-recruit) survival as a function of spawner biomass at Lakes Dora (circles), Eustis (triangles) and Harris (plus).  Survival and spawner biomass observations are point estimates from the length-age model.  Cohort years are indicated for the Lake Dora cohorts.

# CHAPTER 2: EXPLORING REMOVAL STRATEGIES FOR GIZZARD SHAD THAT ACCOUNT FOR UNCERTAINTY IN THE STRENGTH OF COMPENSATION

## Introduction

Compensatory density dependence is an important life history characteristic of fish populations. The strength of compensation determines a population's ability to withstand increased mortality rates and therefore defines the limits of harvest (Myers et al. 1999), which could have implications for biomanipulation efforts. Biomanipulation projects could have unintended consequences for lake ecosystems depending on the shape and strength of density dependence of the target species. For example, fish species with dome-shaped overcompensatory relationships between spawner abundance and age-1 recruits could become more abundant following moderate removals that reduce the population size to a state of optimal productivity (Zipkin et al. 2008). Thus removals may release populations from density-dependent suppression of recruitment due to competition between adults and juveniles. Such compensatory responses could lead to increased rather than decreased grazing of zooplankton, which would have the opposite effect on phytoplankton abundance that is desired (Romare and Bergman 1999). Species with asymptotic relationships between spawner biomass and recruitment (e.g., Beverton-Holt recruitment) may maintain relatively constant recruitment despite reductions in spawner biomass, which would reduce the efficacy of removal efforts.

Accounting for the strength of density dependence of gizzard shad in biomanipulation studies could help improve the efficacy of removal programs. Such studies could guide removal strategies by suggesting removal methods that achieve maximum density reduction or recommending the discontinuation of programs that are unlikely to achieve large enough biomass reductions to reduce phytoplankton biomass. We evaluated the efficacy of removal strategies for gizzard shad biomanipulation in hypereutrophic Florida lakes while accounting for uncertainty in the strength of compensatory density dependence. Catalano et al. (2007) conducted a similar analysis. However, they did not have adequate estimates of the strength of compensation for the Lake Dora gizzard shad population. Rather they used two "best-guess"

estimates (obtained from the literature) of compensation in their simulations. In the chapter we revisited Catalano et al.'s (2007) analyses and incorporated estimates of the strength of compensation from Chapter 1 that were calculated directly from Lake Dora gizzard shad data. We also incorporated observed levels of uncertainty in the strength of compensation. Incorporating uncertainty allowed us to address the efficacy of gizzard shad removal in terms of the probability that a given removal scenario (e.g., mesh size) will result in a given level of biomass reduction (e.g., 75% biomass reduction). Specifically, we evaluated the effect of exploitation rate ($u$), gill net mesh size, and harvest interval (years between removals) on total population biomass and spawning potential ratio (SPR) of gizzard shad.

## Methods

We evaluated the influence of exploitation rate, gill net mesh size, and harvest interval on the percent total biomass reduction and spawning potential ratio of gizzard shad at the Harris Chain of Lakes, Florida, using a simulation model. Percent biomass was evaluated to assess the degree to which a biomanipulation target of 75% biomass reduction (Meijer et al. 1999) was met by a given harvest strategy. Spawning potential ratio (SPR) is a measure of the potential spawner biomass under a given harvest rate relative to the unfished condition and was used to assess the potential for recruitment overfishing (Mace 1994). Simulated population responses to the harvest regime accounted for uncertainty in the strength of density dependence for gizzard shad via a parametric bootstrap procedure.

*Gear Selectivity*

Understanding gear selectivity is essential for simulating potential effects of harvest on fish populations. We evaluated the efficacy of five gillnet mesh sizes: 51, 64, 76, 89, and 102 mm for gizzard shad removal. Estimates of a gear selectivity function were needed for each of these mesh sizes as input parameters for the simulation model. In Chapter 1 we estimated survey and fishery gear selectivity for the gizzard shad removal at Lake Dora. However, the gizzard shad removal had a minimum mesh size restriction of 102 mm and consequently gear selectivity for smaller mesh sizes was unknown and could not be estimated from the removal fishery. Survey gear selectivity estimates from Chapter 1 were also not useful because the survey nets

had multiple panels of different mesh sizes and the estimated selectivity function applied to all of the panels collectively.

To obtain gear selectivity estimates for each mesh size, we estimated the selectivity parameters using a length and age structured population model (see Appendix B for model details). In Chapter 1, we estimated natural mortality, growth and recruitment time series for gizzard shad at Lakes Dora, Eustis, and Harris. Using these parameter estimates as model inputs, we individually estimated gear selectivity for the 51 – 102 mm mesh sizes by fitting the model to length-specific gill net catch data from UF and SJRWMD annual January fishery-independent gill net surveys. The survey gill net data were separated by mesh size, and a three parameter gear selectivity function was fit to the data from each mesh size to estimate mesh-specific gear selectivity parameters. This approach assumed that the point estimates of growth, mortality, recruitment that were used as model inputs were the 'true' values for the lakes and thus the estimates of mesh-specific gear selectivity did not account for uncertainty in these input parameters. Lake-specific gear selectivity parameters were not estimated because we were interested in obtaining 'average' gear selectivity curves across all of the lakes for use as inputs in the simulation model. Therefore, the simulation model represented a generic system with similar fishery characteristics to the Harris Chain of Lakes.

Gill net catch data were obtained from annual fishery-independent gill net surveys conducted by the author (UF) and SJRWMD in January/February at each lake. The UF survey set multi-panel floating gill nets at 20 fixed randomly-selected sites at each lake in January/February (all lakes: 2005 - 2009). The SJRWMD survey set multi-panel gill nets at 10 fixed sites at Lakes Eustis and Harris and 20 sites at Lake Dora (Lake Dora: 2003, 2005 – 2009; Lake Eustis: 2003, 2006-2009; Lake Harris: 2003). Survey gill nets were 2.4-m deep and contained five, 15.3-m long panels of 64, 76, 89, 102, 114, and 127-mm stretch monofilament mesh and nets were set for 2 hours each. The UF gill nets had an additional panel of 51-mm mesh to target age-1 fish. All captured fish were measured in the field and placed in 10-mm length bins to construct length distributions to which the length-age model was fit.

*Uncertainty in Compensation*

The maximum lifetime reproductive rate $\hat{\alpha}$ is a standardized measure of the strength of density dependence for a given fish population and is comparable across species (Myers et al.

1999; Goodwin et al. 2006). This parameter is also known as the Goodyear compensation ratio and describes the ratio juvenile survival at very low population density to juvenile survival in an unfished population (Goodwin et al. 2006; Walters et al. 2006). An estimate of the mean and standard deviation of $\hat{\alpha}$ for gizzard shad was obtained from Chapter 1. We found that the average $\hat{\alpha}$ for gizzard shad was 6.6 with a 95% confidence interval of 1.7 to 15.2 across Lakes Dora, Eustis, and Harris, and this degree of compensation was due primarily to density-dependent changes in juvenile survival and not to changes in growth or maturity. Uncertainty in $\hat{\alpha}$ estimates from Chapter 1 were used to estimate uncertainty in population biomass and SPR as a function of gill net mesh size, exploitation rate and harvest interval using a simulation model.

*Simulations*

We constructed a simple population model to simulate the efficacy (i.e., percent biomass reduction and SPR) of gizzard shad removal over a range of exploitation rate, gill net mesh size, and harvest interval. The model was similar to the one used in Catalano et al. (2007). The model was of the form:

$$N_{a,t} = N_{a-1,t-1}e^{-M}(1 - v_a u_t),$$ (2-1)

where $N_{a,t}$ is the number of fish in the population at age $a$ in year $t$, $M$ is the instantaneous natural mortality rate, $v_a$ is the age-specific gear selectivity term ranging from 0 to 1, and $u_t$ is the finite annual fishing mortality rate. Fishery gear selectivity, $v_a$, was estimated using the function (Thompson 1994):

$$v_a = \left(\frac{1}{1-\gamma}\right)\left(\frac{1-\gamma}{\gamma}\right)^{\gamma}\left(\frac{e^{\beta\lambda(L_{50}-L)}}{1+e^{\beta(L_{50}-L)}}\right),$$ (2-2)

where $L$ is the mean length at age $a$ from the von Bertalanffy growth model, $\gamma$ is the shape parameter that determines the shape, $\beta$ describes the steepness, and $L_{50}$ is the length at 50% selectivity. This is a flexible selectivity function that produces either a dome shaped or sigmoidal curve, depending on parameter values. Values of $\gamma$ are bounded between 0 and 1. The functional form becomes sigmoidal (i.e., knife edge selectivity) as $\gamma$ approaches 0 and increasingly dome-shaped as $\gamma$ approaches 1.

Preliminary analyses suggested that the smaller meshes had strongly dome-shaped selectivity curves. This meant that fish of a particular size interval were vulnerable to capture but that individuals above and below the interval were not vulnerable. If the our simulation model strictly assumed that all fishers used only the minimum mesh size, then fish would only be vulnerable to capture if they were within the size window for the particular mesh. In this case the fishery would not capture large fish and small fish that were not caught could grow out of the vulnerable window and become safe from harvest, which could underestimate the harvest and total biomass reduction  Thus we concluded that dome-shaped gill net selectivity functions would be unrealistic for these simulations because fishers would likely choose to fish larger meshes early in the season to capture any large fish that were available. Fishers would likely then switch to smaller meshed as catches of large fish dropped off. To account for this process, any gear selectivity functions that were dome-shaped were converted to asymptotic curves by setting $\gamma$ equal to zero (Figure 2-1). This was done to mimic occasional fisher use of larger mesh sizes than the minimum by making large fish vulnerable harvest even when the minimum mesh size restriction was small (e.g., 51-mm). Using the dome-shaped selectivity curves would have been unrealistic because fishers would not have used a small mesh if large fish were available in the population and could be caught with a larger mesh. This approach differs from that of Catalano et al. (2007) because they allowed dome-shaped selectivity curves. By assuming asymptotic selectivity, our analysis allowed a greater reduction in gizzard shad populations at a given exploitation rate than Catalano et al.'s (2007) analysis. Thus results of our analysis could be viewed as a best case scenario with respect to total biomass reduction and SPR.

The equilibrium model had deterministic recruitment predicted as a function of spawner biomass using the Beverton-Holt stock-recruitment model (Walters et al. 2006):

$$N_{1,t} = \frac{\dfrac{\hat{\alpha}}{\phi_0} E_{t-1}}{1 + \left(\dfrac{\hat{\alpha}-1}{R_0 \phi_0}\right) E_{t-1}}, \qquad (2\text{-}3)$$

where $\phi_0$ is the equilibrium lifetime spawner biomass per recruit in the absence of fishing, $R_0$ is the equilibrium unfished age-1 recruitment set to a value of 1, and $E_{t-1}$ is the total population spawner biomass from the previous year. The Beverton-Holt model is an asymptotic model such that recruitment is relatively constant across a wide range of spawner biomass. This is a

different model than the Ricker function that was used to obtain the $\hat{\alpha}$ estimates in Chapter 1 Few stock-recruit data sets contain enough observations at extremely high spawner biomass to differentiate between Ricker and Beverton-Holt models (Myers et al. 1999). Estimates of $\hat{\alpha}$ from the Ricker model are relatively robust to varying assumptions regarding the shape of the function (asymptotic or dome-shaped) and should be appropriate for use in the Beverton-Holt model (Myers et al. 1999). Stock-recruit data from Chapter 1 were too sparse to differentiate between the two models. In the absence of knowledge on the shape of the stock recruit function for gizzard shad at the Harris Chain of Lakes, the Beverton-Holt model is appropriate given the life history characteristic of gizzard shad. Beverton-Holt recruitment dynamics are typically associated with pelagic fish with planktivorous diets and ontogenetic diet or habitat shifts such that negative interactions between adults and juveniles are weak. As such, the Beverton-Holt model is appropriate for simulating gizzard shad population dynamics and is a more conservative approach because it does not allow for overcompensatory recruitment dynamics such as increased recruitment following moderate reduction in spawner biomass.

Equilibrium lifetime unfished spawner biomass per recruit was calculated as:

$$\phi_0 = \sum_a s_a m_a w_a , \tag{2-4}$$

where $s_a$ is the survivorship to age $a$, $m_a$ is the age-specific proportion of fish mature, and $w_a$ is the age-specific mean weight. Maturity was estimated using the mean age at 50% maturity from Lakes Dora Eustis and Harris from Chapter 1. Weight at age was estimated using the allometric relationship:

$$w_a = cL^b , \tag{2-5}$$

where $c$ and $b$ are allometric coefficients obtained by fitting the model to gizzard shad collected in UF survey gillnets from 2005-2009.

Annual spawner biomass $E_t$ was estimated as:

$$E_t = \sum_a N_a m_a w_a . \tag{2-6}$$

The model predicted total population biomass and spawning potential ratio (SPR) as a function of exploitation rate, gill net minimum allowable mesh size, and harvest interval (number of years between harvests). Other model inputs were set based on literature values. The model simulated eight age classes and an average unfished recruitment ($R_0$) of 1.0. Instantaneous natural mortality ($M$), asymptotic length ($L_\infty$), the von Bertalanffy metabolic coefficient ($K$), and

time at zero length ($t_0$) were taken from Chapter 1. Each parameter value was obtained by averaging over lake-specific estimates from akes Dora, Eustis, and Harris ($M = 1.01$ yr-1, $L_\infty = 394$, $K = 0.69$, $t_0 = 0.3$). Length at maturity was obtained from a logistic regression model Chapter 1 and was used to estimate the proportion of females mature at each age ($m_a$).

The maximum lifetime reproductive rate $\hat{\alpha}$ is an important term because it defines the degree of compensation in the population and thus determines the limits of harvest. Populations with high $\hat{\alpha}$ will maintain relatively constant recruitment across a wide range of adult population sizes (i.e., large declines), compared to low $\hat{\alpha}$, which indicates that reductions in adult population sizes cause declines in average recruitment. Thus, we varied $\hat{\alpha}$ using the uncertainty from Chapter 1 in a parametric bootstrap analysis. For each combination of exploitation rate (0.1 to 1.0 by 0.1), mesh size (51, 64, 76, 89, 102 mm), and harvest interval (every 1, 2, 3 and 4 years), we drew 1,000 random lognormally-distributed deviates for $\hat{\alpha}$ assuming a mean of 6.6 and standard deviation of 3.7 from Chapter 1. We calculated total population biomass and SPR for each value of $\hat{\alpha}$ across each possible combination of exploitation rate, gill net mesh size, and harvest interval. Biomass and SPR for each $\hat{\alpha}$ value was calculated by averaging the last 50 model years after a 150-yr burn-in period to allow the population to reach equilibrium. The average equilibrium population biomass and SPR was calculated for each possible combination of harvest frequency, mesh size, and exploitation rate by averaging over the 1,000 bootstrap estimates. Uncertainty in biomass and SPR was estimated by calculating the 2.5% and 97.5% quantiles of biomass and SPR across the 1,000 bootstrap estimates. Total population biomass was calculated as:

$$B = \sum_a N_a w_a . \tag{2-7}$$

SPR was calculated as:

$$SPR = \frac{R_0 \phi_0}{R_f \phi_f}, \tag{2-8}$$

where $R_f$ and $\phi_f$ are the equilibrium recruitment and spawner biomass per recruit, respectively, under a given harvest scenario.

To further explore uncertainty in biomass and SPR, we calculated the probability that a given harvest regime would result in a biomass that was less than 25% of the equilibrium unfished value (i.e., 75% biomass reduction) and an SPR of less than 25%. The target level of

75% reduction in total gizzard shad biomass was used to indicate harvest strategies (i.e., fishing frequency, gill net mesh, and exploitation rate) that achieve rates likely to cause changes in lake phytoplankton abundance (Hansson et al. 1998; Meijer et al. 1999). Fishing mortality rates that result in SPR less than 40% increase the risk for recruitment overfishing (i.e., fishing at a rate that prevents a stock from replacing itself; Mace 1994), but this cutoff may be lower for highly productive species such as the gizzard shad (Clark 2002). Thus, we chose 25% as a target SPR to indicate which harvest scenarios presented the greatest probability of causing recruitment overfishing for gizzard shad since gizzard shad are short lived and likely to withstand substantial harvest because of high natural mortality and rapid growth rates.

## Results

Gear selectivity functions were dome-shaped for the 51 to 76-mm gill net mesh and were sigmoidal for the 89 and 102-mm mesh (Figure 2-1a). Lengths at 50% selectivity (L50) ranged from 166 mm for the 51-mm mesh to 339 mm for the 102-mm mesh (Figure 2-1a,b; Table 2-1). Predicted catches of gizzard shad tightly fit the observed length distributions for each mesh size (Figure 2-2).

Equilibrium population biomass was sensitive to changes in gill net mesh size. The 51-mm mesh and a one-year harvest interval drove the population to extinction when the exploitation rate exceeded 0.8 (Figure 2-3a). None of the other mesh sizes reduced the average population biomass to less than 35% of the unfished value even at an exploitation rate of 1.0 (Figure 2-3a,b,c). When accounting for uncertainty in the maximum lifetime reproductive rate, the probability of reducing the population biomass to less than 25% of the unfished value was less than 0.15 for all meshes except 51-mm when the exploitation rate was 0.8 or less (Table 2-2). The 102-mm mesh was the least effective at reducing biomass; the average biomass was 72% of the unfished value at an exploitation rate of 1.0 (Figure 2-3e) and the probability of achieving a biomass of 25% was 0.01 at an exploitation rate of 0.8. Biomass remained greater than 50% of the unfished value for all mesh sizes except 51-mm when the harvest interval was two or more years, regardless of exploitation rate.

Equilibrium SPR was reduced more than total population biomass due to the size-selective nature of the fishery. The 51-mm mesh and a one-year harvest interval reduced SPR to near zero when the exploitation rate exceeded 0.8 (Figure 2-4a), which the model suggested would

eliminate recruitment and drive the population to extinction. The 64, 78, and 89-mm mesh resulted in SPR of 30-50% (Figure 2-4b,c,d). The probability of reducing SPR to less than 25% exceeded 0.85 when exploitation rate exceeded 0.2 for the 51-mm mesh (Table 2-3). The 64 and 76-mm mesh resulted in a less than 0.25 probability of an SPR dropping below 25% when exploitation rate was 0.8 (Table 2-3). The 102-mm mesh was ineffective at reducing SPR (Figure 2-4e). Reducing SPR to less than 25% was highly unlikely with a two-year harvest interval for all mesh sizes except 51 mm (Table 2-3).

## Discussion

Gizzard shad removals at the Harris Chain of Lakes using gill nets are unlikely to achieve large (75%) reductions in biomass or SPR unless a 51-mm mesh size is used, a high exploitation rate is achieved, and fish are harvested every year. Larger mesh sizes left a large proportion of the population biomass invulnerable to harvest due to the selective properties of the gear. High estimated natural mortality rate also dampened the effects of fishing on total biomass of this population because a large proportion of the population resided in young, invulnerable age classes and most fish died naturally before they could be harvested. Failure to reduce SPR to less than 25% indicates that recruitment overfishing is unlikely in this system. Thus, recruitment failure is unlikely and the population would have to be harvested annually to maintain biomass reductions, which would increase removal costs.

We assumed an average $\hat{\alpha}$ value of 6.6 to represent the strength of compensation. This value was obtained directly from our lake Dora analysis in Chapter 1. Catalano et al. (2007) assumed "best guess" $\hat{\alpha}$ values of 18 and 25 to represent assumed low and high levels of compensation based on the literature. Our results from Chapter 1 suggest that Catalano et al. (2007) overestimated the strength of compensation for gizzard shad. Despite this difference, our findings regarding the efficacy of gill net biomanipulation were very similar to Catalano et al. (2007). Both analyses show that current removal efforts are unlikely to attain substantial biomass reductions of gizzard shad in the long term given current exploitation rates of 60-70% (Catalano et al. *in review*). We also show that even higher exploitation rates are very unlikely to cause large gizzard shad reductions unless a smaller mesh size is used. Use of the smallest mesh size (51 mm) would increase biomass reductions and the likelihood for recruitment overfishing but would also increase bycatch of black crappie, which could reduce the value of an important

recreational fishery (Dotson et al. *In press*).  Resource managers and stakeholders for the Harris Chain of Lakes will need to carefully explore the tradeoffs between gizzard shad biomanipulation and black crappie fisheries.

There are several assumptions of our analysis that should be addressed.  We chose a 75% biomass reduction target from the literature because meta-analyses have shown that this level of reduction is associated with higher biomanipulation success rates (Hansson et al. 1998; Meijer et al. 1999).  However, these studies are based primarily on planktivore removals.  Gizzard shad are omnivores capable of consuming zooplankton as well as benthic organic detritus.  Gizzard shad benthivory may provide a source of "new" nutrients to the phytoplankton that were previously unavailable in the sediments (Schaus et al. 1997; Gido 2002).  Thus, gizzard shad may affect phytoplankton biomass via top-down grazing and bottom-up direct nutrient enrichment (DeVries and Stein 1992).  Horpilla et al. (1998) reported substantial reduction in phytoplankton biomass following 79% biomass reduction of omnivorous roach (*Rutilus rutilus*).  The biomass reduction that would reduce phytoplankton biomass at Lake Dora is unknown and may be more or less than the 75% target identified from planktivore removals.  Our data do not address the applicability of this value to Lake Dora.  However, our data suggest that long-term total gizzard shad biomass reductions are unlikely to exceed 40-50% at Lake Dora or similar lakes without substantial increases in the exploitation rate and decreases in gill net mesh size.

Second, we accounted for uncertainty only in the strength of density dependence.  The results of the simulation model are dependent on many other parameters such as growth and natural mortality, which we assumed were known without error in the model.  This approach isolated the effects of recruitment compensation on harvest policies, which in this case was desirable given that we only found changes in juvenile fish survival after fishing.  However, fish stock assessment models can be very sensitive to error in natural mortality estimates.  Upward bias in natural mortality in our analysis would underestimate biomass reduction because the model would overestimate the number of fish dying naturally before reaching a harvestable size.  Similarly, overestimates of growth rates would underestimate biomass reduction and SPR because fish would reach a larger size more rapidly, which would increase stock productivity.  Nevertheless, incorporating uncertainty in the strength of density dependence is an advance over previous analyses of fish removals and the gizzard shad population at the HCL was sensitive to the assumed value for $\hat{\alpha}$ .  For example, the estimated biomass reduction for the 76-mm mesh at

an exploitation rate of 1.0 and an annual harvest interval ranged from 0.18 to 0.7, depending on the assumed $\hat{\alpha}$ value.

Third, we assumed gear selectivity functions were asymptotic when in fact each mesh size had a dome shaped gear selectivity curve. Using the estimated dome-shaped selectivity functions would have been unrealistic because it is unlikely fishers would have exclusively used a particular mesh size if they had the option to use larger mesh sizes. By assuming asymptotic selectivity functions, we assumed that fishers would occasionally choose to use large mesh sizes to exploit fish that had grown large enough to escape minimum mesh size, thus resulting in approximately asymptotic selectivity. This was an attempt to mimic the process of fishers "fishing down" the population and eventually settling on the smallest mesh size allowed after catches in large meshed declined. Moreover, allowing the dome-shaped selectivity function for each mesh would have underestimated the biomass reduction for the smallest mesh sizes and at lower exploitation rates because large fish would have been invulnerable to capture. As such, our gear selectivity assumptions were reasonable and provided the most realistic estimates of biomass reduction and SPR.

Our simulations showed that the 51-mm mesh was most likely to cause substantial biomass reduction but it is not known whether that mesh size would be acceptable to gill net fishers. Smaller mesh sizes are more labor-intensive to process and bycatch of undesirable species would have increased (Dotson et al. *In press*). If biomass were reduced substantially and SPR was reduced enough to cause recruitment failures, then catches would decline drastically. In this case, it would be difficult for fishers to maintain adequate catches to cover costs and they may choose to use a larger mesh size or leave the fishery. Increased price subsidy may be required as catches decline to maintain high harvest rates. Populations of species like the gizzard shad would likely recover rapidly if exploitation were relaxed. Indeed, biomanipulation programs often must be continued indefinitely to maintain changes in phytoplankton biomass due to planktivore removal (McQueen 1998).

The strength and functional form of compensatory density dependence in a population defines the limits of harvest and has important implications for removal efforts. Zipkin et al. (2008) found that experimental removal of smallmouth bass at Little Moose Lake, NY, resulted in increased recruitment, suggesting a Ricker form of the stock-recruitment relationship. They identified several mechanisms that could explain the increase such as high per capita recruitment

at low population size combined with high juvenile survivorship and high maturation rates of age-4 smallmouth bass. Meijer et al. (1999) reported increased age-0 fish abundance following several fish removals. Kim and DeVries (2000) found strong compensatory growth and maturation of gizzard shad at Walker County Lake, Alabama following partial piscicide treatment. In their study, mean length of age-0 gizzard shad in fall was >60% larger at low gizzard shad densities than at high densities. These compensatory responses allowed the gizzard shad population to return to pre-manipulation abundance within one year of treatment. Romare and Bergman (1999) reported a 20-fold increase in juvenile fish abundance following planktivore removal at Lake Ringsjön, Sweden. Thus, compensatory responses of target species have been observed following fish removals.

Despite the importance of compensation in the efficacy of fish removals, only one study to date (Zipkin et al. 2008) has explored the potential effects of compensation. The strength of manipulation is a key consideration for biomanipulation and many studies fail to adequately address this issue (DeVries and Stein 1990). At minimum, the degree to which population biomass was reduced should be quantified to assess biomanipulation strength. However, this analysis is not completed in many cases, thus leading to uncertainty in mechanisms that impact the results of biomanipulation efforts (Meronek et al. 1996). We also recommend that our model should be combined with models describing temperature- and mass-specific gizzard shad nutrient excretion rates. This would allow forecasting of nutrient reductions (attributable to gizzard shad) under various removal scenarios (e.g., mesh size, exploitation rate). These forecast estimates could then be viewed against data on whole-lake nutrient budgets to determine whether the reductions are large relative to other nutrient sources in the lake. Conducting these analyses before removal begins is critical to identify situations in which biomanipulation could be successful, or conversely, to prevent spending large amounts of money on gizzard shad removal subsidies and monitoring for situations that have a low probability of success.

Table 2-1.  Gear selectivity parameter estimates (95% confidence interval) for each gill net mesh
size from the from the length age model.  Point estimates of L50 and b were used in
the simulation model to evaluate competing removal scenarios with varying
exploitation rate, mesh size, and harvest interval.  Parameter subscripts denote the
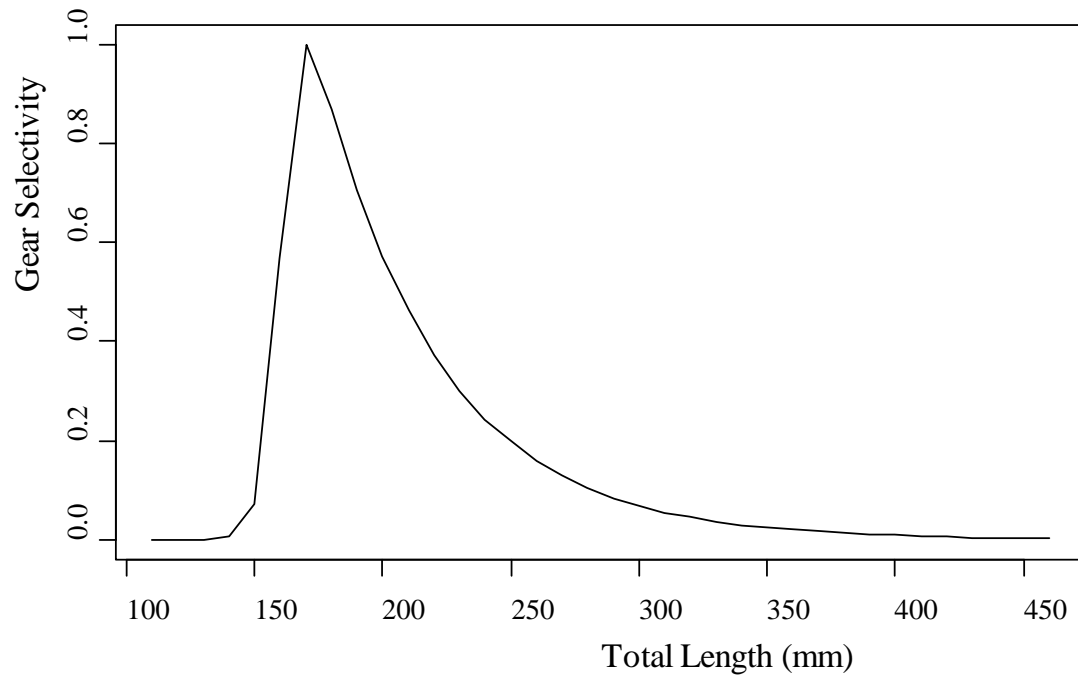mesh size.

| Parameter | Estimate |
|-----------|----------|
| $L50_{51}$ | 165.86 (163.99 - 167.74) |
| $\gamma_{51}$ | 0.07 (0.05 - 0.10) |
| $\beta_{51}$ | 0.28 (0.22 - 0.35) |
| $L50_{64}$ | 217.25 (214.26 - 220.28) |
| $\gamma_{64}$ | 0.13 (0.11 - 0.16) |
| $\beta_{64}$ | 0.13 (0.12 - 0.15) |
| $L50_{76}$ | 251.32 (247.84 - 254.84) |
| $\gamma_{76}$ | 0.05 (0.03 - 0.07) |
| $\beta_{76}$ | 0.10 (0.09 - 0.11) |
| $L50_{89}$ | 290.27 (287.92 - 292.64) |
| $\gamma_{89}$ | 0.00 (0.00 – 0.00) |
| $\beta_{89}$ | 0.07 (0.07 - 0.08) |
| $L50_{102}$ | 340.09 (336.59 - 343.62) |
| $\gamma_{102}$ | 0.00 (0.00 – 0.00) |
| $\beta_{102}$ | 0.05 (0.05 - 0.06) |

Table 2-2. Probability that total population biomass is less than 25% of equilibrium unharvested value for a one and two year harvest interval, a range of exploitation rates (μ), and five gill net mesh sizes ranging from 51 to 102 mm.

| Interval (yrs) | μ | Gill Net Mesh Size | | | | |
|---|---|---|---|---|---|---|
| | | 51 | 64 | 76 | 89 | 102 |
| 1 | 0.4 | 0.44 | 0.03 | 0.02 | 0.01 | 0.00 |
| | 0.6 | 0.97 | 0.07 | 0.05 | 0.02 | 0.00 |
| | 0.8 | 1.00 | 0.14 | 0.09 | 0.03 | 0.01 |
| 2 | 0.4 | 0.04 | 0.01 | 0.00 | 0.00 | 0.00 |
| | 0.6 | 0.12 | 0.02 | 0.02 | 0.01 | 0.00 |
| | 0.8 | 0.43 | 0.06 | 0.04 | 0.02 | 0.00 |

Table 2-3. Probability that transitional spawning potential ratio (SPR) is less than 25% of for a one and two year harvest interval, a range of exploitation rates (μ), and five gill net mesh sizes ranging from 51 to 102 mm.

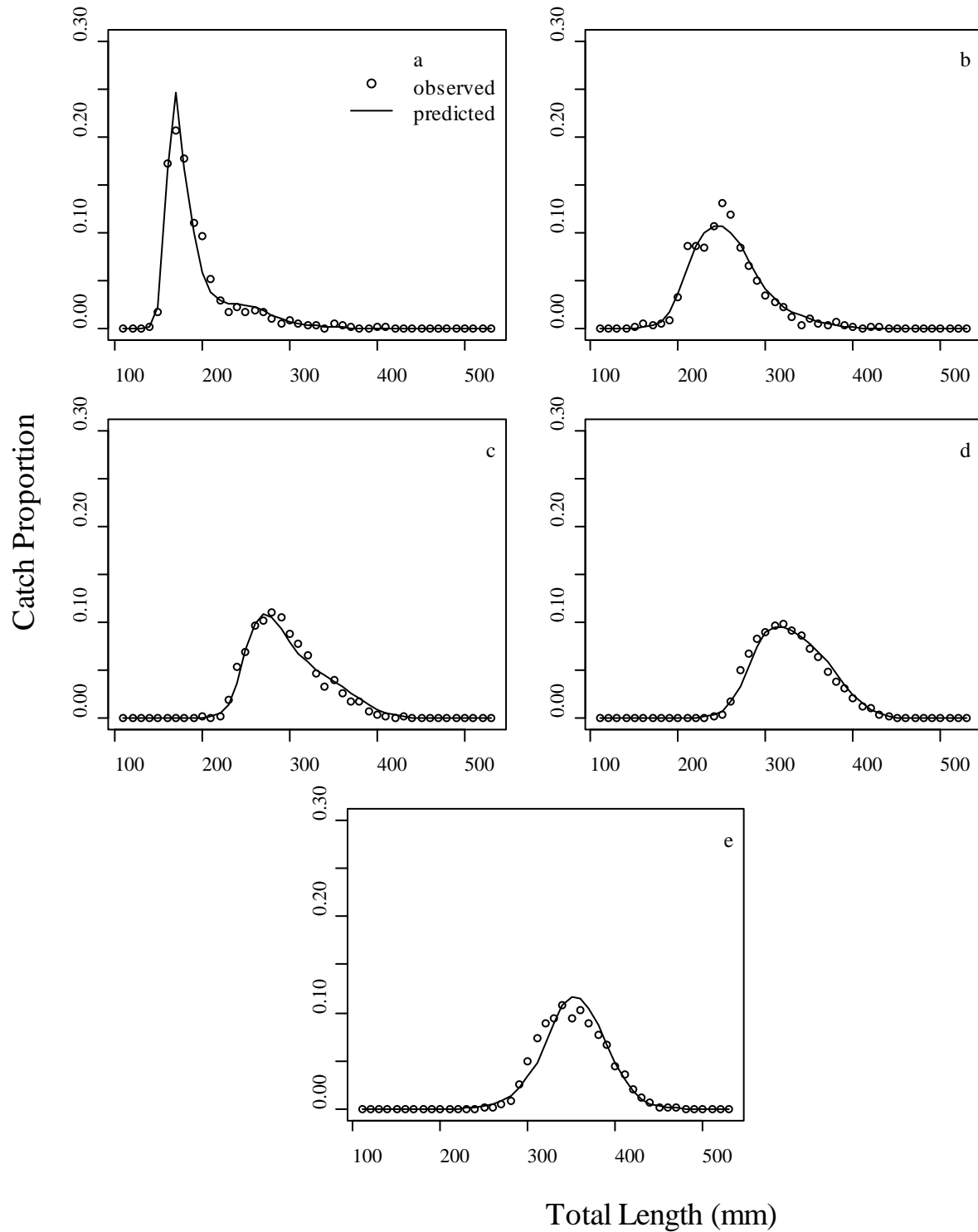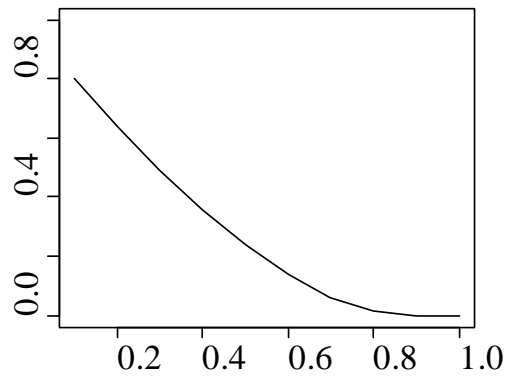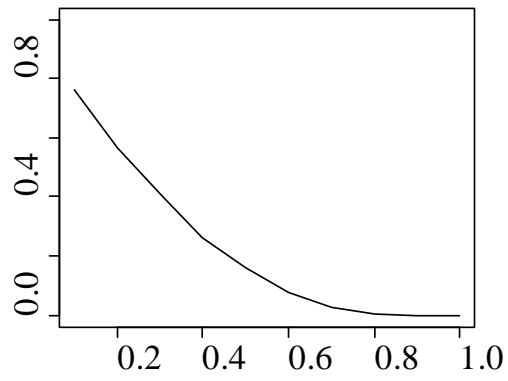| Interval (yrs) | μ | Gill Net Mesh Size | | | | |
|---|---|---|---|---|---|---|
| | | 51 | 64 | 76 | 89 | 102 |
| 1 | 0.4 | 0.84 | 0.03 | 0.03 | 0.01 | 0.00 |
| | 0.6 | 1.00 | 0.09 | 0.07 | 0.02 | 0.00 |
| | 0.8 | 1.00 | 0.23 | 0.15 | 0.04 | 0.01 |
| 2 | 0.4 | 0.11 | 0.01 | 0.00 | 0.00 | 0.00 |
| | 0.6 | 1.00 | 0.04 | 0.03 | 0.01 | 0.00 |
| | 0.8 | 1.00 | 0.15 | 0.11 | 0.02 | 0.00 |

Figure 2-2. Observed (points) and predicted (lines) length distributions of catches for each gill net mesh size. Observations and model predictions were summer over lakes and years.

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| Lake | Site | Latitude | Longitude | Gillnets | Larval Fish | Zooplankton |
|---|---|---|---|---|---|---|
| Dora | 1 | 28.7960 | -81.7320 | X | X | |
| Dora | 2 | 28.7913 | -81.7189 | X | X | X |
| Dora | 3 | 28.7860 | -81.7280 | X | | |
| Dora | 4 | 28.7920 | -81.7260 | X | | |
| Dora | 5 | 28.7960 | -81.7220 | X | | |
| Dora | 6 | 28.7800 | -81.7080 | X | | |
| Dora | 7 | 28.7829 | -81.7000 | X | X | X |
| Dora | 8 | 28.7840 | -81.6980 | X | X | |
| Dora | 9 | 28.7780 | -81.6860 | X | | |
| Dora | 10 | 28.7920 | -81.6800 | X | X | |
| Dora | 11 | 28.7780 | -81.6780 | X | | |
| Dora | 12 | 28.7808 | -81.6811 | X | X | X |
| Dora | 13 | 28.7840 | -81.6720 | X | | |
| Dora | 14 | 28.7976 | -81.6622 | X | X | X |
| Dora | 15 | 28.8040 | -81.6700 | X | | |
| Dora | 16 | 28.7880 | -81.6580 | X | X | |
| Dora | 17 | 28.7787 | -81.6517 | X | | |
| Dora | 18 | 28.7766 | -81.6643 | X | X | |
| Dora | 19 | 28.7724 | -81.6622 | X | X | X |
| Dora | 20 | 28.7703 | -81.6706 | X | | |
| Eustis | 1 | 28.8354 | -81.7420 | X | X | X |
| Eustis | 2 | 28.8160 | -81.7360 | X | X | |
| Eustis | 3 | 28.8220 | -81.7320 | X | | |
| Eustis | 4 | 28.8460 | -81.6980 | X | | |
| Eustis | 5 | 28.8360 | -81.7280 | X | X | |
| Eustis | 6 | 28.8200 | -81.7580 | X | | |
| Eustis | 7 | 28.8459 | -81.7420 | X | X | X |
| Eustis | 8 | 28.8380 | -81.7360 | X | | |
| Eustis | 9 | 28.8380 | -81.7500 | X | X | |
| Eustis | 10 | 28.8440 | -81.7160 | X | | |
| Eustis | 11 | 28.8500 | -81.7060 | X | | |
| Eustis | 12 | 28.8375 | -81.7210 | X | X | X |
| Eustis | 13 | 28.8560 | -81.7480 | X | | |
| Eustis | 14 | 28.8580 | -81.7520 | X | | |
| Eustis | 15 | 28.8606 | -81.7042 | X | X | X |
| Eustis | 16 | 28.8620 | -81.7400 | X | X | |
| Eustis | 17 | 28.8700 | -81.7160 | X | | |
| Eustis | 18 | 28.8700 | -81.7400 | X | | |
| Eustis | 19 | 28.8648 | -81.7273 | X | X | X |
| Eustis | 20 | 28.8720 | -81.7260 | X | X | |
| Harris | 1 | 28.7800 | -81.8660 | X | | |
| Harris | 2 | 28.7829 | -81.8617 | X | X | X |
| Harris | 3 | 28.7960 | -81.8540 | X | X | |
| Harris | 4 | 28.7780 | -81.8540 | X | | |
| Harris | 5 | 28.7740 | -81.8440 | X | | |
| Harris | 6 | 28.7640 | -81.8300 | X | X | |
| Harris | 7 | 28.7619 | -81.8176 | X | X | X |
| Harris | 8 | 28.7520 | -81.8280 | X | | |
| Harris | 9 | 28.7980 | -81.8160 | X | X | |
| Harris | 10 | 28.8200 | -81.7980 | X | | |
| Harris | 11 | 28.7660 | -81.7920 | X | | |
| Harris | 12 | 28.7976 | -81.8071 | X | X | X |
| Harris | 13 | 28.7380 | -81.7860 | X | | |
| Harris | 14 | 28.7840 | -81.7800 | X | | |
| Harris | 15 | 28.7680 | -81.7700 | X | X | |
| Harris | 16 | 28.7556 | -81.7903 | X | X | X |
| Harris | 17 | 28.7320 | -81.7680 | X | X | |
| Harris | 18 | 28.7304 | -81.7567 | X | X | X |
| Harris | 19 | 28.6980 | -81.7520 | X | | |
| Harris | 20 | 28.7140 | -81.7480 | X | | |

# APPENDIX B: AN AGE AND LENGTH STRUCTURED MODEL TO ESTIMATE GIZZARD SHAD GROWTH, MORTALITY, GEAR SELECTIVITY, AND RECRUITMENT

The model estimates a recruitment time series ($R_t$), instantaneous natural mortality rate ($M$), von Bertalanffy growth parameters (asymptotic length, $L_\infty$; metabolic coefficient, $K$; time at zero length, $t_0$), two parameters defining the standard deviation in length-at-age ($\lambda_1$, $\lambda_2$), and three parameters of a flexible gear selectivity function for a fishery-independent survey (shape, $\gamma_s$; steepness, $\beta_s$; length at 50% selectivity, $L_{s50}$) and the fishery ($\gamma_v$, $\beta_v$, $L_{v50}$). The model is conditioned on total annual harvest (biomass) and fit to a time series of survey (e.g., experimental gill net) length-age catch matrices ($n_{l,a,t}$) and fishery length composition data ($f_{l,t}$) using a multinomial maximum likelihood function. The survey length-age data are arranged in an array of dimensions length $\times$ age $\times$ year. The survey length-age component calculates the likelihood of the observed catch of age-$a$ fish in length bin $l$ at time $t$ given a model-generated set of predicted proportions at age, length, and time (Taylor et al. 2005). The survey length-age log likelihood was:

$$\ln \quad (n|\Theta) = \sum_l \sum_a \sum_t n_{l,a,t} \ln(p_{l,a,t}) , \tag{B-1}$$

where $n_{l,a,t}$ is the observed catch of age-$a$ fish in discrete length interval $l$ at time $t$, and $p_{l,a,t}$ is the model-predicted catch proportion of age-$a$ fish in length interval $l$ at time $t$. Predicted catch proportions $p_{l,a,t}$ are estimated as:

$$p_{l,a,t} = \frac{N_{l,a,t} s_l P(l|a)}{\sum_l \sum_a \sum_t N_{l,a,t} s_l P(l|a)} , \tag{B-2}$$

where $N_{l,a,t}$ is the predicted abundance of age-$a$ fish in length interval $l$ at time $t$, $s_l$ is the length-based survey gear selectivity, and $P(l|a)$ is the probability of being in length interval $l$ given age $a$. The $N_{l,a,t}$ term incorporates fishing and natural mortality (described below). The likelihood term for the fishery length distribution data was calculated similarly except that the $N_{l,a,t}$ terms are summed across ages to result in predicted length distributions and the $s_l$ term is replaced by the length-based fishery gear selectivity ($v_l$). Survey and fishery likelihood terms were summed to calculate the total likelihood.

Survey gear selectivity, sl, (and fishery gear selectivity, vl ) was estimated using the function (Thompson 1994):

$$s_l = \left(\frac{1}{1-\gamma_s}\right)\left(\frac{1-\gamma_s}{\gamma_s}\right)^{\gamma_s}\left(\frac{e^{\beta_s \lambda_s (L_{s50}-l)}}{1+e^{\beta_s (L_{s50}-l)}}\right), \tag{B-3}$$

where $\gamma_s$ is the shape parameter that determines the shape, $\beta$ describes the steepness, and $L_{s50}$ is the length at 50% selectivity. This is a flexible selectivity function that produces either a dome shaped or sigmoidal curve, depending on parameter values. Values of $\gamma_s$ are bounded between 0 and 1. The functional form becomes sigmoidal (i.e., knife edge selectivity) as $\gamma_s$ approaches 0 and increasingly dome-shaped as $\gamma_s$ approaches 1.

The $P(l|a)$ term is calculated from a normal probability density function with mean $l_a$ and standard deviation $sd_a$. Mean length-at-age, $l_a$, is assumed to follow the von Bertalanffy (1938) growth model:

$$l_a = L_\infty\left(1 - e^{-K(a-t_0)}\right), \tag{B-4}$$

where $L_\infty$ is the asymptotic length, $K$ is the metabolic coefficient, and $t_0$ is the time at zero length. The standard deviation in length-at-age is estimated using (Fournier et al. 1991):

$$sd_a = \lambda_1 e^{\left(-1+\lambda_2\frac{1-\rho^{a-1}}{1-\rho^{A-1}}\right)}, \tag{B-5}$$

where $\lambda_1$ defines the magnitude of the standard deviations, $\lambda_2$ controls the trend in $sd_a$ over ages, and $\rho$ is the Brody growth coefficient ($\rho = e^{-K}$).

The $N_{l,a,t}$ terms are estimated as the recruitment that occurred $a$-1 years prior ($R_{t-a+1}$) times the survivorship to age $a$ and length $l$ over the time interval $t$-$a$+1 to time $t$:

$$N_{l,a,t} = R_{t-a+1}e^{-Z_{l,a,t}}, \tag{B-6}$$

where $R_{t-a+1}$ is the recruitment that gave rise to the age-$a$ cohort and $Z_{l,a,t}$ is the cumulative lifetime instantaneous total mortality for age $a$ fish that are in length bin $l$ at time $t$. The model assumes fish recruit to the population at age 1, thus one is added to the time-specific recruitment subscript. Cumulative instantaneous mortality represents the total lifetime mortality experienced by a fish of a given length-age-time bin as they grew from age 1 to age $a$ along a growth trajectory with an asymptotic length $L_{\infty(l,t)} = l/(1-\exp(-K*(a-t_0)))$ (Taylor et al. 2005). The model assumes that $K$ is time (years), length, and age invariant, thus a unique asymptotic length $L_{\infty(l,t)}$ (i.e., growth trajectory) is calculated for each length-age bin. The cumulative instantaneous mortality is calculated separately for each length-age bin and year as (Taylor et al. 2005):

$$Z_{l,a,t} = M(a-1) + \sum_{a'} v_{l(a')}F_{t(a')}, \tag{B-7}$$

where $a'$ is a vector of ages from age 1 up to age $a$-1, and $F_{t(a')}$ and $v_{l(a')}$ are vectors of annual instantaneous fishing mortality rates and length-specific fishery gear selectivities, respectively. These terms represent the fishing mortalities and fishery gear selectivities that would have been experienced in the past by fish in a given length-age-time bin. The product of the elements of vectors $F_{t(a')}$ and $v_{l(a')}$ were summed over the age interval $a'$ to calculate the cumulative instantaneous fishing mortality experienced by fish of a given length-age-time bin over their lifetime prior to time $t$.

The fishery gear selectivity ($v_{l(a')}$) terms were calculated by first determining the lengths that fish of a given length-age bin would have been in past years (i.e., at ages $a'$). These are a function of the length-age bin specific asymptotic length $L_{\infty(l,t)}$ using $l_{a'} = L_{\infty(l,t)}(1\text{-}\exp(\text{-}K*(a'\text{-}t_0)))$. The length-specific fishery gear selectivity is then calculated for each of these ages using Equation B-3.

The $F_{t(a')}$ values are subset from a vector of annual instantaneous fishing mortality rates $F_t$. The model is conditioned on aggregate annual catch (i.e., biomass). Thus, the annual instantaneous fishing mortality rate was calculated recursively as:

$$F_t = -\ln\left(1 - \frac{C_t}{B_t}\right) \tag{B-8}$$

where $C_t$ are the annual observed catches and $B_t$ is the model-predicted vulnerable biomass. Biomass is calculated using an assumed length-weight relationship of the form, $w_t = al_a^b$, which was estimated outside the model.

The model requires $F_t$ values for each year during the time span of the surveys and also for the $A$-1 years before the surveys began. This is because the initial $A$-1 $F_t$ values are required to calculate the cumulative instantaneous mortality for fish that were alive before the surveys began. Thus, fishing mortality rates can be calculated only for years in which survey catch data are available because vulnerable biomass cannot be estimated prior to the first survey sample.

The model was fit to catch data from gizzard shad at Lake Dora Florida. Model fits to the age and length data are shown in Figures B-1 and B-2.
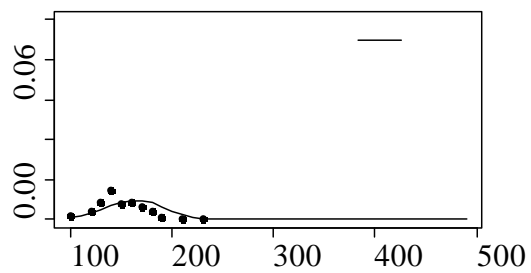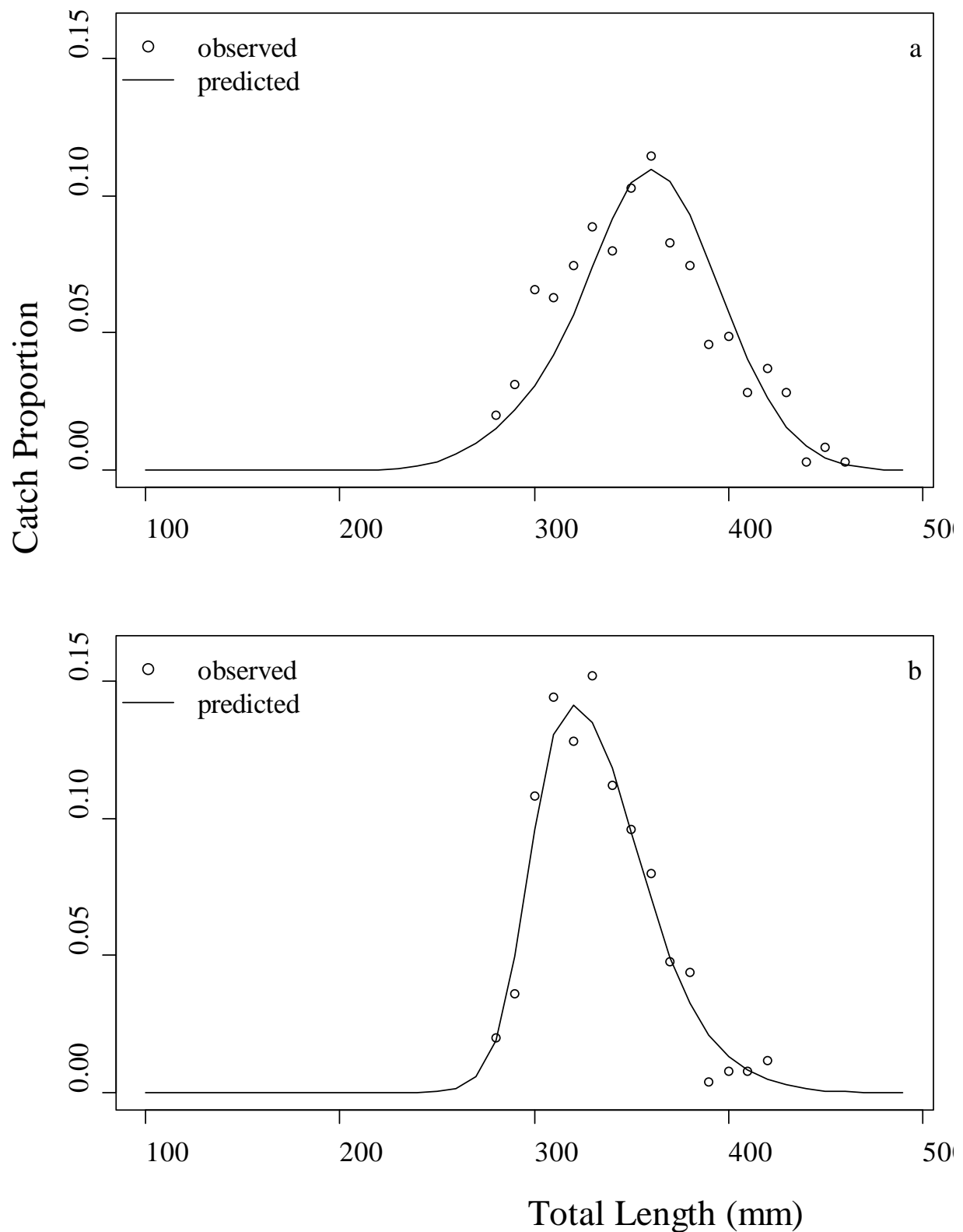
Figure B-2.  Observed (points) and model-predicted (lines) gizzard shad length distributions
from the 2005 (a) and 2006 (b) fishery at Lake Dora, Florida.  Odd ages are shown on
the left column panels and even ages are on the right.