FISH COMPENSATORY RESPONSES FOLLOWING WHOLE-LAKE EXPERIMENTAL DENSITY REDUCTION

By

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# TABLE OF CONTENTS

ACKNOWLEDGMENTS .............................................................................................................. 3

LIST OF TABLES .......................................................................................................................... 6

LIST OF FIGURES ......................................................................................................................... 7

ABSTRACT ..................................................................................................................................... 9

CHAPTER

1 GENERAL INTRODUCTION .............................................................................................. 11

   Introduction ............................................................................................................................. 11
   Compensation During Early Life ........................................................................................... 13
   Evidence from Adult Life Stages ........................................................................................... 14
   Study Objectives ..................................................................................................................... 16

2 A SIZE- AND AGE-STRUCTURED MODEL TO ESTIMATE FISH RECRUITMENT, GROWTH, MORTALITY, AND GEAR SELECTIVITY ................................................................................. 19

   Introduction ............................................................................................................................. 19
   Methods .................................................................................................................................. 20
   Results ..................................................................................................................................... 27
   Discussion ............................................................................................................................... 30

3 DOES INCREASED PRE-RECRUIT SURVIVAL DRIVE FISH DENSITY DEPENDENCE?: EVIDENCE FROM A WHOLE-LAKE EXPERIMENTAL DENSITY REDUCTION ........................................................................ 46

   Introduction ............................................................................................................................. 46
   Study Site ................................................................................................................................ 49
   Methods .................................................................................................................................. 50
   Results ..................................................................................................................................... 58
   Discussion ............................................................................................................................... 62

4 EXPLORING FISH REMOVAL STRATEGIES FOR BIOMANIPULATION THAT ACCOUNT FOR UNCERTAINTY IN THE STRENGTH OF DENSITY DEPENDENCE OF TARGET SPECIES ........................................................................... 74

   Introduction ............................................................................................................................. 74
   Study Site ................................................................................................................................ 75
   Methods .................................................................................................................................. 76
   Results ..................................................................................................................................... 83
   Discussion ............................................................................................................................... 84
## LIST OF TABLES

<table>
<thead>
<tr>
<th>Table</th>
<th>Description</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>2-1</td>
<td>Point estimates and 95% confidence intervals for model parameters estimated from length-age data for gizzard shad at Lake Dora, Florida, USA.</td>
<td>36</td>
</tr>
<tr>
<td>3-1</td>
<td>Parameter estimates (95% confidence intervals) from the length age model for lakes Dora, Eustis and Harris.</td>
<td>67</td>
</tr>
<tr>
<td>3-2</td>
<td>Delta Akaike’s Incormation Criterion (AIC) values for competing models describing associations between growth increments and age, lake, and population density (i.e., total population biomass).</td>
<td>67</td>
</tr>
<tr>
<td>3-3</td>
<td>Delta AIC values for competing models describing associations between gizzard shad maturity and lake, population density ($B_t$), cohort size, year, and cohort.</td>
<td>68</td>
</tr>
<tr>
<td>3-4</td>
<td>Delta AIC values for competing models describing associations between gizzard shad pre-recruit survival and spawner biomass (SB) and year.</td>
<td>68</td>
</tr>
<tr>
<td>4-1</td>
<td>Gear selectivity parameter estimates (95% confidence interval) for each gill net mesh size from the from the length age model.</td>
<td>90</td>
</tr>
<tr>
<td>4-2</td>
<td>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 ($\mu$), and five gill net mesh sizes ranging from 51 to 102 mm.</td>
<td>91</td>
</tr>
<tr>
<td>4-3</td>
<td>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 ($\mu$), and five gill net mesh sizes ranging from 51 to 102 mm.</td>
<td>91</td>
</tr>
</tbody>
</table>
LIST OF FIGURES

<table>
<thead>
<tr>
<th>Figure</th>
<th>Description</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>2-1</td>
<td>Proportional bias of model parameters at constant low fishing mortality (F = 0.2 yr(^{-1})).</td>
<td>37</td>
</tr>
<tr>
<td>2-2</td>
<td>Proportional bias of model parameters with fishing mortality increasing annually to a low level (F = 0.2 yr(^{-1})).</td>
<td>38</td>
</tr>
<tr>
<td>2-3</td>
<td>Proportional bias of model parameters at constant high fishing mortality (F = 0.7 yr(^{-1})).</td>
<td>39</td>
</tr>
<tr>
<td>2-4</td>
<td>Proportional bias of model parameters with fishing mortality increasing annually to a high level (F = 0.7 yr(^{-1})).</td>
<td>40</td>
</tr>
<tr>
<td>2-5</td>
<td>Observed (points) and model-predicted (lines) length-age survey catch proportions for gizzard shad at Lake Dora, Florida from January 20005 to January 2009.</td>
<td>41</td>
</tr>
<tr>
<td>2-6</td>
<td>Observed (points) and model-predicted (lines) gizzard shad length distributions from the 2005 (upper) and 2006 (lower) fishery at Lake Dora, Florida.</td>
<td>42</td>
</tr>
<tr>
<td>2-7</td>
<td>Gizzard shad recruitment estimates (millions of age-1 recruits) from 1999 to 2009. Error bars represent 95% confidence intervals.</td>
<td>43</td>
</tr>
<tr>
<td>2-8</td>
<td>Model-estimated gear selectivity curves for the fishery-independent gill net survey (solid line), 2005 fishery (dashed line), and 2006 fishery (fine dashed line).</td>
<td>44</td>
</tr>
<tr>
<td>2-9</td>
<td>Observed (points) and model-predicted (solid line) gizzard shad mean length-at-age from a fishery-independent gill net survey from 2005-2009 at Lake Dora, Florida.</td>
<td>45</td>
</tr>
<tr>
<td>3-1</td>
<td>Annual age-1 recruitment estimates (+/- 95% confidence interval) for lakes Dora (a), Eustis (b) and Harris (c) from the length-age model.</td>
<td>69</td>
</tr>
<tr>
<td>3-2</td>
<td>Cohort-specific maturity ogives for gizzard shad at lakes Dora (a), Eustis (b) and Harris (c) with respect to fish length.</td>
<td>70</td>
</tr>
<tr>
<td>3-3</td>
<td>Time series of predicted spawner biomass for 2003 – 2008 at lakes Dora (a), Eustis (b), and Harris (c) from the length-age model.</td>
<td>71</td>
</tr>
<tr>
<td>3-4</td>
<td>Loge pre-recruit survival as a function of spawner biomass at lakes Dora (circles), Eustis (triangles) and Harris (plus).</td>
<td>72</td>
</tr>
<tr>
<td>3-5</td>
<td>Kernel density of maximum lifetime reproductive rate estimates for lakes Dora (solid line), Eustis (dashed line) and Harris (fine dashed line).</td>
<td>73</td>
</tr>
<tr>
<td>4-1</td>
<td>Estimated gear selectivity curves for 51, 64, 76, 89, and 102-mm gill net mesh sizes.</td>
<td>92</td>
</tr>
</tbody>
</table>
4-2  Observed (points) and predicted (lines) length distributions of catches for each gill net mesh size..........................................................................................................................93

4-3  Total population biomass as a function of exploitation rate and gill net mesh size for an annual harvest interval. ........................................................................................................94

4-4  Spawning potential ratio (SPR) as a function of exploitation rate and gill net mesh size for an annual harvest interval. .................................................................95
I evaluated fish compensatory responses following a whole-lake experimental density reduction of gizzard shad at Lake Dora, Florida. Gizzard shad were removed in 2005 and 2006 via a subsidized commercial fishery by the St. Johns River Water Management District. Approximately 30% of the total gizzard shad biomass and 70% of the total spawner biomass was removed. My first objective was to develop an age and length-structured population model that could be used to assess recruitment responses following density reduction. The model provided unbiased estimates of mortality, growth, gear selectivity and recruitment for long-lived species. For short-lived species there was a small upward bias in early recruitment estimates when the time series length was half of the maximum age, but all other scenarios provided unbiased estimates. My second objective was to evaluate compensatory responses of gizzard shad growth, maturity, and pre-recruit survival following density reduction. I found no evidence for density dependence in growth and maturity. Pre-recruit survival was negatively related to spawner biomass suggesting density dependence in early life survival. The strength of density dependence in pre-recruit survival was quantified by estimating the maximum lifetime reproductive rate, which was 7.3 (95% confidence interval: 1.9 – 16.5) at Lake Dora. Thus, pre-recruit survival increases 7.3 -fold at very low spawner abundance when compared to the
unfished condition at Lake Dora. My third objective was to assess the relative efficacy of different gill net mesh sizes, exploitation rate, and harvest interval (number of years between removals) on total biomass reduction and spawning potential ratio of gizzard shad following removals at hypereutrophic Florida lakes using a simulation model. Specifically, I was interested in whether various combinations of these factors could achieve a 75% reduction in total population biomass and Spawning potential ratio (SPR). These targets were obtained from the literature and represent the reductions needed to achieve changes in phytoplankton biomass and to effectively reduce fish recruitment following biomanipulation. Gizzard shad biomass reduction failed to meet the target of 75% reduction for all mesh sizes and harvest intervals except for the smallest (51-mm) mesh size. Reductions in spawning potential ratio exceeded total biomass reductions but remained above a 75% reduction target except when using the smallest mesh size (51 mm). I conclude that gill net removals are unlikely to result in substantial biomass reductions at Lake Dora unless removals adopt very small mesh sizes, which may not be preferred by commercial fishers.
Density dependent population regulation is a pervasive theme in ecology. Populations of living organisms are density dependent if their birth and death rates are functions of some measure of population density (Murray 1994; Gotelli 1995). Ecologists typically refer to two types of density dependence: depensatory and compensatory. Depensatory density dependence is a positive feedback on population size whereby population growth increases as density increases (Gotelli 1995; Rose et al. 2001). Depensation can result in reduced reproduction at low population densities, which is known as the Allee effect (Allee et al. 1949). Compensatory density dependence is the opposite; population growth decreases as density increases (Gotelli 1995; Rose et al. 2001). Compensation results in high per capita reproductive rates in fishes at low spawner abundance and relatively low reproductive rates at high abundance (Myers et al. 1999). There is considerable debate about the relative importance of stochastic versus equilibrium (density dependent regulation) dynamics in animal populations, but density-dependence likely plays an important role in regulating populations (Murdoch 1994; Brooks and Bradshaw 2006). Understanding the mechanisms and specific life history stages leading to density dependence can provide insight into how populations might respond to perturbations such as harvest (Fogarty et al. 1992) and changes in habitat quality and quantity.

Density dependence is a particularly important concept in the life history of fish populations. There is strong support for the existence of compensatory density dependence in fish populations (Goodyear 1980; Myers et al. 1999; Rose et al. 2001). Sustainable harvest of fish populations is predicated on the assumption that fish populations can compensate for harvest of individuals via increases in survival and reproduction. Without compensation, only
populations with positive intrinsic rates of population growth could be harvested sustainably (Rose et al. 2001). However, such populations would increase unbounded in the absence of harvest, which is unrealistic and typically not observed in nature (Murdoch 1994). Evidence for compensation in fish populations led to the early development surplus production models (Schaefer 1954), which predict harvest rates that fully utilize this ‘surplus’ fish biomass. Depensatory density dependence, although important for many animal populations, does not have similar broad support in the fisheries literature (Myers et al. 1995).

Compensatory population regulation processes must affect the number of individuals in the population in order to act as a stabilizing force on population growth. These processes can act directly, via changes in survival and reproduction, or indirectly via changes in growth or behavioral processes that in turn affect survival and reproduction (Rose et al. 2001). Compensation in fish populations is thought to occur through reproduction and early life dynamics and can result from changes in vital rates such as larval/juvenile survival and growth, which leads to changes in age-specific fecundity and survival. Such changes may result from shifts in availability of food and space due to relaxation of intraspecific competition. Larval and juvenile life stages are particularly important regulators of fish populations (Hjort 1914; reviewed by Heath 1992), and even small changes in these rates can cause substantial change in subsequent adult abundance (Houde 1989). Density dependence in adult life stages such as changes in maturation schedules, length-specific fecundity, egg size and quality, and growth can also regulate population growth (Trippel 1995; Rochet 1998; Rochet 2000), but these mechanisms are thought to be subordinate to processes operating during early life. However, few studies have evaluated the relative importance of various compensatory mechanisms at the population level.
Understanding recruitment in fish populations is critical to evaluating effects of compensatory population regulation. Recruitment is the “conversion of eggs, through density dependent and density-independent processes, to the fish that reproduce in the next generation” (Myers 2002). Definition of the age and size at which recruitment occurs lacks standardization but is generally considered the age or size at which fish become vulnerable to a fishery. Average annual recruitment is relatively constant over a wide range of spawner abundance for many species, but exhibits high lognormal variation around expected values due largely to environmental variation (Walters and Martell 2004). This has led some to conclude that recruitment is independent of spawner abundance. However, density-dependence must be strong in order for average recruitment to remain stable over a wide range of spawner abundances. Recent meta-analyses of spawner-recruit data have confirmed that fish populations are subject to strong compensatory density-dependence through reproduction (Myers and Barrowman 1996; Myers et al. 1999; Myers 2001; Myers 2002).

**Compensation During Early Life**

Density-dependent survival during early life stages can result in large changes in subsequent recruitment. Early researchers surmised that survival during the larval stage was most important and that starvation during some “critical period” had the greatest influence on recruitment (Hjort 1914). More recently, results from individual-based-model simulations indicate that density dependent feedbacks on recruitment are more likely during the late larval to early juvenile phase (Cowan et al. 2000) because total cohort consumption rates are highest during this period. Cushing (1990) proposed the match/mismatch hypothesis as a model explaining recruitment variability in fish populations. The model states that the degree of temporal overlap between peak larval abundance and maximum prey abundance determines the magnitude of recruitment (Cushing 1990), and has been supported by empirical data. Density-
dependent change in juvenile survival is thought to be the primary mechanism for compensation in fish populations (Rose et al. 2001).

There are several proposed mechanisms for density dependent survival of juvenile fishes. 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 habitat refugia and spend more time in predator-dense feeding zones in order to maintain adequate growth rates when density of conspecifics is high. Conversely, juveniles can procure adequate prey without substantial risk taking when density is low. This hypothesis has not been fully tested empirically, but Gilliam and Fraser (1987) showed that predation risk and food availability interact to affect individual behavior leading to increased predation risk when food availability is low.

Density dependent growth rates of juveniles can also affect recruitment to adulthood. Growth rates of age-0 fish are often density-dependent (Zijlstra and Witte 1985; van der Veer 1986; Peterman and Bradford 1987). 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; Hovenkamp 1992; Sogard 1997). In addition, smaller individuals may have higher rates of starvation-induced mortality during winter (Post and Evans 1989).

**Evidence from Adult Life Stages**

Density-dependence in adult stages can also result in compensation although these mechanisms are generally considered subordinate to juvenile survival. Fecundity can change
with adult density through changes in condition, food availability, and growth rate (Baccante and Reid 1988; Henderson et al. 1996). Individuals of higher condition may have greater length-specific fecundity (Henderson et al. 1996; Marshall and Frank 1999; Oskarsson and Taggart 2006). Density reduction via exploitation has caused increased length-specific fecundity for many species (e.g., Koslow et al. 1995), although with changes in the age structure after fishing the total population fecundity will typically decline.

Many fish species exhibit phenotypic plasticity in maturation schedules. Age at maturity 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). Rochet (1998) reported that plasticity in maturation has led to decreased age at maturity and increased size at maturity across 77 commercially exploited fish stocks. Other studies have documented decreased age and size at maturity following exploitation (Beacham 1983). Shifts in maturation schedules may be controlled by feeding conditions during nutritionally sensitive periods in gametogenesis (Burton 1994). Juvenile growth rates have also been linked to density dependent changes in maturation schedules (Brophy and Danilowicz 2003; Scheuerell 2005).

Somatic growth is often density dependent in fish populations. 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 (Millner and Whiting 1996; Rijnsdorp and van Leeuwen 1996; Helser and Almeida 1997). Healey (1980) reported increases in growth that were proportional to the degree of exploitation in experimentally manipulated lake whitefish *Coregonus clupeiformis* populations. Lorenzen (2002) concluded
that density dependent growth alone could explain compensatory population regulation in several species.

Understanding compensation in fish populations has been hindered by a lack of experimental manipulations. Large-scale, controlled, population-level experimental manipulations are needed but are rare in the literature. Few studies have manipulated fish populations experimentally at the whole-lake scale and tested mechanisms for compensation. Fish biomanipulation projects are ideal situations for testing compensatory density dependence. In these cases, target species are often unharvested prior to biomanipulation and total harvest and exploitation rate can usually be estimated. Nearby unharvested lakes can be used as control systems against which to evaluate population responses at harvested lakes.

**Study Objectives**

I evaluated fish compensatory responses following whole-lake size-selective density reduction. My model species was gizzard shad *Dorosoma cepedianum*. Gizzard shad are an important component of aquatic food webs in North American rivers, lakes, and reservoirs, and are native to Florida lakes. They are omnivores, feeding on organic detritus and zooplankton. This flexible feeding strategy allows gizzard shad to simultaneously influence lake primary productivity and piscivore biomass through “middle-out” processes (DeVries and Stein 1992). Detritus feeding by gizzard shad may increase lake primary productivity via excretion of sediment derived nutrients into the water column (Schaus et al. 1997). This mechanism represents a source of “new” nutrients to the phytoplankton and may contribute substantially to total lake phosphorus loading in some systems (Schaus et al. 1997; Vanni et al. 2006). Gizzard shad larvae and juveniles may reduce survival of economically important piscivores via grazing effects on zooplankton during early life (Stein et al. 1995). Moreover, gizzard shad are dominant organisms in freshwater ecosystems and can constitute over 90% of fish biomass in eutrophic
and hypereutrophic lakes (Allen et al. 2000; Vanni et al. 2006). Management of gizzard shad populations has important implications for lake management and consequently has been a target species for attempts at biomanipulation to alter lake primary productivity and food web structure.

The St. Johns River Water Management District in Florida has sought to manipulate gizzard shad populations in hypereutrophic Florida lakes to reduce lake primary productivity. Such biomanipulations have previously been carried out at Lakes Apopka, Denham, and Griffin by subsidizing commercial fishers to harvest gizzard shad using gillnets. However, these manipulations did not include a rigorous evaluation of responses in nutrient cycling, lake primary productivity, and shad population dynamics. A new study was initiated in 2005 to reduce the population density of gizzard shad at Lake Dora, using two other lakes as reference systems. This provided a unique opportunity to evaluate the response of a previously unexploited fish population to density reduction to assess density dependence and the causal mechanisms. Gizzard shad density reduction was carried out at one treatment lake (Lake Dora) and two unharvested reference lakes (Lakes Eustis and Harris) at the Harris Chain of Lakes, Florida. Removals occurred at Lake Dora in March-April 2005 and January-March 2006. Gizzard shad were removed via an experimental gillnet fishery by hired commercial fishers. Removal was highly size-selective owing to a minimum mesh size restriction of 102 mm. Therefore, gillnetting reduced the density of gizzard shad approximately > 300 mm. The primary mechanism for the predicted improvements in water quality was the reduction in phosphorus loading via removal of large detritivorous gizzard shad that excrete previously sediment-bound nutrients into the water column via sediment feeding. It was thought that removal of gizzard shad would reduce this benthic-pelagic nutrient loading.
My primary objective was to evaluate compensatory responses of gizzard shad growth, maturation, and pre-recruit survival following density reduction (Chapter 3). To estimate pre-recruit survival, I developed a novel age and length structured population model that estimated mortality, growth, gear selectivity, and recruitment parameters (Chapter 2). Finally, I incorporated estimates of the strength compensatory density dependence of gizzard shad to evaluate the efficacy of removal methods (exploitation rate, gill net mesh size, harvest interval) to gizzard shad biomanipulation (Chapter 4).
CHAPTER 2
A SIZE- AND AGE-STRUCTURED MODEL TO ESTIMATE FISH RECRUITMENT,
GROWTH, MORTALITY, AND GEAR SELECTIVITY

Introduction

Rates of mortality and reproduction in fish populations are often a function of fish size rather than age (Sauer and Slade 1987). However, stock assessments have widely adopted methods that rely solely on fish age to estimate mortality, gear selectivity, and recruitment rates (e.g., statistical catch-at-age, virtual population analysis). There is substantial variation in growth rates within cohorts resulting in a distribution of lengths around each age. Size-selective fishing practices therefore result in differential fishing mortality rates among fish of the same age (Hansen and Chouinard 1992), which is not accounted for in most age-based population models. Stock assessments and management policies could be improved if data on length as well as age could be incorporated into estimation procedures.

Length and age-structured models have an additional advantage because they can estimate growth parameters that account for gear selectivity and the cumulative effects of size-selective harvest (Taylor et al. 2005). Gear selectivity affects age and length samples due to the selective properties of a survey or fishery gear. Fishing gears typically have greater capture efficiencies for larger individuals. Thus, mean length-at-age of age classes recruiting to the gear may be overestimated due to higher capture probabilities for the largest (fastest-growing) individuals of the cohort (Taylor et al. 2005). Cumulative size-selective harvest effects refer to the decay of the largest individuals in the population over time via fishing mortality. These removal effects would be strongest on fully recruited age classes by removing the largest individuals in a cohort, and therefore the remaining fish that are collected in length-age samples may represent primarily slow-growing animals (Kristiansen and Svåsand 1998; Sinclair et al. 2002). These effects can
lead to underestimation of the asymptotic length parameter \((L_\infty)\) and overestimation of the metabolic parameter \((K)\) of the von Bertalanffy growth model (Taylor et al. 2005).

Taylor et al. (2005) proposed a method for estimating mortality, gear selectivity, and growth parameters simultaneously from a length-age catch matrix (collected in a single year) using a multinomial maximum likelihood framework. Growth parameters obtained using Taylor et al.’s (2005) approach were unbiased with respect to gear selectivity and the cumulative effects of size-selective harvest. This method has the potential to allow estimation of critical population parameters with realistic data requirements (i.e., one year of data) and may be particularly useful for species for which large amounts of catch data are lacking due to minimal exploitation. The model is unique in that it accounts for variation in length-at-age by carrying out survival calculations for each length-age bin explicitly.

Here I developed a new model that uses the Taylor et al. (2005) formulation but extends the model to estimate historical recruitment (i.e., the number of age-1 fish in the population each year) for situations where sequential years of survey length-age catch matrices are available. The model estimates recruitment, growth, mortality, and gear selectivity parameters from a time series of survey catches of length and age, the length distribution of the harvest, and total annual harvest in biomass. The objectives of this chapter were to (1) introduce the model structure, (2) evaluate model performance using a series of simulation-estimation procedures, and (3) demonstrate the model using data on gizzard shad from a whole-lake biomanipulation experiment in Florida.

**Methods**

**Model**

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, \(L_{50}\)) and the fishery (\(\gamma_v, \beta_v, L_{50}\)). 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:

\[
\ln \mathcal{L}(\theta | n) = \sum_l \sum_a \sum_t n_{l,a,t} \ln(p_{l,a,t}),
\]

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:

\[
p_{l,a,t} = \frac{N_{l,a,t}s_lP(l|a)}{\sum_l \sum_a \sum_t N_{l,a,t}s_lP(l|a)},
\]

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):

\[
s_i = \left( \frac{1}{1 - \gamma_s} \right) \left( \frac{1 - \gamma_s}{\gamma_s} \right)^{\gamma_s} \left( \frac{e^{\beta_s \lambda_s (L_{50} - l)}}{1 + e^{\beta_s (L_{50} - l)}} \right),
\]

(2-3)

where \(\gamma_s\) 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 \(\gamma_s\) 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 \(sda\). Mean length-at-age, \(l_a\), is assumed to follow the von Bertalanffy (1938) growth model:

\[
l_a = L_\infty \left( 1 - e^{-K(a-t_0)} \right),
\]

(2-4)

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):

\[
sda = \lambda_1 e^{-\frac{1 - e^{-\rho \tau}}{1 - \rho}},
\]

(2-5)

where \(\lambda_1\) defines the magnitude of the standard deviations, \(\lambda_2\) controls the trend in \(sda\) 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 \(t\):

\[
N_{l,a,t} = R_{t-a+1} e^{-Z_{l,a,t}},
\]

(2-6)
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 $L_{x(l,t)} = l/(1-\exp(-K*(a-t_0)))$ (Taylor et al. 2005). The model assumes that $K$ is time (years), length, and age invariant, thus a unique asymptotic length $L_{x(l,t)}$ (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):

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

(2-7)

where $a'$ is a vector of ages from age 1 up to age $a-1$, and $F_{l(a')}$ 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 $F_{l(a')}$ 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 $L_{x(l,t)}$ using $l_{a'} = L_{x(l,t)}(1-\exp(-K*(a'-t_0)))$. The length-specific fishery gear selectivity is then calculated for each of these ages using Equation 2-3.
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:

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

(2-8)

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, $w_i = al_i^b$, 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. However, 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. This presents a problem if the fishery developed before the first survey occurred. The model can accommodate this situation by estimating an additional parameter: the initial average fishing mortality rate ($F_0$). This parameter represents the annual instantaneous fishing mortality for the years leading up to the collection of the first survey. This is accomplished by setting the first $A$-1 values of the $F_t$ vector equal to $F_0$. This assumes that $F$ was relatively constant for one generation time leading up to the first sample collection. The $F_0$ parameter can be fixed at a value of zero if there is prior knowledge that the population was unfished before the first sample was collected.

**Model Performance**

Model performance was evaluated by fitting the model to simulated data and estimating parameter bias for situations that would commonly occur in stock assessment situations. The
model was used to generate data for all possible combinations of fish longevity (short-lived: $A = 8$ years; long-lived: $A = 15$ years), survey sampling duration (i.e., years of data; short: $0.5 \times A$ yrs; long: $A$ yrs), survey gear selectivity (asymptotic and dome-shaped), instantaneous fishing mortality rate ($F_i = 0.2$ and $0.7 \text{ yr}^{-1}$) and fishing mortality trend (stable and increasing). For asymptotic sampling gear selectivity, the age at 50% selectivity was $0.3 \times L_\infty$ and fish attained 90% selectivity at $0.4 \times L_\infty$. For dome-shaped gear selectivity, fish attained 50% selectivity at $0.3 \times L_\infty$, maximum (100%) selectivity at $0.5 \times L_\infty$, and 50% at $L_\infty$. For all scenarios, fishery gear selectivity was asymptotic with 50% selectivity at $0.6 \times L_\infty$. The increasing $F$ scenario allowed $F$ to increase gradually from 0 to $F_i$ over the years in which survey data were collected. Annual recruitment variation was log-normally distributed with a coefficient of variation (CV) of 50%, and observation errors on length- and age-specific catches each year were drawn from a multinomial distribution. All other parameters were held constant in the simulations. Monte Carlo simulation was used to generate data and estimate parameters for each combination of longevity, sampling duration, gear selectivity, and fishing mortality schedule. Parameter bias was calculated for each Monte Carlo iteration by dividing the difference between the estimated and true parameter values by the true values. The median, 2.5%, 25%, 75%, and 97.5% quantiles for bias over 200 Monte Carlo iterations were plotted for each parameter. Additional iterations (>200) resulted in no change in bias estimates.

**Application to Gizzard Shad**

The model was used to estimate parameters of a gizzard shad population that experienced a biomanipulation at Lake Dora, central Florida, USA. Biomanipulation was achieved with an experimental commercial gill net fishery by the St. Johns Water Management District (SJRWMD). Prior to fish removal, the gizzard shad population was unfished. Commercial
fishers removed gizzard shad during March-April 2005 and again during January-March 2006. Gizzard shad were removed using gill nets with a minimum mesh size restriction of 102 mm, which selected for fish larger than approximately 300-mm total length. The SJRWMD used onboard observers to (1) record commercial catch-per-effort in 102-mm gill nets, and (2) measure a subsample of 100 harvested gizzard shad per week to characterize the length composition of the fishery harvest. The cumulative catch and total harvest (kg) each year were estimated from mandatory trip tickets, which were submitted to the SJRWMD daily by each fisher.

An annual fishery-independent survey was conducted at Lake Dora to obtain data on the length-age composition of the gizzard shad population. Survey data were collected by setting 20 multi-panel floating gill nets at 20 fixed sites in late January or early February from 2005 to 2009. The 2005 sample was conducted prior to the initial biomanipulation and thus represented an unfished population size/age structure. The final removal occurred in 2006, thus the 2008 and 2009 samples represented a rebuilding population. Gill nets were 2.4-m deep and contained eight, 15.3-m long panels of 38, 51, 64, 76, 89, 102, 114, and 127-mm stretch monofilament mesh. Each net was set for 2-3 hrs. Captured fish were measured for total length (mm) and counted, and otoliths were removed from a subsample of 10 fish per 10-mm group for ageing. Otoliths were sectioned using a South Bay Tech© Model 650 low-speed saw and read by three independent readers using a dissecting microscope at 40X magnification. Aged fish were extrapolated to the entire catch using an age-length key to estimate the age and length composition of the catch each year.

Data inputs used in the model were five years of survey length-age catch matrices, gizzard shad length distributions from the 2005 and 2006 fishery via onboard observers, and total
harvested biomass in 2005 and 2006. The model was fitted using the optim() minimization function in program R. Parameter uncertainty was evaluated by inverting the Hessian matrix. Parameters that must be positive values (e.g., recruitments, \( M, L_\infty \)) were constrained using a logarithmic transformation and parameters on a fixed interval from 0 to 1 (i.e., \( g_s \) and \( g_v \)) were fit using the logit transformation.

**Results**

**Model Performance**

Median proportional bias was less than 0.1 for all parameters and scenarios except for the short-lived, short time period simulations, which had a slight upward recruitment bias early in the time series (Figures 2-1, 2-2). Simulations with low fishing mortality (\( F = 0.2 \) yr\(^{-1} \); Figures 2-1 and 2-2) had greater bias than those with higher fishing mortality (\( F = 0.7 \); Figures 2-3 and 2-4). Median bias and bias uncertainty were greater for the short-lived than for the long-lived species (all Figures, panels a and b vs. c and d), and with a short rather than long time series of data (i.e., \( n = 0.5A \) yrs; all figures 2, panels a and c vs. b and d). Bias was greater for scenarios with increasing \( F \) than with constant \( F \) (Figures 2-1 and 2-3 vs. Figures 2-2 and 2-4). Simulations that assumed a dome-shaped survey gear selectivity function exhibited greater bias than simulations with asymptotic selectivity, but the model could adequately determine the shape of the selectivity curve in most cases. Overall, the bias was relatively small, with parameters being biased by less than 5% in most cases but up to 40% in the worst case scenarios (i.e., \( R_2 \) in Figure 2-2a).

The amount of bias varied among parameters. Growth parameters had median bias of less than 2% and low uncertainty in bias across all scenarios except for \( t_o \) which had a slight upward bias in the long-lived short time series constant high \( F \) scenario. However, the true value of the \( t_o \) parameter was near zero therefore very small absolute biases led to large proportional biases.
even though bias in mean length-at-age was negligible. Gear selectivity parameters also had low median bias and bias uncertainty across all scenarios. Natural mortality, fishing mortality and recruitment parameters were the most biased due to moderate to high confounding among these parameters. Recruitment (i.e., particularly early in the time series) was correlated with natural mortality, and therefore overestimates in recruitment led to overestimates in natural mortality because fish had to die more rapidly to explain the catches. Recruitment overestimates would then lead to underestimates of fishing mortality because biomass was overestimated and because there would be an upward bias in natural mortality that would also reduce the impact of the removals on the population. Despite these correlations, parameter uncertainty was low with CVs around recruitment estimates ranging from 10 to 35% and most other parameter CVs less than 10%. This indicated that the data contained enough information to reliably estimate all of the parameters except for the first few recruitment values.

The first few recruitments produced the oldest age classes in the first year of survey catch data. These cohorts were captured in only one or two years of catch data and catches were very low due to cumulative mortality of the cohorts. Thus, the recruitment parameters for these cohorts were not well-defined in the data resulting in higher uncertainty in the model estimates. I used AIC to determine which of the early recruitment parameters were justifiably estimated by comparing AIC values from full models (all recruitment parameters estimated) with reduced models in which one or more recruitment values were fixed at the mean value of all other estimates. In general, the first recruitment parameter was not estimable for the short-lived species and the first three were not estimable for the long-lived species. Thus, these simulations identified the limitations of the model for estimating early recruitments in a time series, but
demonstrated that in nearly all other cases the model provided reliable estimates of the other parameters.

**Application to Gizzard Shad**

The total harvested biomass of gizzard shad was 124,989 kg (54 kg/ha) in 2005 and 135,095 kg (58 kg/ha) in 2006. The model fit the survey length-age data reasonably well although there was some under-prediction of proportional catches of age-1 fish in 2006, 2007 and 2009 (Figure 2-5). Modal length-at-age for age-1 fish was over-predicted in 2006 and 2009 suggesting slower than average pre-recruit growth in 2005 and 2008 (Figure 2-5). Length distributions from the fishery were predicted well by the model (Figure 2-6).

Annual recruitment estimates varied from 0.5 to 4 million age-1 gizzard shad and strong year classes occurred in 2000, 2004 and 2006 (Figure 2-7). Preliminary fits indicated that the first recruitment value ($R_{1998}$) was not estimable, and thus I fixed that value to the average of all other recruitment values. There was evidence for alternating strong and weak year classes although the pattern was not evident in 2001-2002 and 2008-2009 (Figure 2-7). Von Bertalanffy growth parameter and natural mortality estimates were precise with CVs less than 10% (Table 2-1).

The length at 50% selectivity and $\gamma$ (shape parameter) parameters were estimated precisely for all three gear selectivity functions (i.e., survey, 2005 fishery, 2006 fishery) with CVs less than 10%, but the steepness parameters were less certain (CV range: 15-36%; Table 2-1). The survey gear selectivity function was dome-shaped with selectivity increasing exponentially up to 400 mm then peaking at 430 mm and declining to 0.75 at 450 mm (Figure 2-8). Gear selectivity curves for the fishery were asymptotic and suggested that length at 50% selectivity decreased in 2006 (Figure 2-8). This agreed with on-board observer data showing that fishers used mesh sizes.
of 102, 144 and 127 mm in 2005 but only used 102-mm mesh in 2006 due to declining catches in the large mesh sizes.

Discussion

The model estimated recruitment, growth, natural mortality, and gear selectivity using only survey length-age and fishery length composition data. Parameter bias in these models should be lowest when fitting to long-lived species, by collecting data for at least one generation time of the species of interest, and if fishing mortality is relatively constant and moderate ($F = 0.7$). However, performance was reasonable in other scenarios as well.

The gizzard shad example represented what should be a relatively high-bias scenario because (1) gizzard shad are short lived, (2) only 5 years of data were collected (i.e., 63% of $A$), (3) survey gear selectivity was dome shaped, and (4) $F$ increased dramatically over two years. As a check on the gizzard shad model performance, I compared model-predicted exploitation rates to ones obtained via an in-season depletion analysis. Catalano et al. (in review) estimated an annual exploitation rate of 0.7 in 2005 and 0.65 in 2006 from a depletion of fisher catch per effort (kg per 100 m of net per hr) vs. cumulative catch of the fishery over the course of each annual harvest period. Model-predicted exploitation rates were 0.67 in 2005 and 0.75 in 2006, which were similar in magnitude to the depletion estimates.

As a second set of checks, gizzard shad growth and mortality estimates were compared with literature values. Observed mean lengths-at-age were calculated directly from the age-length key data using methods of DeVries and Frie (1996) and these estimates were similar to model-predicted values (Figure 2-9). Mean lengths from the age-length key exceeded model predictions for older ages (ages 3-5 and 7). This was plausible considering that the survey gill nets should have selected for the largest individuals of these age classes due to an estimated steep selectivity curve from 300-400 mm (Figure 2-8). The model natural mortality rate estimate of
0.87 yr\(^{-1}\) was greater than estimates of 0.61 yr\(^{-1}\) from Pauly’s equation (Pauly 1980; \(M = f\{L_\infty, K, ^\circ\text{C}\}\)) and 0.53 yr\(^{-1}\) from Hoenig (1983; \(M = f\{A\}\)), but was similar to an estimate of 0.9 yr\(^{-1}\) from Jensen (1996; \(M = 1.5K\)). However, the Hoenig (1983) and Pauly (1980) values were derived from empirical models based on many fish populations and may not accurately represent gizzard shad life history characteristics. The mean and standard deviation of these literature \(M\) estimates could be used as priors in future uses of this model in a Bayesian framework.

I also obtained \(M\) estimates using a simple catch curve for unfished Lake Dora (2005) and a pooled estimate over five years from two nearby unharvested control lakes (Lakes Eustis and Harris, 2005-2009) that had similar gizzard shad populations and were sampled with the same gear during the same time period as Lake Dora (Catalano et al. 2007). Catch curve \(M\) estimates were 0.6 yr\(^{-1}\) for Lake Dora in 2005 and 0.76 yr\(^{-1}\) from Lakes Eustis and Harris. Thus, the model \(M\) estimate was greater than the catch curve values suggesting that one of the two estimates was biased. Downward bias in the catch curve estimates could have resulted from an increase in survey gear selectivity with fish length, which would over-represent older fish in the catch. This selectivity trend was estimated to be the case by the model (Figure 2-8). Size selectivity is common for survey gears (Bayley and Austen 2002) but such biases are rarely considered when catch curves are estimated. The advantage of the model is that the \(M\) estimates account for gear selectivity. If \(M\) was in fact overestimated by the model, then there was likely a concurrent upward bias in recruitment values to produce a large enough population to explain the observed harvest.

Taylor et al. (2005) reported that prior knowledge of the shape of the gear selectivity function was required for their model; however, my simulations suggested that the model could obtain unbiased estimates of the shape of the gear selectivity function with no prior information.
The flexible selectivity function could accommodate the dome-shaped survey gear selectivity for gizzard shad, which differed from the asymptotic selectivity assumption used by Taylor et al. (2005) for northern pikeminnow *Ptychocheilus oregonensis*. Although the model showed a dome-shaped survey gear selectivity with peak selectivity at 430 mm, it should be noted that gizzard shad exceeding 430 mm should be extremely rare in this population due to high natural mortality, an asymptotic length of 394 mm, and an estimated standard deviation in length-at-age of age-5 to age-8 fish of around 30 mm. This dome-shaped gear selectivity pattern could have been an artifact of size-dependent natural mortality rates in which faster-growing individuals had higher natural mortality rates. Nevertheless, failure to account for selectivity patterns could bias abundance estimates of large (older) fish in the age structure. Hansen et al. (1997) found that total annual mortality of Lake Superior lake trout *Salvelinus namaycush* was underestimated by 20% when catch-age samples were not corrected for dome-shaped gear selectivity. This model could be very useful for evaluating populations where the shape of the gear selectivity function is unknown.

The model used only survey catches at length and age as well as fishery length distributions, but estimates could be improved with the inclusion of additional data types. For example, survey CPUE trend indices could be included to help define the magnitude of biomass reductions, which would provide information on the recruitment and mortality levels that would have been necessary to result in the observed catches and CPUE trend. Additional survey length-age catch matrices could also be included, which reduced parameter bias and uncertainty in these models in preliminary simulation analyses (Catalano unpublished data). I did not allow for time, age, or cohort specific variation in growth, natural mortality, or gear selectivity. However, the model fits to the data suggested that mean age-1 length may have varied among
years suggesting time or cohort-specific growth rates. Inclusion of growth variation in the simulated data would likely have reduced model performance. Uncertainty in growth parameters was very low in these trials, thus there may be enough information in the data to estimate variable growth rates by adding additional time-varying growth parameters. As another example, it was assumed that instantaneous natural mortality was constant across age classes. Work by Lorenzen (2000) suggests natural mortality declines with age inversely proportional to fish length. Thus, the model could be adapted to estimate time- or size-varying natural mortality rates as well.

The Taylor et al. (2005) accounting structure used in the model was unique compared to other existing length-age models. Stock synthesis 2 (Methot 2005) uses a growth-type-group accounting method where the stock is divided into several growth morphs each with its own von Bertalanffy growth parameters. The dynamics of each morph are calculated separately through time as fish stay in the same morph throughout life. This method can be very efficient if only a few groups are needed but can become computationally demanding with many groups. The number of groups necessary has not been studied and likely varies depending on the species. Another approach is the matrix transition approach such as the Fleksibest model by Frøysa et al. (2002). This accounting structure calculates probabilities of transition from a given length bin and age to other length bins at the next age and time step. These calculations can be rather complicated because fish from a single length-age bin will transition to multiple length bins in the next time step. The Taylor accounting structure can be thought of as a type of growth type group (GTG) model (Walters and Martell 2004) because it assumes that fish grow along a growth trajectory although it does not explicitly calculate the dynamics of each growth morph through time. Instead, the dynamics of each length-age bin are explicitly accounted for by
calculating back in time rather than calculating forward as in the typical GTG formulation. In addition, population numbers at length and age are predicted directly rather than aggregating fish into length-age bins from growth morphs (in the typical GTG formulation) by assuming a length distribution for fish of a given age and morph.

The most common model bias encountered in the simulation-estimation experiments was overestimation of recruitment values, particularly early in the time series. In these situations, \( M \) is often overestimated and there were trends in recruitment bias with larger recruitment biases for older cohorts than for more recent ones. These early recruitments represent cohorts that were not tracked fully through the age structure. The potential for these biases can be reduced by collecting data over a sufficiently long time series, by including additional survey data types, and by not estimating several of the earliest recruitment values but rather setting them equal to the average of the estimated recruitments. This would be problematic for short time series of data where few cohorts are tracked through the entire age structure.

The model requires an adequate number of aged fish. I simulated the aging of 2,000 fish annually from survey data and 200 lengths from the fishery harvest, which represents a substantial data investment but is not uncommon for most high-profile marine fisheries (e.g., groupers and snappers). Taylor et al. (2005) found that at least 500 fish were needed for their model to perform adequately. Model performance also depends on the number and width of the length bins. The model performed best when length bins widths were between 2 and 5% of \( L_\infty \). Parameter bias increased substantially when length bins were greater than 10% of \( L_\infty \). This coarse level of discretization can cause some age classes to be represented by only 1-2 length bins, which can introduce parameter bias due to random sampling error on these
underrepresented age classes. As with other length-based models, care should be taken when setting the level of length discretization in the model.

Demographic parameter estimates for gizzard shad are rare in the literature and the model estimates presented here could be useful for fishery management in eastern North America. Gizzard shad are hypothesized to control food webs in eutrophic lakes through complex “middle-out” processes by larval overgrazing of zooplankton and adult detritivorous foraging (DeVries and Stein 1992). Therefore, gizzard shad have received attention from managers as targets for biomanipulation (Kim and DeVries 2000) and as prey for recreational fishes (Cyterski and Ney 2005). However, there are few published estimates of gizzard shad growth, gear selectivity and natural mortality with which to inform these studies. Bodola (1965) estimated an $L_\infty$ of 395 mm and $K$ of 0.78 yr$^{-1}$ for Lake Erie, and Perry et al. (2003) reported estimates of 370 for $L_\infty$ and 0.58 yr$^{-1}$ for $K$ in the Ohio River, which are similar to my estimates. Gear selectivity estimates would be particularly useful for biomanipulation efforts that utilize gill nets as the removal method. Van den Avyle et al. (1995) estimated retention probabilities for gizzard shad in various gill net mesh sizes but their estimates assumed equal encounter rates among fish lengths and did not represent gear selectivities that could be used in a modeling context. I could find no peer-reviewed estimates of natural mortality for adult gizzard shad.

This model could be useful for estimating critical population parameters of fishes. There have been no peer-reviewed evaluations of the performance of age-length structured assessment models to date. I showed that these models can provide unbiased estimates of population parameters under most conditions and explored situations in which biases could arise to test the limits of the approach. One important advantage of a fully age and length-structured model is the ability to directly estimate growth parameters in the model. The models would likely
outperform traditional age-based models when biases in growth parameters are suspected due to

<table>
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<th>Description</th>
<th>Estimate</th>
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<th>U95%CI</th>
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<td>$M$ (yr-1)</td>
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gear selectivity and the cumulative effects of size-selective harvest on age/size distributions.

Table 2-1. Point estimates and 95% confidence intervals for model parameters estimated from length-age data for gizzard shad at Lake Dora, Florida, USA.
Figure 2-1. Proportional bias of model parameters at constant low fishing mortality ($F = 0.2 \text{ yr}^{-1}$) for a short-lived (panels a, b) and long-lived (panels c, d) species and for a short (panels a, c) and long (panels b, d) time series. Every fourth recruitment parameter estimate is shown for efficiency.
Figure 2-2. Proportional bias of model parameters with fishing mortality increasing annually to a low level (F = 0.2 yr⁻¹) for a short-lived (panels a, b) and long-lived (panels c, d) species and for a short (panels a, c) and long (panels b, d) time series. Every fourth recruitment parameter estimate is shown for efficiency.
Figure 2-3. Proportional bias of model parameters at constant high fishing mortality ($F = 0.7$ yr$^{-1}$) for a short-lived (panels a, b) and long-lived (panels c, d) species and for a short (panels a, c) and long (panels b, d) time series. Every fourth recruitment parameter estimate is shown for efficiency.
Figure 2-4. Proportional bias of model parameters with fishing mortality increasing annually to a high level (F = 0.7 yr\(^{-1}\)) for a short-lived (panels a, b) and long-lived (panels c, d) species and for a short (panels a, c) and long (panels b, d) time series. Every fourth recruitment parameter estimate is shown for efficiency.
Figure 2-5. Observed (points) and model-predicted (lines) length-age survey catch proportions for gizzard shad at Lake Dora, Florida from January 2005 (a, f) to January 2009 (e, j). Odd ages are shown on the left column panels (a – e) and even ages are on the right (f – j).
Figure 2-6. 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.
Figure 2-7. Gizzard shad recruitment estimates (millions of age-1 recruits) from 1999 to 2009. Error bars represent 95% confidence intervals.
Figure 2-8. Model-estimated gear selectivity curves for the fishery-independent gill net survey (solid line), 2005 fishery (dashed line), and 2006 fishery (fine dashed line).
Figure 2-9. Observed (points) and model-predicted (solid line) gizzard shad mean length-at-age from a fishery-independent gill net survey from 2005-2009 at Lake Dora, Florida. Error bars represent 95% confidence intervals for observed length-at-age and dashed lines signify the 95% confidence interval for model-predicted length-at-age.
CHAPTER 3
DOES INCREASED PRE-RECRUIT SURVIVAL DRIVE FISH DENSITY DEPENDENCE?:
EVIDENCE FROM A WHOLE-LAKE EXPERIMENTAL DENSITY REDUCTION

Introduction

Compensatory density-dependence is a negative feedback on population growth rate via functional relationships between population density and vital rates. Understanding the strength and mechanisms of compensation is a pervasive theme in ecology because these factors determine the ability of animal populations to withstand anthropogenic perturbations. Density-independent processes are important in determining year-to-year variability in demographic rates of animals, but density-dependence must play a critical role in regulating population size (Murdoch 1994; Brooks and Bradshaw 2006); without it, populations would increase unbounded or be driven to extinction stochastically. However, detection of density dependence in natural populations has been elusive (but see Brooks and Bradshaw 2006) due to inadequate analyses (Rotella et al. 2009), environmental noise, and the difficulty of experimentally manipulating animal population density at an appropriate spatial or time scale. Compensation occurs through density-dependent changes in rates of survival, reproduction or migration. Understanding the vital rates and life stage where density dependence occurs can provide insight into how populations might respond to perturbations such as harvest and changes in habitat quality and quantity.

There is strong support for the existence of compensatory density dependence in fish populations (Goodyear 1980; Myers et al. 1999; Rose et al. 2001). Recent meta-analyses of spawner-recruit data have confirmed that fish populations are subject to strong compensatory density-dependence via changes in reproduction (Myers and Barrowman 1996; Myers et al. 1999; Myers 2001; Myers 2002). Compensation results in high per capita reproductive rates in fishes at low spawner abundance and relatively low reproductive rates at high abundance (Myers
et al. 1999). The strength of density dependence varies widely across species and likely depends on life history strategy (Winemiller and Rose 1992), habitat structure, and species interactions (Rose and Cowan 2000). Such changes may result from shifts in availability of food and space due to relaxation of intraspecific competition.

There is considerable debate about the relative contributions of changes in various demographic rates to compensation in fish populations. Compensation may occur through changes in demographic rates during early life (larval and juvenile) and adult life stage. Larval and juvenile life stages are particularly important regulators of fish populations (Hjort 1914; reviewed by Heath 1992), and even small changes in these rates can cause substantial change in subsequent adult abundance (Houde 1989). Compensation during the early life phase can occur through changes in growth (Zijlstra and Witte 1985; van der Veer 1986; Peterman and Bradford 1987) or variation in survival related to risk-sensitive foraging behaviors (Walters and Juanes 1993). Density dependence in adult life stages such as changes in maturation schedules, condition (leading to increased fecundity), egg size and quality, and growth can also regulate population growth (Trippel 1995; Rochet 1998; Rochet 2000). Despite extensive research on fish density dependence, few studies have evaluated the relative importance of early versus adult life stages to compensation at the population level.

A central problem in understanding compensation in animal populations is the difficulty in manipulating population densities on a large enough scale to measure density-dependent responses. Many studies have treated exploited fish populations as replicates from which to draw inferences regarding the strength and mechanisms of density dependence (Rijnsdorp 1993; Myers et al. 1999; Goodwin et al. 2006). However, these studies rarely include reliable data before fishing, and there are no observations from unmanipulated control systems against which
population trends of the harvested populations could be compared. Moreover, management
practices often aim to maintain exploited populations within bounds to maximize production,
which can reduce contrast in population density and limit its utility for evaluating density
dependence. Whole-lake experiments provide the appropriate scale for detecting meaningful
management of ecosystems whereby individual fish stocks are treated as replicates and subject to
varying levels of exploitation, some of which cause population failure. Such studies are rarely
feasible and are politically challenging because of the many individuals who depend on these
stocks for their livelihoods (Walters and Martell 2004). Thus, few studies have evaluated density
reductions in an experimental framework at the population (e.g., lake) scale.

In Florida, U.S.A, the St. Johns River Water Management District (SJRWMD) has used
biomanipulation of omnivorous gizzard shad *Dorosoma cepedianum* as a lake restoration tool to
reduce phytoplankton abundance and improve water clarity at hypereutrophic natural lakes.
Biomanipulation is the selective removal of fish to reduce grazing pressure on zooplankton
thereby increasing water clarity via trophic cascades (Shapiro et al. 1975; Carpenter et al. 1987).
The SJRWMD evaluated the efficacy of the gizzard shad removal via a whole-lake experimental
density reduction of gizzard shad at Lake Dora in 2005 and 2006. The biomanipulation removed
approximately 30% of total gizzard shad biomass from Lake Dora in 2005 and 2006 (Catalano et
al. *in review*) and larger amounts of adult gizzard shad because the fishery selectively removed
large gizzard shad (> 300 mm). The removal provided the opportunity to evaluate compensatory
responses of the gizzard shad population following density reduction. Here I assessed the
relative importance of three mechanisms for compensatory density dependence of gizzard shad
following whole-lake density-reduction. I measured changes in adult growth, maturation, and pre-recruit survival at an experimental lake (Lake Dora) and two unharvested control lakes.

**Study Site**

The study was conducted at lakes Dora, Eustis and Harris, Lake County, Florida, USA. Lake Dora was the experimental lake where gizzard shad density reduction occurred, and the other lakes served as unmanipulated control systems. All lakes were large (>2,000 ha) shallow (3 m average depth) hypereutrophic lakes (mean chlorophyll a concentrations > 50 ug/L) with similar fish communities. Lake Dora is composed of two distinct basins: Lake Dora and the smaller Lake Beauclair. The two basins are separated by a 300-m long by 80-m wide canal. Gizzard shad harvest occurred in both basins, so they were treated as one system for these analyses and will be referred to collectively as Lake Dora hereafter. Narrow canals (<30 m wide, > 1.0 km long) also connected Lake Dora to Lake Eustis and Lake Harris to Lake Eustis. The degree to which gizzard shad moved among the lakes was unknown.

Biomanipulation at Lake Dora was achieved with a government-subsidized commercial gill net fishery by the SJRWMD. Prior to fish removal, gizzard shad populations in both 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 SJRWMD used onboard observers to obtain data on commercial catch-per-effort and catch composition.
Methods

I evaluated density-dependence in growth, maturity, and pre-recruit survival using data from the density reduction at Lake Dora and two control lakes. 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, I was 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. I 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

Data regarding the magnitude of the gizzard shad density reduction were collected by SJRWMD from a fishery-dependent onboard observer program. Onboard observers recorded fishery catch-per-effort in 102-mm gill nets and measure a subsample of 100 harvested gizzard shad per week to characterize the length composition of the catch. The cumulative catch and total harvest (kg) each year were tabulated from mandatory trip tickets, which were submitted to the SJRWMD daily by each fisher.

Gizzard shad demographic information (growth, maturity, pre-recruit survival) was collected via annual fishery-independent gill net surveys conducted by the author (UF) and SJRWMD 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) 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 five, 15.3-m long panels of 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, 64-mm mesh to target age-1 fish.

I 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 model (Chapter 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). I 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 Pre-recruit 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:

\[
R_{t,i} = \bar{R}e^{\omega_{t,i} - 0.5\sigma^2_{R,i}}
\]  

(3-1)

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

\[
-\ln P(\omega_{t,i} \mid \sigma_{R,i}) = \sum_i \ln(\sigma_{R,i}) + \frac{\omega^R_{i,t}}{2\sigma^2_{R,i}},
\]  

(3-2)

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 at lakes Eustis and Harris.

**Growth**

I tested for density dependence of 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 produces 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**

I 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. 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. I 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. Individuals with a model-predicted probability of maturity exceeding 0.5 were classified as mature and all others were classified as immature.

I modeled maturation as a cohort-specific process, with each cohort potentially maturing according to its own cohort-specific ogive. I 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 \( \times \) length interactions with logistic regression. The lake \( \times \) 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.

**Pre-recruit Survival**

Lake- and time-specific pre-recruit survival \((S_{t,i})\) was estimated from the length-age 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:

\[
B_{t-1,i} = \sum_l \sum_a N_{l,a,t-1,i} m_{l,a,t-1,i} w_l H_{t-1},
\]

(3-3)
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 \( H_{t-1,i} \) 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 \textit{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-invariant allometric relationship \( w_l = 6.97 \times 10^{-7} l^{3.49} \). 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 I subtracted from the \( B_t \) an estimate of the spawner biomass that was removed just prior to the spawn in the previous year:

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

(3-4)

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). Pre-recruit 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 pre-recruit 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 pre-recruit survival as a function of spawner biomass and environmental factors using the linear form of the Ricker stock-recruit function:

\[ \ln(S_{i,t}) = \ln(\alpha) - b_i B_{i,t} + w_i t + \varepsilon_{i,t}, \]  

(3-5)

where \( \alpha \) is the maximum pre-recruit 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 \( w_i \) terms represent annual environmental effects on pre-recruit survival that act on all of the lakes. Including these shared environmental affects in the model may help ameliorate bias due to serial autocorrelation in pre-recruit 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 \( \alpha \). However, the magnitude of \( \alpha \) is not comparable among populations unless it is compared to pre-recruit survival in an equilibrium unharvested population. Thus, the more valuable measure of density-dependence of pre-recruit 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). I calculated \( \hat{\alpha} \) for each lake as:
\[ \hat{\alpha}_i = \alpha \phi_{0,i}, \]  
\[ (3-6) \]

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

\[ \phi_{0,i} = \sum_a s_{a,i} w_a m_{a,i}, \]  
\[ (3-7) \]

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.

Observation error in spawner biomass and serial correlation between pre-recruit survival and spawner biomass can cause overestimates of \( \alpha \) (reviewed by Walters and Martell 2004). Monte Carlo simulation was used to explore these potential biases. I simulated a fish population using length-age model estimates of gizzard shad population parameters, simulated a time series of random recruitments and subsequent spawner biomass assuming a known \( \alpha \), sampled from stock and recruit pairs with observation error, fit the Ricker model and evaluated bias in \( \alpha \) estimates.

**Results**

**Recruitment**

Estimated recruitment time series showed some degree of temporal synchrony in year class strength among lakes (Figure 3-1). Lake Dora had strong age-1 recruitment in 2000 and 2006 (1999 and 2005 year classes; Figure 3-1a). Lake Eustis had above average recruitment in 2000 as well, but also had high recruitment in 1999 and 2009, as did Lake Harris (Figure 3-1b,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 3-1a). All other model parameter estimates are listed in Table 3-1.

**Growth**

Annual growth increments differed among ages, but not among lakes or with population density (Table 3-2). The model with age only had the best AIC support (Table 3-2; 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 3-2). The best model (age) fit the data considerably better than the single parameter (null) model (Table 3-2). Thus I conclude that growth was not density dependent and 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 are likely to be mature if their GSI exceeds 2%. Because of the high classification rates, I was 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 my prediction (Table 3-2). The minimum AIC model was an additive model with length, lake, and population density (Table 3-3). However, there were seven other models
with nearly equivalent AIC support ($\Delta \text{AIC} < 5$), each of which included lake (Table 3-3). Thus maturity varied among lakes (Figure 3-2); models excluding lake had $\Delta \text{AIC}$ values near 50. Including density resulted in marginal improvements in model parsimony over the model with just length and lake ($\Delta \text{AIC} = 3$) and including cohort size resulted in no improvement in AIC (Table 3-3). 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 I 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 $= 0.041\pm0.002$; lake $= -1.52\pm0.23$; $df = 1166$), and was selected as the most parsimonious, biologically plausible model, and was used in subsequent calculations of spawner biomass (see below).

**Pre-Recruit Survival**

Spawner biomass at Lake Dora decreased to 28% of the average unharvested biomass in 2006 following the second year of harvest (Figure 3-3a). This reduction exceeded the natural variation in spawner biomass observed at control lakes (Figure 3-3). Spawner biomass decreased steadily from 2003-2009 at control lakes due to natural mortality of large year classes in 1999 and 2000 (Figure 3-3b,c). Pre-recruit survival was greatest at Lake Dora in 2005-2007 just after density reduction as recruitment was near the long-term average despite substantially reduced spawner biomass (Figure 3-4). However, pre-recruit survival at Lake Dora after density reduction was exceeded by survival rates at control lakes in 2009 (Figure 3-4).

Juvenile survival was negatively related to spawner biomass across lakes and years (Figure 3-4). The most parsimonious model included additive spawner biomass and year effects (Table
The point estimate of $\alpha$ (maximum pre-recruit survival at low spawner abundance) was 0.07 at the maximum likelihood estimates for recruitment and spawner biomass from the length-age model. Lake-specific point estimates of the maximum lifetime reproductive rate, $\hat{\alpha}$, were 10.0 at Lake Dora, 9.2 at Lake Eustis, and 6.9 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 the largest $\phi_0$, which resulted in a large $\hat{\alpha}$ estimate. The point estimates of $\hat{\alpha}$ were higher than the average estimates across the posterior parameter samples from the MCMC simulation of the length-age model (Lake Dora mean: 7.3; lake Eustis mean: 7.0; Lake Harris mean: 5.5; Figure 3-5). Thus, $\hat{\alpha}$ values less than the point estimates were more likely than higher values across the posterior parameter samples from MCMC simulation.

A value for $\hat{\alpha}$ of 1.0 results in a linear relationship between pre-recruit survival and spawner biomass and signifies a lack of density dependence in pre-recruit 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 3-5). Monte Carlo simulations used to assess potential biases in $\alpha$ suggested that in the case of gizzard shad from these three lakes, time series bias and observation error in stock biomass would cause an underestimation of $\alpha$ rather than overestimation. These estimates of the maximum lifetime reproductive rate should therefore be viewed as conservative, which is preferable to an overly-optimistic estimate from a management perspective.
Discussion

There are many peer reviewed studies showing increased pre-recruit 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 pre-recruit survival would be the dominant compensatory
mechanisms at very low population sizes. My results disagree with Lorenzen and Enberg’s
(2002) findings and indicate that under a moderate change in population density, pre-recruit
survival increased substantially at Lake Dora whereas growth and maturation schedules
remained relatively unchanged. This suggests that changes in pre-recruit 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. I 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 my study. Gizzard shad may have relatively weak compensation when compared to other clupeids, or alternately, the estimates from other species could be biased. For example, 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). I was able to use an experimental density reduction with control systems to evaluate \( \hat{\alpha} \), 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’, e.g., 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 survivors are adapted to quickly invade and exploit highly variable resources (Stearns 1992). My 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.

My study assessed the relative importance of density dependence of several demographic rates, but was unable to assess specific mechanisms influencing changes in those rates. I observed increased pre-recruit 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 pre-recruits 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; Hovenkamp 1992; Sogard 1997). Additional growth and survival studies on pre-recruits are needed within the context of experimental density reduction to evaluate mechanisms for density-dependent survival that could not be addressed by my study.

I 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). Rjinsdorp (1993) considered the exploitation of the North Sea plaice Pleuronectes platessa an experimental density manipulation and reported decreases in length and age at maturity since 1900, and Beacham (1983) documented decreased age and size at maturity following exploitation. Shifts in maturation schedules may be controlled by feeding conditions during nutritionally limited periods in gametogenesis (Burton 1994). 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 (Millner and Whiting 1996; Rjinsdorp and van Leeuwen 1996;
Helser and Almeida 1997). 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 my 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 many 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 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 pre-recruit survival. Future density reduction studies should achieve stronger total biomass reductions so that changes in all demographic rates can be evaluated.

There are few examples of whole-lake density manipulations to test fish compensatory responses. Healey (1978; 1980) manipulated lake trout (Salvelinus namaycush) and lake whitefish densities in a Canadian shield lake and reported compensatory changes in growth,
recruitment, and fecundity, but the magnitude of these changes was not proportional to the amount of density reduction. Experimentally-manipulated mountain brook trout (*Salvelinus fontinalis*) populations have provided good insights into compensation. DeGisi (1994) manipulated seven lakes in the Sierra Nevada Mountains, California, and found that the maximum lifetime reproductive rate in these populations was approximately 19 (Myers 2002). At a smaller scale, Silliman and Gutsell (1958) and Silliman (1968), experimentally reduced laboratory populations of guppies (*Lebistes reticulatus*) and examined trends in abundance and yield at varying exploitation and feeding rates. They found dome-shaped relations between exploitation rate and yield that conformed to theoretical compensatory predictions, but they did not explicitly assess the strength of density dependence (Beverton and Holt 1957). However, results of these small-scale studies may not be appropriate for making conclusions about responses at larger scales and in more complex environments (Schindler 1998). Experimental manipulation of the Lake Dora gizzard shad population contributes substantially to the body of experimental research on compensation and is unique in that changes in demographic rates in the adult as well as pre-recruit phase were assessed to evaluate the relative importance of the two life stages in density dependence.
Table 3-1. Parameter estimates (95% confidence intervals) from the length age model for lakes Dora, Eustis and Harris.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Dora</th>
<th>Eustis</th>
<th>Harris</th>
</tr>
</thead>
<tbody>
<tr>
<td>$M$</td>
<td>0.94 (0.86 - 1.02)</td>
<td>1.02 (0.92 - 1.13)</td>
<td>1.07 (0.99 - 1.16)</td>
</tr>
<tr>
<td>$K$</td>
<td>0.61 (0.60 - 0.63)</td>
<td>0.70 (0.66 - 0.74)</td>
<td>0.76 (0.73 - 0.79)</td>
</tr>
<tr>
<td>$L_\infty$</td>
<td>387.89 (385.08 - 390.73)</td>
<td>406.85 (401.87 - 411.89)</td>
<td>389.67 (386.91 - 392.45)</td>
</tr>
<tr>
<td>$t_0$</td>
<td>0.16 (0.13 - 0.18)</td>
<td>0.34 (0.29 - 0.40)</td>
<td>0.39 (0.34 - 0.44)</td>
</tr>
<tr>
<td>$\lambda_1$</td>
<td>30.86 (30.43 - 31.29)</td>
<td>33.80 (32.86 - 34.77)</td>
<td>30.39 (29.17 - 31.66)</td>
</tr>
<tr>
<td>$\lambda_2$</td>
<td>0.06 (0.04 - 0.09)</td>
<td>-0.19 (-0.24 - -0.14)</td>
<td>-0.11 (-0.16 - -0.05)</td>
</tr>
<tr>
<td>$L_{50_{UF}}$</td>
<td>462.45 (445.64 - 479.89)</td>
<td>440.15 (428.78 - 451.82)</td>
<td>471.28 (460.62 - 482.19)</td>
</tr>
<tr>
<td>$\gamma_{UF}$</td>
<td>0.84 (0.71 - 0.97)</td>
<td>0.65 (0.56 - 0.74)</td>
<td>0.81 (0.62 - 1.00)</td>
</tr>
<tr>
<td>$b_{UF}$</td>
<td>0.09 (0.04 - 0.2)</td>
<td>0.06 (0.05 - 0.08)</td>
<td>0.14 (0.05 - 0.40)</td>
</tr>
<tr>
<td>$L_{50_{SRWMD}}$</td>
<td>319.46 (312.66 - 326.42)</td>
<td>395.05 (374.20 - 417.07)</td>
<td></td>
</tr>
<tr>
<td>$\gamma_{SRWMD}$</td>
<td>0.00 (0.00 – 0.00)</td>
<td>0.00 (0.00 – 0.00)</td>
<td>0.14 (0.05 - 0.40)</td>
</tr>
<tr>
<td>$b_{SRWMD}$</td>
<td>0.04 (0.03 - 0.04)</td>
<td>0.03 (0.03 - 0.03)</td>
<td>0.14 (0.05 - 0.40)</td>
</tr>
<tr>
<td>$\sigma_R$</td>
<td>0.61 (0.40 - 0.92)</td>
<td>0.77 (0.50 - 1.18)</td>
<td></td>
</tr>
<tr>
<td>$L_{50_{05}}$</td>
<td>357.80 (340.36 - 376.13)</td>
<td>395.05 (374.20 - 417.07)</td>
<td></td>
</tr>
<tr>
<td>$b_{05}$</td>
<td>0.04 (0.03 - 0.06)</td>
<td>0.00 (0.00 – 0.00)</td>
<td>0.14 (0.05 - 0.40)</td>
</tr>
<tr>
<td>$\gamma_{05}$</td>
<td>0.00 (0.00 – 0.00)</td>
<td>0.00 (0.00 – 0.00)</td>
<td>0.14 (0.05 - 0.40)</td>
</tr>
<tr>
<td>$L_{50_{06}}$</td>
<td>300.86 (297.06 - 304.70)</td>
<td>395.05 (374.20 - 417.07)</td>
<td></td>
</tr>
<tr>
<td>$b_{06}$</td>
<td>0.15 (0.11 - 0.21)</td>
<td>0.00 (0.00 – 0.00)</td>
<td>0.14 (0.05 - 0.40)</td>
</tr>
<tr>
<td>$\gamma_{06}$</td>
<td>0.00 (0.00 – 0.00)</td>
<td>0.00 (0.00 – 0.00)</td>
<td>0.14 (0.05 - 0.40)</td>
</tr>
</tbody>
</table>
Table 3-2. Delta AIC values for competing models describing associations between growth increments and age, lake, and population density (i.e., total population biomass).

<table>
<thead>
<tr>
<th>Model</th>
<th>AIC</th>
<th>ΔAIC</th>
</tr>
</thead>
<tbody>
<tr>
<td>age</td>
<td>5.5</td>
<td>0.0</td>
</tr>
<tr>
<td>age+lake</td>
<td>7.2</td>
<td>1.7</td>
</tr>
<tr>
<td>age+density</td>
<td>7.4</td>
<td>1.9</td>
</tr>
<tr>
<td>intercept only (null)</td>
<td>130.7</td>
<td>125.2</td>
</tr>
</tbody>
</table>

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

<table>
<thead>
<tr>
<th>Model</th>
<th>AIC</th>
<th>ΔAIC</th>
</tr>
</thead>
<tbody>
<tr>
<td>length+lake+density</td>
<td>614.1</td>
<td>0.0</td>
</tr>
<tr>
<td>length+lake+density+length:lake</td>
<td>615.4</td>
<td>1.3</td>
</tr>
<tr>
<td>length+lake+density+cohort size</td>
<td>616.0</td>
<td>1.9</td>
</tr>
<tr>
<td>length+lake</td>
<td>617.1</td>
<td>3.0</td>
</tr>
<tr>
<td>length+lake+cohort size+length×lake</td>
<td>617.2</td>
<td>3.1</td>
</tr>
<tr>
<td>length+lake+cohort size</td>
<td>617.4</td>
<td>3.3</td>
</tr>
<tr>
<td>length+lake+lake×length</td>
<td>618.5</td>
<td>4.4</td>
</tr>
<tr>
<td>length+lake+cohort size+length×lake</td>
<td>618.5</td>
<td>4.4</td>
</tr>
<tr>
<td>length+density</td>
<td>662.9</td>
<td>48.8</td>
</tr>
<tr>
<td>length</td>
<td>664.1</td>
<td>50.0</td>
</tr>
<tr>
<td>length+cohort size</td>
<td>664.2</td>
<td>50.1</td>
</tr>
<tr>
<td>intercept only (null)</td>
<td>1501.5</td>
<td>887.4</td>
</tr>
</tbody>
</table>

Table 3-4. Delta AIC values for competing models describing associations between gizzard shad pre-recruit survival and spawner biomass (SB) and year.

<table>
<thead>
<tr>
<th>Model</th>
<th>AIC</th>
<th>ΔAIC</th>
</tr>
</thead>
<tbody>
<tr>
<td>SB+year</td>
<td>26.0</td>
<td>0.0</td>
</tr>
<tr>
<td>SB</td>
<td>31.9</td>
<td>5.9</td>
</tr>
<tr>
<td>intercept only (null)</td>
<td>37.6</td>
<td>11.6</td>
</tr>
</tbody>
</table>
Figure 3-1. Annual age-1 recruitment estimates (+/- 95%CI) for lakes Dora (a), Eustis (b) and Harris (c) from the length-age model.
Figure 3-2. Cohort-specific maturity ogives for gizzard shad at lakes Dora (a), Eustis (b) and Harris (c) with respect to fish length.
Figure 3-3. Time series of predicted spawner biomass for 2003 – 2008 at lakes Dora (a), Eustis (b), and Harris (c) from the length-age model.
Figure 3-4. Loge 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.
Figure 3-5. Kernel density of maximum lifetime reproductive rate estimates for lakes Dora (solid line), Eustis (dashed line) and Harris (fine dashed line). Estimates were obtained by repeated fitting of a stock-recruit model across 1,000 parameter sets of the length-age model that were simulated from the posterior parameter distributions using Markov Chain Monte Carlo simulation.
CHAPTER 4
EXPLORING FISH REMOVAL STRATEGIES FOR BIOMANIPULATION THAT ACCOUNT FOR UNCERTAINTY IN THE STRENGTH OF DENSITY DEPENDENCE OF TARGET SPECIES

Introduction

Fish biomanipulation has been used to reduce phytoplankton biomass and improve water transparency in eutrophic lakes via increased grazing pressure by zooplankton on phytoplankton (Shapiro et al. 1975; DeMelo et al. 1992; Hansson et al. 1998; Drenner and Hambright 1999; Meijer et al. 1999). This has been achieved by addition of predatory fish species to increase predation on planktivorous fish or direct removal of planktivores themselves (Carpenter et al. 1987; Meronek et al. 1996; Drenner and Hambright 1999). Direct planktivore removals typically are achieved with a large-scale commercial fishery to rapidly and efficiently remove large amounts of planktivore biomass (Drenner and Hambright 1999). Consequently, the population dynamics of planktivorous fish species may have important consequences for the efficacy of direct planktivore removals (Romare and Bergman 1999).

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 fisheries. Biomanipulation fisheries 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 (e.g., Ricker recruitment) 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 target organisms 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. In this study, I evaluated the efficacy of removal strategies for biomanipulation while accounting for uncertainty in the strength of density dependence of the target species. I 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 the target species. My study species was the gizzard shad in hypereutrophic Florida lakes, and this species has been the target of biomanipulation in eastern North America (DeVries and Stein 1990; Kim and DeVries 2000; Catalano et al. in review).

**Study Site**

Gizzard shad biomanipulation was conducted at Lake Dora, Lake County, Florida, USA. Gizzard shad populations at two nearby unmanipulated lakes were also studied to serve as unfished control populations. The lakes were part of the Harris Chain of Lakes (HCL) in central Florida, USA. The lakes were shallow (3 m average depth) hypereutrophic lakes (mean chlorophyll a concentrations $> 50$ ug/L) with similar fish communities. Biomanipulation at Lake Dora was achieved with a government-subsidized commercial gill net fishery by the regional
water management agency, the St. Johns River Water management District (SJRWMID). 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).

**Methods**

I 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 HCL 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. I 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. Catalano (Chapter 2) 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. Survey gear selectivity estimates from Catalano (Chapter 2) 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, I estimated the selectivity parameters using a length and age structured population model (see Chapters 2 and 3 for model details). Catalano (Chapter 3) estimated natural mortality, growth and recruitment time series for gizzard shad at lakes Dora, Eustis, and Harris. Using these parameter estimates as model inputs, I 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 I was 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 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 Density Dependence**

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 pre-recruit survival at very low population density to pre-recruit 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 Catalano (Chapter 3). Catalano (Chapter 3) 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 pre-recruit survival and not to changes in growth or maturity. Uncertainty in \( \hat{\alpha} \) estimates 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

I 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 of the form:

\[ N_{a,t} = N_{a-1,t-1}e^{-M}(1-v_a u_t), \]  

(4-1)

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):

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

(4-2)

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.

Estimated selectivity functions that were dome-shaped were converted to asymptotic curves by setting \( \gamma \) equal to zero (Figure 4-1). This was done to mimic occasional fisher use of larger mesh sizes than the minimum to exploit large individuals that were invulnerable to small mesh sizes due to dome-shaped selectivity. 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.
The equilibrium model had deterministic recruitment predicted as a function of spawner biomass using the Beverton-Holt stock-recruitment model (Walters et al. 2006):

\[
N_{t+1} = \frac{\hat{\alpha} E_{t-1}}{\phi_0 + \left(\frac{\hat{\alpha} - 1}{R_0 \phi_0}\right) E_{t-1}},
\]

(4-3)

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 (Catalano, Chapter 3). 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 Catalano (Chapter 3) 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:

\[ \phi_0 = \sum_a s_a m_a w_a, \]  

(4-4)

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 Catalano (Chapter 2). Weight at age was estimated using the allometric relationship:

\[ w_a = cL^b, \]  

(4-5)

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:

\[ E_t = \sum_a N_a m_a w_a. \]  

(4-6)

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 Catalano (Chapter 3). Each parameter value was obtained by averaging over lake-specific estimates from lakes 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 by Catalano (Chapter 3) 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, I varied $\hat{\alpha}$ using the uncertainty from Chapter 3 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), I drew 1,000 random lognormally-distributed deviates for $\hat{\alpha}$ assuming a mean of 6.6 and standard deviation of 3.7 from Catalano (Chapter 3). I 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:

$$B = \sum_a N_a w_a. \quad (4-7)$$

SPR was calculated as:

$$SPR = \frac{R_f \phi_f}{R_j \phi_j}, \quad (4-8)$$

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, I 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, I 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 4-1a). Lengths at 50% selectivity (L50) ranged from 166 mm for the 51-mm mesh to 339 mm for the 102-mm mesh (Figure 4-1a,b; Table 4-1). Predicted catches of gizzard shad tightly fit the observed length distributions for each mesh size (Figure 4-2).

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 4-3a). 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 4-3a,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 4-2). 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 4-3e) 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 4-4a), 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 4-4b,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 4-3). 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 4-3). The 102-mm mesh was ineffective at reducing SPR (Figure 4-4e). Reducing SPR to less than 25% was highly unlikely with a two-year harvest interval for all mesh sizes except 51 mm (Table 4-3).

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.

These findings have implications for gizzard shad biomanipulation. The SJRWMD has been harvesting gizzard shad since 1995 to reduce phytoplankton biomass in hypereutrophic Florida lakes using a 102-mm mesh size restriction to reduce bycatch of black crappie, a recreationally important fish species. My findings suggest that this approach is unlikely to attain substantial biomass reduction of gizzard shad in the long term given current exploitation rates of 60-70% (Catalano et al. in review). 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). In such situations resource managers and stakeholders will need to carefully explore the tradeoffs between gizzard shad biomanipulation and black crappie fisheries.

There are several assumptions of my analysis that should be addressed. I 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 plaktvore removals. My data do not address the applicability of this value to Lake Dora. However, my 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, I 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 I 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 I only found changes in juvenile fish survival after fishing. However, fish stock assessment models can be very sensitive to error in natural mortality estimates (Mertz and Myers 1997; Clark 1999; Quinn and Deriso 1999). Upward bias in natural mortality in my 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, I 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, I 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, my gear selectivity assumptions were reasonable and provided the most realistic estimates of biomass reduction and SPR.

My 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). Ideally, simulations such as those presented here should be carried out prior to manipulation to determine the levels of biomass reduction that could be expected given current knowledge of mortality, growth, and gear selectivity. Such simulations should attempt to incorporate compensatory density dependence.
One problem with this approach is that the strength of density dependence is often not known for a particular population and likely depends on many factors that could be specific to a particular system (Walters and Martell 2004). However, there is a growing body of knowledge on general patterns in density dependence across species that could be used to inform simulations that account for compensation (Myers et al. 1999; Goodwin et al. 2006). Goodwin et al. (2006) related the strength of density dependence to life history characteristics of 54 fish stocks. Thus, one could choose a range of values of $\hat{\alpha}$ based on these patterns.
Table 4-1. Gear selectivity parameter estimates (95% confidence interval) for each gill net mesh size 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.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Estimate</th>
</tr>
</thead>
<tbody>
<tr>
<td>L50_{51}</td>
<td>165.86 (163.99 - 167.74)</td>
</tr>
<tr>
<td>γ_{51}</td>
<td>0.07 (0.05 - 0.10)</td>
</tr>
<tr>
<td>β_{51}</td>
<td>0.28 (0.22 - 0.35)</td>
</tr>
<tr>
<td>L50_{64}</td>
<td>217.25 (214.26 - 220.28)</td>
</tr>
<tr>
<td>γ_{64}</td>
<td>0.13 (0.11 - 0.16)</td>
</tr>
<tr>
<td>β_{64}</td>
<td>0.13 (0.12 - 0.15)</td>
</tr>
<tr>
<td>L50_{76}</td>
<td>251.32 (247.84 - 254.84)</td>
</tr>
<tr>
<td>γ_{76}</td>
<td>0.05 (0.03 - 0.07)</td>
</tr>
<tr>
<td>β_{76}</td>
<td>0.10 (0.09 - 0.11)</td>
</tr>
<tr>
<td>L50_{89}</td>
<td>290.27 (287.92 - 292.64)</td>
</tr>
<tr>
<td>γ_{89}</td>
<td>0.00 (0.00 - 0.00)</td>
</tr>
<tr>
<td>β_{89}</td>
<td>0.07 (0.07 - 0.08)</td>
</tr>
<tr>
<td>L50_{102}</td>
<td>340.09 (336.59 - 343.62)</td>
</tr>
<tr>
<td>γ_{102}</td>
<td>0.00 (0.00 - 0.00)</td>
</tr>
<tr>
<td>β_{102}</td>
<td>0.05 (0.05 - 0.06)</td>
</tr>
</tbody>
</table>
Table 4-2. 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 ($\mu$), and five gill net mesh sizes ranging from 51 to 102 mm.

<table>
<thead>
<tr>
<th>Interval (yrs)</th>
<th>$\mu$</th>
<th>Gill Net Mesh Size</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>51</td>
</tr>
<tr>
<td>1</td>
<td>0.4</td>
<td>0.44</td>
</tr>
<tr>
<td></td>
<td>0.6</td>
<td>0.97</td>
</tr>
<tr>
<td></td>
<td>0.8</td>
<td>1.00</td>
</tr>
<tr>
<td>2</td>
<td>0.4</td>
<td>0.04</td>
</tr>
<tr>
<td></td>
<td>0.6</td>
<td>0.12</td>
</tr>
<tr>
<td></td>
<td>0.8</td>
<td>0.43</td>
</tr>
</tbody>
</table>

Table 4-3. 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 ($\mu$), and five gill net mesh sizes ranging from 51 to 102 mm.

<table>
<thead>
<tr>
<th>Interval (yrs)</th>
<th>$\mu$</th>
<th>Gill Net Mesh Size</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>51</td>
</tr>
<tr>
<td>1</td>
<td>0.4</td>
<td>0.84</td>
</tr>
<tr>
<td></td>
<td>0.6</td>
<td>1.00</td>
</tr>
<tr>
<td></td>
<td>0.8</td>
<td>1.00</td>
</tr>
<tr>
<td>2</td>
<td>0.4</td>
<td>0.11</td>
</tr>
<tr>
<td></td>
<td>0.6</td>
<td>1.00</td>
</tr>
<tr>
<td></td>
<td>0.8</td>
<td>1.00</td>
</tr>
</tbody>
</table>
Figure 4-1. Estimated gear selectivity curves for 51, 64, 76, 89, and 102-mm gill net mesh sizes (panel a). The dome-shaped curves were converted to asymptotic functions for the simulation analysis to simulate the choice by fishers to occasionally use of larger mesh sizes than the minimum when large fish are available for capture. (panel b). Length at 50% selectivity is identical between the two panels for each mesh size.
Figure 4-2. 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.
Figure 4-3. Total population biomass as a function of exploitation rate and gill net mesh size for an annual harvest interval. Panels are arranged as follows: panel a, 51-mm mesh; panel b, 64-mm mesh; panel c, 76-mm mesh; panel d, 89-mm mesh; panel e, 102-mm mesh. Dashed lines represent the 95% confidence intervals obtained via parametric bootstrap of the maximum lifetime reproductive rate.
Figure 4-4. Spawning potential ratio (SPR) as a function of exploitation rate and gill net mesh size for an annual harvest interval. Panels are arranged as follows: panel a, 51-mm mesh; panel b, 64-mm mesh; panel c, 76-mm mesh; panel d, 89-mm mesh; panel e, 102-mm mesh. Dashed lines represent the 95% confidence intervals obtained via parametric bootstrap of the maximum lifetime reproductive rate.
CHAPTER 5  
SYNTHESIS AND FUTURE RESEARCH

Gizzard shad populations appear to be regulated by density dependence in juvenile survival at least at the level of density reduction achieved by the experimental removal at Lake Dora. This is not surprising considering the abundance of literature suggesting that density likely plays a key role in the survival of pre-recruits. One clear weakness of the study was the strength of the total biomass reduction. The reduction in spawner biomass was substantial and provided good contrast in the data to evaluate changes in juvenile survival, but total biomass reduction was moderate due to the size-selective nature of the fishery and high estimated natural mortality rate. The lack of density dependence in adult growth and maturity may have been due to the relatively weak total density reduction. Future studies should achieve stronger total biomass reductions to fully assess the relative importance of compensation among life stages. I would expect large total biomass reductions to result in changes in growth and maturity of gizzard shad based on data from gizzard shad biomanipulation in Alabama (Kim and DeVries 2000) and apparent density related effects on growth at Acton lake, Ohio (Schaus et al. 2002). Thus, I view my estimates of the strength of density dependence as conservative.

Biomanipulation studies could provide information on compensatory density dependence of target species. However, analysis of density reduction levels and compensatory responses are rarely rigorous enough for such investigations as the focus of biomanipulation is usually on the responses of phytoplankton and zooplankton communities. With some additional effort, I argue that more detailed data should be collected from these manipulations. These could provide a very large sample size of density reduction experiments to make strong inferences about fish compensation.
My study was not able to examine specific mechanisms for changes in pre-recruit survival. Understanding these mechanisms would be interesting from an ecological and population dynamics perspective. Future density reduction studies should collect data on the juvenile life stage to assess possible mechanisms such as growth or risk-sensitive foraging behavior. These studies will be difficult because of problems in capturing small juvenile fishes in such a way that is comparable throughout the first year of life. This is challenging because juvenile fishes grow rapidly and therefore vulnerability to sampling gears is constantly changing. In addition, these animals undergo complicated ontogenetic shifts in habitat and diet, and the processes controlling density dependence may occur at very fine spatial and temporal scales. Controlled pond studies may provide the best means for studying mechanisms of juvenile fish density dependence.

I introduced a maximum likelihood model to estimate a recruitment time series along with mortality, growth, and gear selectivity. This model was useful for exploring gizzard shad population dynamics. The model provided an alternative to other existing length-age fish stock assessment models. In addition, my analysis evaluated potential biases in parameter estimates, which to my knowledge has yet to be published for length-age structured models. Future work should compare estimates from my model with those of other length-age models such as Flexibest and Stock Synthesis 2. In addition, investigators should assess model efficiency in terms of the amount of computation time required for estimation. My model was computationally demanding but likely could have been run more efficiently with a program that uses automatic differentiation such as AD Model Builder (ADMB). ADMB is much more efficient than program R in estimating complicated models with many parameters. Thus, my model will likely perform better using the ADMB platform.
I introduced a simple simulation study showing how uncertainty in density dependence could be incorporated into forecasts of the efficacy of fish removal for biomanipulation. This study could serve as a guide for planning biomanipulation experiments. In my view, biomanipulation studies could do a better job of quantitatively assessing how the proposed removal could affect the target population. These modeling efforts could be extended further to include ecosystem dynamics to attempt to predict effects of biomanipulation on phytoplankton biomass and other ecosystem components. These models would represent testable hypotheses of system function and would promote more structured thinking regarding when, where and why biomanipulation could be successful. Current ecosystem models such as ECOPATH/ECOSIM could be used in these exploratory modeling exercises. However, other models may need to be developed for omnivorous fish biomanipulation that incorporate bottom-up nutrient enrichment due to benthivory, as well as top-down effects of zooplankton grazing by juvenile omnivores on phytoplankton dynamics. These dynamics could be quite complicated and therefore a modeling exercise would force investigators to clarify our understanding of system function as well as identify data needs that could resolve uncertainties.

Few biomanipulation studies to date have used basic fish population dynamics methods to understand the effects of harvesting on target populations. Incorporation of estimates of gear selectivity and natural mortality could clarify how many fish should be removed to attain biomanipulation targets. These studies should be conducted before biomanipulation occurs to ensure that funds are not wasted by removing only a relatively small part of the population, which would have minimal impacts on water quality. These analyses need not be complicated and could provide excellent guidance in planning of biomanipulation projects.
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BIOGRAPHICAL SKETCH

Matt is from Lorain, Ohio and grew up within a stone’s throw of Lake Erie. He received a Bachelor of Science degree in Zoology from Miami University (Ohio) in 1997. After graduation, he worked as a field technician at Yellowstone National Park where he assisted in a study of the effects of non-native lake trout on the cutthroat trout population in Yellowstone Lake. He also spent two years working as a fisheries technician at the Illinois Natural History Survey in Salem, Illinois. Matt received his Master of Science degree in 2002 at the University of Wisconsin-Stevens Point where he evaluated the effects of low-head dam removal on fish communities in the Baraboo River, Wisconsin. He then worked for two years as a research biologist with the Wisconsin Department of Natural Resources in Madison, Wisconsin. After working as a fisheries research biologist for one year under Mike Allen at the University of Florida, Matt began his Ph.D. working on population dynamics of gizzard shad in 2005.