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FINAL REPORT



**Biomanipulation Impacts on
Gizzard Shad Population Dynamics,
Lake Water Quality, and a
Recreational Fishery**

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Period of Study: 1 November 2004 to 31 May 2007

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LAKE WATER QUALITY AND A RECREATIONAL FISHERY

EXECUTIVE SUMMARY

Reversing the effects of eutrophication can be challenging and requires the reduction of external nutrient sources and internal nutrient loading. Omnivorous gizzard shad *Dorosoma cepedianum* can facilitate nutrient loading from the sediments as a consequence of their foraging activity at the sediment-water interface and subsequent excretion of nutrients in the water column. This feeding activity may contribute considerably to the release of nutrients from the sediments in eutrophic Florida lakes.

Biomanipulation via removal of gizzard shad has been proposed as a management strategy for improving water clarity by reducing internal nutrient loading from the sediments. Preliminary studies at Lake Denham, Florida, suggested that strong biomass reductions of gizzard shad using haul seines may reduce phytoplankton biomass. Recently, biomanipulations have been attempted on several lakes of the Harris Chain of Lakes, Florida using gill nets, but the results of these efforts have yet to be experimentally evaluated. Understanding how fish life history metrics respond to density reductions is critical to understanding the potential impact of biomanipulation on lake food webs. We used a whole-lake gizzard shad reduction experiment, hereafter referred to as a biomanipulation, to 1) assess impacts of a commercial gizzard shad removal on their population dynamics (i.e., recruitment, growth, mortality), 2) measure diet contents of gizzard shad to indicate mode of feeding, 3) explore the potential for gizzard shad removal to influence lake water quality, and 4) evaluate the potential for bycatch impacts on black crappie *Pomoxis nigromaculatus* fisheries.

We tested the hypothesis that gizzard shad removal at Lake Dora would result in compensatory changes in reproductive rates of the gizzard shad population. We sought to understand the mechanisms for compensatory responses by evaluating changes in growth, reproductive investment, maturation schedules, larval fish densities, juvenile survival, and recruitment of gizzard shad. Lakes Eustis and Harris were used as reference sites with no commercial fishing. Commercial fishing with gill nets (minimum of 4 inch mesh) occurred in March and April of 2005 and January – March 2006. We collected data on gizzard shad population dynamics at all three lakes from November 2004 to May 2007. The total harvest of gizzard shad from Lake Dora was estimated at 124,989 kg (54 kg/ha) in 2005 and 135,095 kg (58 kg/ha) in 2006. Leslie depletion analysis estimated an exploitation rate on vulnerable-sized fish of 0.61 (95% confidence interval = 0.42 to 0.73) in 2005 and 0.46 (95% confidence interval = 0.30 to 0.63) in 2006.

Total biomass reduction for the gizzard shad population was about 40% from both years of harvest combined. Compensatory responses of individual vital rates were weak following biomanipulation with the exception of length-at-maturity. Gizzard shad at Lake Dora matured at a size 40 mm smaller in 2007 than in 2005, and we observed no changes in size at maturity for Lakes Eustis or Harris. We detected no change in growth, the gonadosomatic index (an index of fecundity), and juvenile survival, but we found a small decrease in average larval fish density after fishing at Lake Dora. Despite small changes in vital rates, we found increased gizzard shad recruitment to age-1 from 2005 to 2007 at Lake Dora, indicating no reduction in gizzard shad recruitment despite substantial decrease in population egg production. Changes in individual vital rates that led to increased recruitment may have been very small or were obscured by sampling variation. Age-1 recruitment estimates were uncertain due to low vulnerability of these small fish to the experimental gill nets. Further sampling in 2008 and 2009 will track these cohorts as they become more vulnerable to the gill nets at age 2. If future samples confirm preliminary conclusions from age-1 recruitment estimates, we would conclude that the population compensated through increased reproduction and maintained constant or possibly increased recruitment despite a 40% total biomass reduction. This finding would have important implications for biomanipulation efforts because compensatory reproduction may dampen biomass reductions by maintaining or increasing the numbers of age-0 gizzard shad, even if the

mechanisms for compensation are difficult to detect in field data. Future sampling will refine our conclusions regarding recruitment compensation of the gizzard shad population at Lake Dora.

We used a simulation model to evaluate the relative performance of alternative gizzard shad removal strategies. The 4-inch mesh nets used in the commercial fishery showed dome-shaped vulnerability schedules for gizzard shad, with fish not fully vulnerable to the gear until age 3.5 and vulnerability declining after age 4. Our results show that gill net fisheries for gizzard shad are unlikely to cause large total biomass reductions for gizzard shad (i.e., $\geq 75\%$ declines) under current gear and fishery configurations. Achieving a 75% reduction in total shad biomass, which is often the target in biomanipulation efforts, could only be achieved by 1) use of smaller mesh sizes, especially 3-inch mesh, 2) very high fishing mortality rates, and 3) fishing every year. We chose a 75% biomass reduction target based on literature reviews of many previous biomanipulation studies, but the degree of reduction required to reduce phytoplankton biomass in Florida lakes is unknown. Our results 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 fishing mortality (i.e., fishing effort) and decreases in gill net mesh size.

Gizzard shad diets were evaluated using stable isotopes of sulfur and gut content analysis. Gizzard shad $\delta^{34}\text{S}$ values confirmed the ontogenetic changes in the diet composition reported in literature. During the summer of 2006, gizzard shad $\delta^{34}\text{S}$ signatures showed clear evidence of an ontogenetic shift from water column to benthic food items. The $\delta^{34}\text{S}$ values of young gizzard shad were initially high (9-10‰) and associated with pelagic modes of feeding, but declined rapidly to values between 0.1‰ and 2.4‰ once a TL size of 100-200 mm was reached, suggesting increased importance of benthic feeding. Gut content analysis showed that nearly all gizzard shad stomachs contained evidence of both pelagic and benthic feeding. Gizzard shad in the 100 – 200 mm length class probably derive most of their food from the microflora associated with sediment detritus, whereas larger fish likely spend more time in the water column foraging on zooplankton (copepods and cladocerans), although their foreguts still contained plant and mud detritus. The size relationship with $\delta^{34}\text{S}$ suggested some size-dependent diet shifts to zooplankton in gizzard shad populations.

Our analysis of zooplankton and water quality data from 2003 to 2007 showed no changes in water quality and macrozooplankton biomass following gizzard shad removal at Lake Dora. The removal resulted in no change in chlorophyll *a* concentration, Secchi depth, or total phosphorus concentration. There were also clearly no changes in copepod or cladoceran biomass.

Macrozooplankton communities may be controlled by a number of other factors including juvenile gizzard shad, threadfin shad *D. penetense*, invertebrate predators, or density of inedible filamentous algae. We expected gizzard shad removal to reduce water column phosphorus and chlorophyll *a* based on previous studies evaluating omnivore removals. Our results suggest that either 1) these effects are not likely via gizzard shad removal in Florida lakes, or 2) the biomass reduction was not strong enough to elicit a response in the phytoplankton community or total phosphorus concentrations. Although gizzard shad clearly contribute to internal phosphorus loads in eutrophic lakes, the magnitude of this loading relative to external inputs, sediment fluxes, and wind resuspension is unknown. Our results suggested that these other phosphorus loads substantially exceeded those attributable to the two-year gizzard shad removal at Lake Dora.

Black crappie is the primary sport fish targeted by recreational anglers at Lake Dora, and our results show that the population could be negatively impacted by increases in exploitation resulting from either the recreational fishery or bycatch from the commercial gill net fishery for gizzard shad. The estimated recreational exploitation rate in 2006 was approximately the total sustainable exploitation rate, and increases due to recreational fishing and/or commercial bycatch greatly increase the probability of recruitment overfishing. Resource managers must evaluate policy trade-offs to consider the benefit of the gizzard shad removal and the negative impacts of bycatch mortality on recreational fisheries. Total bycatch estimates in 2006 (January – March) were nearly twice as high as total bycatch estimates in 2005 (March – April). These results suggest that bycatch could be reduced by timing the commercial fishing season to prevent fishing during winter and early spring when black crappie are more abundant in open-water areas where gill netting occurs. Bycatch impacts on black crappie fisheries may be acceptable if the gizzard shad reduction is successful in improving water clarity and increasing aquatic macrophyte abundance. Possible management alternatives are to 1) discontinue the gill net fishery to

eradicate bycatch and prevent any harm to the black crappie recreational fishery, or 2) increase commercial effort and gizzard shad exploitation to optimize the success of the biomanipulation. The results of this study showed that continuing the program at the current level of commercial effort did not optimize either management objective at Lake Dora.

Results of this study show that current commercial fishing gear configurations for gizzard shad reductions are unlikely to achieve large ($> 75\%$) reductions in total gizzard shad biomass. We cannot conclude that biomanipulation is not a viable management tool for restoration of Florida lakes, but our results clearly show that 40% biomass reduction over two years did not significantly influence lake nutrients and zooplankton abundance at Lake Dora. Future biomanipulations targeting water quality improvements should seek to maximize biomass reductions for gizzard shad and should be conducted using control lakes to verify any shifts that occur. Lower mesh sizes and higher commercial fishing effort are recommended, but resource managers should recognize that substantial impacts to black crappie fisheries could occur.

MANAGEMENT RECOMMENDATIONS

- Substantial literature indicates that a minimum of a 75-80% reduction in total omnivore biomass is required to achieve changes in water clarity via biomanipulation.
- Gill net fishery configurations conducted to date (i.e., 4-inch mesh size) are unlikely to cause 75% reductions in total gizzard shad biomass in eutrophic Florida lakes, even if commercial fishing effort was higher than that achieved at Lake Dora. Resource managers should consider either smaller mesh sizes for gill nets or different fishing gears that are less size selective for future biomanipulation projects.
- The whole-lake experiment did not achieve reductions in chlorophyll *a* or water clarity at Lake Dora, suggesting that a stronger manipulation would be required to attain these objectives.
- Bycatch from commercial fishing can harm recreational fisheries in cases where recreational fishing mortality on black crappie is also high (e.g., Lake Dora).
- Future biomanipulation efforts targeting water quality improvements should seek to maximize impact on omnivorous fish populations for Florida lakes through lower mesh sizes and higher levels of commercial fishing effort. Achieving these objectives could require making recreational fishery objectives secondary to biomanipulation objectives.

COOPERATORS AND ACKNOWLEDGMENTS

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PROJECT INTRODUCTION

Gizzard shad (*Dorosoma cepedianum*) are important prey fish in lakes and reservoirs and may influence lake water chemistry and species interactions. Gizzard shad serve as prey for predators but can also influence fish communities and nutrient cycling, particularly in hypereutrophic lakes where gizzard shad often dominate total fish biomass (Heidinger 1983). Juvenile gizzard shad are obligate zooplanktivores (Guest et al. 1990; Allen and DeVries 1992), whereas adult gizzard shad are usually detritivores but can be zooplanktivorous depending on zooplankton availability (Heidinger 1983; Michaletz 1988; DeVries and Stein 1992). At high densities, gizzard shad can influence recruitment of other fishes by reducing crustacean zooplankton densities to nil, thereby reducing food availability for other fishes during early life (DeVries and Stein 1992; Stein et al. 1995).

Biomanipulation via removal of planktivorous and detritivorous fishes is a strategy that has potential for improving water clarity in lakes. Removal of gizzard shad could reduce physical disruption of bottom sediments by benthivorous shad and cycling of nutrients from the fish to the water column via excretion. Because adult gizzard shad often consume detritus and resuspend nutrients in the water column (Drenner et al. 1996; Schaus and Vanni 2000), reducing adult gizzard shad biomass could lower nutrient availability in the water column and thus reduce phytoplankton abundance. Vanni et al. (2006) showed that gizzard shad can influence lake nutrient concentrations across broad spatial scales and may contribute relatively more to phosphorus loading as lake productivity increases. Schaus et al. (1997) and Gido (2002) found that gizzard shad provide available nutrients to phytoplankton by consuming organic detritus from the sediments and excreting soluble forms of nitrogen (N) and phosphorus (P) in the water column. The magnitude of nutrient excretion from gizzard shad was found to be significant relative to external sources of nutrient loading for reservoirs in Ohio (Schaus et al. 1997; Vanni et al. 2006) and Oklahoma (Gido 2002).

Impacts of gizzard shad on lake nutrient cycling likely vary with their feeding strategy. Adult gizzard shad most commonly feed on detritus but can also consume zooplankton and phytoplankton depending on their availability and quality (Michaletz 1988; DeVries and Stein 1992). Gizzard shad consuming detritus have the most potential to take unavailable nutrients from the sediment and make them available to phytoplankton. Conversely, gizzard shad feeding on phytoplankton or zooplankton could cycle nutrients that are already present in the water column. Schaus and Vanni (2000) found that gizzard shad excluded from the sediments failed to stimulate phytoplankton biomass in enclosures, whereas with fish access to bottom sediments phytoplankton concentrations increased substantially within a period of days. Thus, there is a need to understand feeding strategies of gizzard shad when considering impacts of gizzard shad on nutrient cycling.

The magnitude of nutrient excretion by omnivorous fishes varies with total fish biomass, size structure, fish feeding, and season. Effects of nutrient resuspension by fish appear to be magnified in eutrophic and hypereutrophic systems that support high omnivorous fish biomass, based on mesocosm experiments (Drenner et al. 1996; Drenner et al. 1998; Schaus and Vanni 2000). Schaus et al. (1997) found that small gizzard shad excrete more N and P per body mass than large shad, suggesting that for a given level of total biomass, populations composed of small gizzard shad would release more nutrients to the water column than populations composed of large fish. Similarly, Schaus and Vanni (2000) found that enclosures containing small gizzard shad had greater increases in phytoplankton abundance than enclosures containing a similar biomass of large shad. Fish metabolism increases with temperature (Moyle and Cech 1996), and thus excretion are expected to vary with latitude and season. Omnivorous fishes found in cold climates may have less influence on in-lake nutrient cycling than fish populations at lower latitudes due to warmer temperatures and higher metabolism throughout the year. However, annual rates of nutrient excretion have not been determined, and studies thus far have included only temperate regions with relatively long winters (Schaus et al. 1997; Gido 2002). Impacts of gizzard shad on nutrient cycling in Florida lakes could be important throughout the year due to the warm climate.

Selective reduction or removal of gizzard shad using rotenone has been attempted in small impoundments and reservoirs, but the impacts were often short lived. Kim and DeVries (2000) evaluated treatment of a 66-ha Alabama reservoir with 0.1 mg/L of rotenone for reducing gizzard shad biomass. In the year following treatment, age-0 gizzard shad density was low but fish growth was rapid relative to pre-treatment rates. In the second year post-treatment, the gizzard shad population returned to pre-treatment levels (Kim and DeVries 2000; Irwin et al. 2003). DeVries and Stein (1990) reviewed effects of shad removal studies on sport fish populations and found highly variable results. They surmised that major reductions (i.e., > 50 %) in shad biomass would be required to see a measurable benefit to other fishes. Zeller and Wyatt (1967) found that use of selective rotenone for a gizzard shad reduction in a Georgia reservoir reduced gizzard shad biomass for four years. Duration of impact for rotenone studies is likely influenced by the extent of gizzard shad kill, which varies widely (reviewed by Zeller and Wyatt 1967).

In Florida, gizzard shad removal projects using gill nets and/or haul seines have been conducted in an attempt to improve lake water clarity and reduce algal blooms. The St. Johns River Water Management District (SJRWMD) has conducted gizzard shad reductions on three hypereutrophic lakes (Lakes Denham, Apopka, and Griffin) from the late 1980's to current day. Improved water clarity occurred concurrent with gizzard shad reductions at all three lakes (M. Coveney, SJRWMD, pers. comm.), but the causal mechanisms were not clearly identified.

However, no studies have evaluated the population response of gizzard shad to biomass reductions using gill nets. Gill nets impart highly size-selective mortality and reduced biomass of large shad, whereas rotenone treatment reduces density of all size groups. Thus, any effects of the gill net reductions could be short lived because smaller shad would remain in the population to grow and reproduce. Reductions could be followed by increases in growth rate (e.g., Kim and DeVries 2000), possibly causing large year classes to occur from reproduction of the remaining fish. Alternately, selective removal of large gizzard shad could reduce population fecundity and cause lower gizzard shad recruitment. Thus, there is a need to assess how reducing large gizzard shad density with gill nets influences overall gizzard shad size structure, reproduction, growth rate, and the potential for decreased nutrient excretion.

Bycatch occurs in all commercial fisheries and has the potential to harm sport fisheries if bycatch rates are high. The concern about bycatch for commercial gizzard shad fisheries in Florida revolves primarily around black crappie (*Pomoxis nigromaculatus*) fisheries. Black crappie support popular fisheries in many eutrophic Florida lakes (Allen et al. 2000), and for much of the year black crappie are found in open-water areas where commercial gill nets are fished. No previous studies have evaluated the impact of commercial gill netting on black crappie populations, and understanding these potential impacts is important when considering commercial gill netting as a biomanipulation tool.

The purpose of this project was to experimentally assess impacts of a commercial gizzard shad removal (i.e., biomanipulation) on their population dynamics (i.e., recruitment, growth, mortality), to explore the potential for gizzard shad removal to influence nutrient cycling in Florida lakes, and to evaluate the potential for bycatch impacts on black crappie fisheries. Our objectives were to:

1. assess gizzard shad population dynamics (recruitment, growth, mortality) before and after an experimental removal project and compare to two reference lakes (Chapter 1),
2. develop a population model for gizzard shad and predict effects of varying levels of commercial fishing on gizzard shad population dynamics (Chapter 1),
3. assess feeding strategies of various size groups of gizzard shad using stable isotope analysis (Chapter 2), and
4. evaluate effects of gizzard shad removal on water quality and macrozooplankton communities (Chapter 3), and
5. quantify the impacts of gill net bycatch on a recreational black crappie fishery (Chapter 4).

Each project objective was addressed in a series of interrelated studies, and they are presented as chapters of this report.

CHAPTER 1: COMMERCIAL FISHING IMPACTS ON A GIZZARD SHAD POPULATION WITH IMPLICATIONS FOR BIOMANIPULATION STRATEGIES

INTRODUCTION

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: densatory and compensatory. Densatory density dependence is a positive feedback on population size whereby population growth increases as density increases (Gotelli 1995; Rose et al. 2001). However, densation 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 stages affected by 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.

When considering biomanipulation as a lake restoration tool, understanding how fish life history metrics respond to commercial fishing is critical to understanding the potential impact of biomanipulation on lake food webs. Gizzard shad are highly fecund with mean annual fecundity increasing from about 60,000 to 300,000 eggs per female as size increases from 200 to 400 mm, respectively (Heidinger 1983). Thus, low numbers of adult gizzard shad can produce large year classes if environmental conditions are favorable. Gizzard shad are a relatively short lived fish with high natural mortality (Heidinger 1983), which means that fishing mortality may not substantially influence total mortality relative to long-lived species. In this chapter, we

addressed project objectives 1 and 2: the gizzard shad population responses to commercial fishing and evaluation of the level of commercial fishing required to reduce gizzard shad abundance. We tested the hypothesis that gizzard shad removal at Lake Dora would result in compensatory changes in reproductive rates of the gizzard shad population. We sought to understand the mechanisms for these compensatory responses by evaluating changes in growth, reproductive investment, maturation schedules, larval fish densities, juvenile survival, and recruitment of gizzard shad. We also used a population model to explore harvest policies that would result in varying levels of gizzard shad population suppression.

BIOMANIPULATION TIMELINE AND STUDY SITES

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

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

METHODS

Abundance and size structure

Gizzard shad relative abundance and size structure were measured for Lakes Dora, Eustis, and Harris from samples collected in November/December, January/February, and May of each year. Horizontal floating gill nets were used to sample fish at 20 fixed, randomly-selected sites per lake (Figure 1-1; Appendix A). Gill nets were 2.4-m deep and contained eight, 15.3-m long panels of 1.5, 2.0, 2.5, 3.0, 3.5, 4.0, 4.5, and 5.0-in stretch monofilament mesh. Each net was set for approximately two hours during daytime, and time of net deployment and retrieval was recorded. Captured fish were measured for total length (TL; mm) and counted separately for each mesh panel.

The main comparison of interest regarding catch per effort (CPE) was differences in catch rates of fish that were vulnerable to the fishery at Lake Dora. Therefore we tested for differences in the ratio of the catch of vulnerable:invulnerable fish (hereafter referred to as the length ratio) among lakes and years. The length ratio was calculated for each year, lake, and site as:

$$LR = \ln \left(\frac{\# \text{ fish } < 330 \text{ mm} + 1}{\# \text{ fish } \geq 330 \text{ mm} + 1} \right), \quad (1-1)$$

where the number of fish over and below 330 mm total length was calculated for each of 20 gill net sets per lake per year. We were particularly interested in whether differences in the length ratio among lakes were consistent across years. We used a repeated measures ANOVA (SAS Proc Mixed) using sites as subjects in the analysis and lake, year, and the lake*year interaction as factors. If the interaction term was significant, it could indicate that commercial gill netting influenced the size structure of gizzard shad at Lake Dora relative to the other lakes, depending on the cause of the interaction. If a significant interaction was detected, we used Bonferoni pairwise comparisons to test whether the length ratio differed between years for each lake (N = 9 pairwise comparisons; $\alpha = 0.05/9 = 0.005$).

One problem with a size structure analysis across years is that length distributions can be affected by recruitment variation, which could confound conclusions regarding the shad removal.

We conducted a second analysis that tested for differences in the length ratio between January and May 2005, again using repeated measures ANOVA with sites as the subject. Pairwise comparisons were carried out using the Bonferroni correction if there was a significant lake*month interaction (N = 6 pairwise comparisons; $\alpha = 0.05/6 = 0.0083$). This before/after comparison was not affected by recruitment variation but could be affected by seasonal changes in catchability due to growth or changes in behavior. We excluded fish less than 270 mm to remove age-1 fish from this analysis, which were more vulnerable in May than January because of growth between the two time periods. We also evaluated gizzard shad size structure by constructing relative length frequency histograms for each lake, year, and month.

Gizzard shad age structure and growth

We evaluated gizzard shad age structure at Lakes Dora, Eustis and Harris in January/February of 2005, 2006, and 2007. During each sampling event, gizzard shad were collected using gill nets (described above) at 20 fixed, randomly selected sites at each lake (Appendix A). Otoliths were removed from a subsample of 10 fish per 10-mm group for aging. Otoliths were either read in whole view or sectioned using a South Bay Tech[®] Model 650 low-speed saw. All otoliths with three or more annuli were sectioned due to difficulty in detecting annuli in older fish. Otoliths were read by three independent readers using a dissecting microscope at 40X magnification. Aged fish were extrapolated to the entire catch of gizzard shad using an age-length key (Ricker 1975) to estimate the age frequency of the sample (number of fish of each age).

Gizzard shad growth was evaluated using length and age data from January/February of each year. We estimated shad growth parameters using the von Bertalanffy model:

$$L_t = L_\infty (1 - e^{-K(t-t_0)}) \quad (1-2)$$

where L_t is the length (mm) at time t , L_∞ is the asymptotic mean length, K is the metabolic coefficient, and t_0 is the theoretical age at zero length (von Bertalanffy 1938). The model was fit to data from an age-length key using maximum likelihood assuming a log-normal error structure. Because subsampling of fixed-length intervals produces biased parameter estimates (Devries and Frie 1996), we fit the model with age-length key data using weighted average lengths-at-age, weighted by the number of fish in each 10-mm group at each age. The growth model was

simultaneously fit to total length and age for all lakes and years combined, and differences in growth parameters among lakes/years were evaluated by comparing alternative nested models with Akaike's information criterion (AIC). It should be noted that these growth parameter estimates, although unbiased with respect to the sampling gear used, are biased with respect to the true underlying growth parameters of the population due to the size selectivity of the gear. This selectivity tends to overestimate the K parameter and underestimate L_{∞} (Taylor et al. 2005). However, the above comparisons are valid because the same gear was used at all lakes and times. Recently, methods have been developed to estimate unbiased growth parameters and we employed those methods in *Strength of Biomanipulation*, below (Taylor et al. 2005).

The model fitting procedure above is not a direct way to evaluate the influence of commercial fishing on fish growth, because the older age classes underwent most of their growth before the removal. Thus, we tested for differences in mean length-at-age 1 and age 2 as a more direct method for assessing if growth changed in response to fishing. For age-1 fish we compared data from 2005, 2006 and 2007. For age-2 fish, we compared 2005 and 2007 data. Data from 2006 were excluded because age 2 fish in 2006 spent only half of their lifetime at the reduced density. A modified analysis of variance (ANOVA) was then used to compare mean length-at-age from the age length key (Larson 1992; Devries and Frie 1996). The analysis generates data from summary statistics to facilitate fitting of the ANOVA model when individual data records (i.e., age estimates of every fish) are not available. This method provides unbiased estimates of mean lengths at age and their standard deviation from an age length key (Devries and Frie 1996). We tested for a significant lake*time interaction and evaluated whether mean length-at-age differed through time for each lake using Bonferoni pairwise comparisons if interactions were significant.

We conducted marginal increment analysis on gizzard shad otoliths to verify the timing of annulus formation at Lakes Dora, Eustis, and Harris. Otoliths were extracted from approximately 50-100 gizzard shad per month from January 2005 through February 2006. Otoliths for marginal increment analysis were sectioned as described above. Measurements were taken using a Moticam© 2000 digital imaging system with Java software. Marginal increment distance (mm) was defined as the width of the hyaline zone beyond the outer edge of the last opaque band on the otolith. The mean monthly marginal increment was calculated for each lake.

Plots of marginal increment distance vs. time were examined to identify marginal increment minima. These minima indicate the time of gizzard shad annulus formation for verification of age estimates.

Gizzard shad reproduction

Time of reproduction and reproductive output of gizzard shad was estimated at each of the three lakes by measuring ovarian weight and by calculating the gonadosomatic index (GSI) from fish captured in experimental gill nets. Ovaries were removed at two-week intervals from approximately 50 females per lake from January through May of 2005, 2006, and 2007. The GSI was calculated by dividing the ovary weight by the ovary-free whole fish weight. Mean monthly GSI values and ovary weights were plotted against time (month) to identify peaks in gizzard shad spawning activity. We tested for effects of gizzard shad removal on mean GSI using a before-after-control-impacts paired series (BACIPS) analysis. The analysis tests whether differences in a control and an impact system are consistent through time. We calculated mean GSI values for each lake and sample date using fish that were greater than 330 mm to ensure inclusion of only mature fish. Lakes Eustis and Harris data were averaged for each sample date and served as the control dataset (Bence et al. 1996). The difference between average Lake Dora and control GSI values for each sample date are hereafter referred to as ‘deltas’. The time series of data was divided into three time periods: 2005, 2006, and 2007. We used Welch’s t-test for unequal variances to test for differences in mean delta values among years ($\alpha = 0.05$) to identify effects of commercial fishing on GSI values.

Larval fish were collected at Lakes Dora, Eustis, and Harris from late January through June (2005 - 2007) to assess gizzard shad reproductive success. Larval tows were collected at two-week intervals at 10 fixed, randomly selected sites (Appendix A) at each lake using a 0.75-m diameter ichthyoplankton net with 500 micron mesh. Each tow was three minutes in duration at 1-1.5 m/s and the water volume sampled was estimated with a General Oceanics Model 2030 flowmeter mounted in the mouth of the net. Samples were stored in 95% ethanol for processing. The total number of shad was counted in each sample, and a random subsample of 50 shad was removed for length measurement and species determination. We separated larval gizzard shad

from threadfin shad (*D. penetense*) by counting total myomeres for fish < 19 mm (Santucci and Heidinger 1986) and anal fin rays for fish ≥ 19 mm (Shelton 1972). We used anal fin ray counts for fish ≥ 19 mm because larval shad attain their full complement of fin rays at that size (Shelton 1972). Fish with more than 46 myomeres or 27 anal fin rays were considered gizzard shad, and fish with fewer than 46 myomeres and 27 anal rays were considered threadfin shad (Shelton 1972; Santucci and Heidinger 1986). Species proportions from subsamples were applied to the total catch to estimate density (fish/m³) in each sample.

We used the BACIPS type approach for evaluating differences in larval density among the lakes. One of the key assumptions of the BACIPS is additivity of control and impact differences through time. This assumption is violated, for example, if the values of the impact system are a multiple (e.g., 50%) of the control system values. Our larval fish data violated this assumption and consequently were analyzed with the ‘predictive BACIPS’ approach, which models the impact system as a function of the control and requires no additivity assumption (Bence et al. 1996). We calculated mean larval fish densities (across sites; N = 10) for each lake and sample date. Lake Harris and Eustis were averaged for each sample date and served as control densities. We modeled the Lake Dora larval fish densities as a function of the control densities using a zero intercept linear model. The zero intercept was used because model fit was not improved by including the additional intercept parameter based on Akaike’s information criterion. The data were divided into three time periods, 2005, 2006, and 2007 and a separate analysis was conducted for each pairwise comparison of years. For each analysis, effect size (change in the difference between control and impact system) was calculated at each value of the control as the difference between year 1 and year 2 model-predicted impact values (Bence et al. 1996). Confidence intervals for effect size were calculated using methods in Bence et al. (1996). Effect size was considered statistically significant if zero fell outside the 95% confidence interval.

We evaluated changes in size and age-at-maturity by examining histological sections and GSI index values from 2005 and 2007 at Lakes Dora and Eustis. We excluded Lake Harris from this analysis because of the extra expense of the histology preparation and because samples sizes of immature fish from this lake were relatively small. Our approach was to use histology samples (histology was not available for 2005 ovaries) from a subset of 2007 females to estimate the GSI

level at which fish were likely to be mature. Females were considered mature if histological sections showed the presence of vitellogenic (yolked) oocytes. We then plotted maturity as a function of GSI for these 2007 fish to estimate the cutoff GSI value at which fish became mature. This cutoff was used to classify all 2005 and 2007 fish as mature or immature based on their GSI value. Ovaries from 2007 were preserved in 10% buffered formalin and histological cross sections were prepared at the University of Florida College of Veterinary Medicine, Department of Tissue Pathology. Ovary sections were stained with hematoxylin and eosin, embedded in paraffin, sectioned, and mounted on a glass slide. Maturity was modeled as a function of length and age with maximum likelihood using a binomial distribution where the probability of maturity was a function of fish length (l ; or age a) using:

$$P = \frac{1}{1 + e^{-s(l-L50)}} \quad (1-3)$$

where s is the steepness parameter, and $L50$ is the length (or age) at 50% maturity. We compared alternative nested model parameterizations using AIC to determine whether $L50$ and s differed between lakes and years.

Recruitment of gizzard shad to age 1 was evaluated as another index of the reproductive response to commercial fishing. We used mean CPE (fish/hr) of age-1 fish from gill nets set in January/February as an index of recruitment. We tested for differences in CPE of age-1 gizzard shad using repeated measures ANOVA with lake and year as main effects and site as the subject. Means were compared using the Bonferroni multiple comparisons procedure if the interaction was significant ($N = 9$ pairwise comparisons; $\alpha = 0.05/9 = 0.005$).

We evaluated potential changes in survival between the larval stage and age 1 by calculating a survival index. The index was computed as the mean larval fish density from the previous year divided by the age-1 CPE from the current year. The index was calculated for 2006 and 2007 at each lake. Survival index values were compared qualitatively among lakes and years, but were not statistically analyzed.

Strength of Biomanipulation

We used two approaches to estimate the fishing mortality rate on the gizzard shad population at Lake Dora. The first approach estimated the annual exploitation rate (u ; proportion of vulnerable-sized gizzard shad removed) of the commercial removal with a Leslie depletion analysis, which is a linear regression of catch-per-effort (CPE) of commercial vessels though time against cumulative catch (Van Den Avyle and Hayward 1999). We calculated 95% parametric bootstrap confidence intervals for u by using the standard error of the slope and intercept to simulate 1,000 iterations of the regression.

The second approach used a statistical catch at age model (SCA) to estimate u by fitting model-predicted catch proportions at age to observed annual catch-at-age proportions from our fishery-independent experimental gill nets. The SCA model predicted population numbers at age and time ($N_{a,t}$) as a function of an annual survival rate from natural mortality, growth parameters, dome-shaped gill net vulnerability parameters, unknown annual recruitment anomalies (estimated by the model), and unknown annual exploitation rates (estimated by the model) using:

$$N_{1,t} = R_t \quad (1-4)$$

$$N_{2+,t} = N_{a-1,t-1} S(1 - u_t f_a), \quad (1-5)$$

where R_t are a time series of annual recruitment anomalies scaled to a median of 1, S is the annual survival rate from natural mortality, which was assumed constant across age classes, u_t are annual exploitation rates of the commercial fishery for 2005 and 2006, and f_a are age-specific vulnerability parameters to the commercial fishery. The model predicted the age and time specific catch proportions in the fishery-independent experimental gill nets using:

$$C_{a,t} = \frac{N_{a,t} v_a}{\sum_a N_{a,t} v_a}, \quad (1-6)$$

where v_a is the age-specific vulnerability to the experimental nets. Vulnerability to the fishery (f_a) and to experimental nets (v_a) was a function of fish length using the dome shaped model:

$$v_a \text{ (or } f_a) = \left(\frac{1}{1-\gamma} \right) \left(\frac{1-\gamma}{\gamma} \right)^\gamma \left(\frac{e^{\beta\gamma(V50-L_a)}}{1 + e^{\beta(V50-L_a)}} \right), \quad (1-7)$$

where γ determines the strength of the dome shape, β is the steepness parameter, V_{50} is the length at 50% vulnerability, and l_a is the mean length-at-age (Thompson 1994). Asymptotic vulnerability curves with a sigmoidal shape are commonly used in fishery assessments and also were considered in this analysis. However, the dome-shaped model (equation 1-7) is flexible and can assume a sigmoidal form as γ approaches 0. Consequently, using the dome-shaped equation allowed the maximum likelihood estimates of the vulnerability parameters to determine the shape of the vulnerability schedule. Mean length-at-age was predicted from the von Bertalanffy growth model (von Bertalanffy 1938).

Vulnerability, natural survival, and unbiased von Bertalanffy growth parameters are essential for the SCA model. These parameters were obtained independent of the SCA by fitting a length and age structured model to size-age catch data from experimental nets using a multinomial maximum likelihood function (Taylor et al. 2005). This model estimates what natural mortality, growth, and vulnerability rates were most likely to result in catches at length and age that most closely match our observed catches. The Taylor et al. (2005) Model 1 assumes no harvest and stable recruitment, so we pooled January/February length-age data from all unfished lake years (Dora 2005, Harris 2005-2007, and Eustis 2005-2007). Pooling of all lake years was necessary to reduce the influence of strong and weak year classes and to achieve robust parameter estimates by increasing the sample size. We estimated vulnerability parameters for experimental gill nets, 2005 commercial mesh sizes (mainly 4.5-in mesh), and 2006 commercial meshes (mainly 4-in mesh). This was accomplished by repeating the analysis on subsets of length-age data from each of the mesh sizes. The growth parameters estimated from this model are unbiased because they account for sampling gear size selectivity, unlike growth models fit only to length-age data from gill nets (see *Gizzard Shad Age Structure and Growth*, above). One potential problem with pooling the lake data is if growth differed among lakes. Our growth parameter estimates indicated that K was lower at Lake Dora than at Lakes Eustis and Harris (see *Gizzard Shad Age Structure and Growth*, above), suggesting that pooling the length-age data should be interpreted with caution. However, the combined growth models performed nearly as well as models with separate K values, indicating that this assumption was not strongly violated.

Using growth, survival, and vulnerability parameters estimated from the Taylor et al. (2005) model, we used maximum likelihood (multinomial distribution) to estimate annual recruitment anomalies and exploitation rates (2005-2006) by fitting model-predicted catch-at-age proportions to observed catch-at-age proportion data from our annual experimental gill net surveys conducted in January/February. Essentially, this model estimates what the exploitation rates and past recruitments would had to have been to produce experimental gill net catches similar to our observed catches. Exploitation rates from the age structured model were compared to depletion estimates.

The change in total population biomass and spawning potential ratio was estimated from 2004 to 2007. We used an age-structured population model that used monthly time steps to estimate the average and maximum biomass reduction for the post-manipulation time period. The model included growth and mortality parameters estimated from the Taylor et al. (2005) model and exploitation rates from the Leslie depletion. We assumed stable recruitment because of the high degree of uncertainty in our recent annual recruitment estimates. Confidence intervals (95%) were estimated from 1,000 parametric bootstrap iterations. Each iteration generated random exploitation rates drawn from a normal distribution with mean and variance estimated from Leslie depletion. The SPR was calculated at each time step using:

$$SPR_t = \frac{\sum_a N_{a,t(f)} F_a}{\sum_a N_{a,t(0)} F_a}, \quad (1-8)$$

where $N_{a(f)}$ is the numbers at age at time t , $N_{a(0)}$ is the numbers at age in the unfished population at time t , and F_a is the age-specific relative fecundity. Relative fecundity was calculated as;

$$F_a = W_a - W_{mat}, \quad (1-9)$$

where W_a is the average weight at age and W_{mat} is the weight at maturity.

Optimal Biomanipulation strategies

We explored optimal biomanipulation strategies for gill net fisheries using an age structured population model that simulated equilibrium population biomass and SPR across a range of exploitation rates, gill net mesh sizes, harvest frequencies (number of years between harvest), and assumptions about the compensatory ability of gizzard shad. The model was similar in structure to the SCA, but instead of estimating annual recruitment anomalies, we assumed that recruitment was deterministic as a function of spawner biomass. This allowed the model to fully simulate a self-regenerating fish population with density-dependent recruitment. Density-dependent recruitment was a function of spawner biomass using the asymptotic Beverton-Holt model, which predicts a declining per-capita recruitment rate as spawner abundance increases. We used the compensation ratio form of the Beverton and Holt model (Walters and Martell 2004) to predict annual recruitment (R_t) as:

$$R_t = \frac{\frac{recK}{\phi_0} E_t}{1 + \left(\frac{recK - 1}{R_0 \phi_0} \right) E_t}, \quad (1-10)$$

where ϕ_0 is the average unfished lifetime egg production per recruit (calculated by summing the product of unfished survivorship and age-specific fecundity), R_0 is the average unfished recruitment (arbitrarily set to zero to scale the population), $recK$ is the Goodyear recruitment compensation ratio (Goodyear 1980) representing the ratio of juvenile fish survival in the unfished population to juvenile survival in a population fished down to very low levels, and E_t is the population egg production in year t . Values of E_t were calculated by summing the product of the numbers at age and the age-specific fecundity in year t , thus accounting for greater individual contributions of old fish to the population fecundity. We allowed half of the catch to be taken before E_t was calculated to account for reduced population fecundity due to pre-spawn harvest of gizzard shad in January and February.

The compensation ratio is an important term because it defines the degree of compensation in the population and thus determines the limits of harvest. Populations with high $recK$ would be expected to maintain similar average recruitment across a wide range of adult population sizes (i.e., large declines), compared to low $recK$, which would suggest that reductions in adult

population sizes cause declines in average recruitment. The compensation ratio was not known for the gizzard shad populations. However, we can infer reasonable estimates from meta-analyses of *recK* from fish stocks having similar life history as the gizzard shad (Myers et al. 1999; Goodwin et al. 2006). These analyses suggest that *recK* for gizzard shad likely ranges between 10 and 25. Therefore, we conducted two population models, one for a population with low compensation (*recK* = 10) and one for relatively high compensation (*recK* = 25).

For each level of *recK*, we simulated four harvest frequencies (harvest every year, every second, third, and fourth years), four different commercial gill net mesh sizes (2.5, 3.0, 3.5, and 4.0 inch stretch mesh), and a range of exploitation rates (0 to 1). Vulnerability parameters for each mesh size were obtained from the Taylor et al. (2005) model described above. We calculated average equilibrium population biomass and SPR for each possible combination of harvest frequency, mesh size, and exploitation rate. The mean was calculated by averaging the last fifty model years after a 150-yr burn-in period to allow the population to reach equilibrium. A recent review of lake restoration studies in Denmark found that reductions in benthivorous fishes of about 80% must be obtained to improve lake water clarity (Sondergaard et al. 2000). We used a target level of 75% reduction in total gizzard shad biomass 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; Sondergaard et al. 2000). Fishing mortality rates that result in SPR less than 0.35 increase the risk for recruitment overfishing (i.e., fishing at a rate that prevents a stock from replacing itself; Clark 2002). We chose 0.35 as a target SPR to indicate which harvest scenarios presented the greatest probability of causing recruitment overfishing for gizzard shad.

RESULTS

Gizzard shad size, age structure and growth

Gizzard shad catch rates during December were extremely low, particularly at Lakes Harris and Eustis. Low December catch rates may have resulted from seasonal changes in movement patterns and shad activity levels. Consequently, this report will present data from only January/February and May. The ratio of the number of gizzard shad >300 mm to shad < 300 mm decreased significantly from 2005 to 2006 and from 2006 to 2007 at Lake Dora (all $P < 0.0055$; Figure 1-2). The length ratio also decreased significantly at Lake Eustis from 2006 to 2007 ($P = 0.0005$), but not from 2005 to 2007 ($P = 0.0073$, $\alpha = 0.0055$) or from 2005 to 2006 ($P = 0.4$). Lake Harris showed no changes in the length ratio through time (all $P > 0.13$). The large change in length ratios at Lake Dora relative to Lakes Eustis and Harris suggest that the size structure of gizzard shad was influenced by fishing at Lake Dora (Figure 1-2). However, these changes could have been influenced by recruitment variation. Changes in the length ratio from January (pre-fishing) to May 2005 (post fishing) were not affected by changes in recruitment but could have been influenced by seasonal shifts in fish vulnerability to the gill nets. These seasonal changes in vulnerability were evident at all three lakes because the length ratio was higher in January than in May 2005 at all lakes (all $P \leq 0.0001$, $\alpha = 0.008$; Figure 1-2). However, the magnitude of the differences between these time periods was substantially greater at Lake Dora than at the other two lakes. These results indicate that commercial fishing reduced the relative abundance of large (> 330 mm) gizzard shad at Lake Dora.

Gizzard shad length frequencies shifted downward at Lake Dora after commercial harvest (Figure 1-3). Modal January/February lengths at Lake Dora shifted from 360 mm in 2005 (before harvest) to 280 mm in 2006 (after harvest), to 260 mm in 2007 (after harvest), likely reflecting the harvest of shad >330 mm. Conversely, modal January/February length distributions at Lakes Eustis and Harris changed less between years than at Lake Dora (Figure 1-3).

Gizzard shad age structure and growth

Examination of age structure indicated variable recruitment across lakes, and a pattern of alternating high and low recruitment years was evident at all lakes but particularly at Lake Eustis (Figure 1-4). Large and small year classes tracked fairly consistently between years. There also appeared to be some among-lake synchrony in patterns of strong and weak year classes. For example, age-2 fish were relatively abundant in 2005 at Lakes Dora and Eustis, and age-3 fish were relatively abundant the next year at all three lakes. This suggests that the lakes may experience similar environmental or possibly density-dependent factors that influence recruitment across years. The Lake Dora age structure was truncated substantially after gizzard shad removal in 2005, and ages 6, 7, and 8 were not collected in post-removal age samples. Age structure at lakes Eustis and Harris was relatively consistent across years.

Gizzard shad growth was similar among lakes and years (Figure 1-5). The best fitting model indicated that asymptotic length (L_{∞}) was 420 mm for all lakes and years with the exception of Lakes Dora and Harris in 2007, which had a value of 431 mm (AIC = -184.5). The higher L_{∞} for Lake Dora in 2007 likely resulted from the loss of older age classes, which left the asymptote poorly defined. The metabolic coefficient (K) was lower at Lake Dora ($K = 0.53 \text{ yr}^{-1}$) than at Lakes Eustis and Harris ($K = 0.64 \text{ yr}^{-1}$) and did not vary temporally within lakes. Time at zero length (t_0) was 0.06 yrs for all lakes and years with the exception of Lake Eustis in 2007 and Lake Harris in 2006 and 2007, which had a value of 0.22 yr.

Mean length at age 1 decreased significantly at Lake Eustis from 191 and 192 mm in 2005 ($P = 0.0008$, $\alpha = 0.0055$) and 2006 ($P = 0.02$) to 170 mm in 2007, but did not differ significantly among years at either Lake Dora or Lake Harris (all $P > 0.008$). Mean length at age 2 decreased significantly from 300 to 278 mm between 2005 and 2007 at Lake Eustis ($P < 0.001$, $\alpha = 0.008$). Mean length at age 2 did not differ significantly among years at Lake Dora.

Marginal increment analysis validated opaque zones on gizzard shad otoliths as annuli. All three lakes exhibited a pattern of reduced marginal increment distance during May-August, indicating that annuli were fully formed by summer (Figure 1-6).

Gizzard shad reproduction

The GSI, used as an indicator of energy allocated to reproduction, was highest for all lakes in either February or March in all years (Figure 1-7). The BACIPS analysis indicated that from 2005 to 2007, GSI values for Lake Dora decreased from -0.3% to -1.9% relative to control lakes, but this difference was not statistically significant (Welch's ANOVA, $P = 0.26$, $\alpha = 0.05$)

Larval density peaked during mid to late April 2005 and 2007 and during mid March 2006 at Lake Dora (Figure 1-8). Lake Dora had higher larval densities than Lakes Eustis and Harris each year. Peak larval density in 2006 was about half of 2005 and 2007 densities. Predictive BACIPS analysis indicated that larval gizzard shad densities at Lake Dora were marginally lower (zero was excluded from the 95% confidence interval for effect size) relative to Lakes Eustis/Harris in 2007 than in 2005 (Figure 1-9). The average effect size between 2005 and 2007 was -0.82 fish/m^2 , suggesting that Lake Dora larval gizzard shad densities declined by 0.82 fish/m^3 relative to the other lakes. Average effect sizes for the 2005 vs. 2006, and 2006 vs. 2007 comparisons were -0.23 fish/m^3 and 0.41 fish/m^3 , respectively, but neither was statistically significant. These results suggest that larval density marginally declined after fishing at Lake Dora relative to the other lakes. However, confidence intervals for effect size for all three comparisons were large and sample sizes were low, suggesting that results should be interpreted with caution.

We detected changes in length and age-at-maturity at Lakes Dora and Eustis from 2005 to 2007. Gizzard shad matured at a smaller size after fishing (2007) compared to before fishing (2005) at Lake Dora. The best fitting model indicated that length-at-maturity (L_{50}) decreased significantly from 272 to 237 mm between 2005 and 2007 at Lake Dora but not at Lake Eustis (AIC = 517.7; Figure 1-10). In comparison to Lake Dora, gizzard shad at Lake Eustis matured at a significantly larger size (305 mm) in both years. The rate of increase in probability of maturation with length (steepness parameter) decreased significantly from 0.05 in 2005 to 0.035 in 2007 and did not differ between lakes. Gizzard shad matured at an older age at Lake Eustis in 2007 than in 2005. The best fitting model for age-at-maturity indicated that age-at-maturity (A_{50}) increased significantly from 1.9 to 2.5 yrs at Lake Eustis but did not differ between years at Lake Dora

($A50 = 1.9$ yrs; $AIC = 367.8$; Figure 1-11). The steepness parameter for age-at-maturity did not differ between lakes or years ($s = 2.8$).

Catch rate of age-1 fish in January/February was used as an index of gizzard shad recruitment. There was a significant lake*year interaction ($P < 0.001$), which was due to a significant increase in recruitment at Lake Dora from 2005 to 2006 and 2006 to 2007 (all $P < 0.0004$, $\alpha = 0.0055$). There was no significant interannual change in age-1 CPE at Lakes Eustis or Harris (all $P > 0.01$). Thus, our catch rate indices suggested that gizzard shad recruitment to age-1 was higher at Lake Dora than the other lakes in all years, and the catch rates at Lake Dora increased significantly each year of the study.

The survival index, or ratio of age-1 CPE in year t to average larval density in year $t-1$, increased from 2.1 in 2006 to 16.9 in 2007 at Lake Dora (7.8-fold increase), from 0.5 to 6.1 at Lake Eustis (11.9-fold increase), and from 0.2 to 3.3 at Lake Harris (13.8-fold increase). Thus, we did not detect increases in the index at Lake Dora relative to the other lakes. Consistent across-lake increases from 2006 to 2007 indicated that survival from the larval stage to age 1 was greater for the 2006 cohort, which had low larval abundance, than for the abundant 2005 cohort for all lakes. These results infer that even though recruitment (CPE of age-1 fish) increased each year at Lake Dora, the increase relative to larval densities was not significantly different than that expected based on data from the two unfished lakes. Nevertheless, the gizzard shad population at Lake Dora appeared to compensate for harvest with higher recruitment, because recruitment increased each year at this lake despite large reductions in population fecundity.

Strength of Biomanipulation

The total harvest of gizzard shad from Lake Dora was estimated at 124,989 kg in 2005 and 135,095 kg in 2006. These values equate to harvest levels of 54 and 58 kg/ha from Lake Dora. Catch per effort (CPE) of commercial fishers declined with increasing cumulative catch in both years and catch rates were higher in 2005 than in 2006 (Figure 1-13). The Leslie depletion analysis estimated an exploitation rate of 0.61 (95% confidence interval = 0.42 to 0.73) in 2005 and 0.46 (95% confidence interval = 0.30 to 0.63) in 2006. The larger catch, but lower

exploitation rate in 2006 can be explained by an increase in the vulnerable biomass due to the use of smaller mesh sizes in that year, and the presence of a strong cohort of age-3 fish that entered the fishery in 2006 (Figure 1-4, top center panel).

The Taylor model estimated an instantaneous natural mortality rate (M) of 0.51 yr^{-1} , metabolic parameter K of 0.52 yr^{-2} , and an L_{∞} of 435 mm. An important finding from the Taylor model was a dome-shaped vulnerability schedule for both the commercial fishery and the experimental gill nets (Figure 1-14). Lengths at maximum vulnerability increased from 210 mm (age 1.75) for 2.5-in mesh nets to 375 mm (age 3.5) for 4.0-in mesh nets. The experimental gill nets had the largest length at maximum vulnerability (395 mm; age 4.2) but also captured small gizzard shad better than the commercial gill nets. The SCA model used these rates of mortality, growth, and vulnerability as input parameters and estimated an exploitation rate of 0.51 in 2005 and 0.61 in 2006. However, likelihood profile confidence intervals were very large and values close to zero and 1 were nearly as likely as the point estimates. This high uncertainty resulted from having only three years of age structure data from which to estimate the parameters. Annual recruitment estimates also had large confidence intervals. Estimates of recruitment for 2005 and 2006 were unrealistically large (20 to 40-fold greater than the median), further suggesting that more years of age structure data are needed to refine the exploitation and recruitment estimates. Nevertheless, the point estimates for exploitation rate from this model were close to those estimated from the depletion analysis, suggesting two similar estimates of u based on independent analyses.

The total population biomass at Lake Dora likely decreased by a maximum of about 40% and SPR decreased to 0.44 (Figure 1-15) following two years of removals, assuming constant recruitment. However, both metrics increased in late 2006 and 2007 due to recruitment and growth. The average biomass for the entire post-manipulation period was about 72% of the unfished value and the average SPR was 0.57, indicating that harvest levels at Lake Dora were well short of the target level of a 75% reduction in total biomass.

Optimal Biomanipulation strategies

The low compensation model indicated that gizzard shad removals were unlikely to reach a target biomass reduction of 75% unless fish were harvested every year (Figure 1-16). Gill net mesh sizes of 3.5 and 4.0 inch will likely not achieve target total biomass reductions unless exploitation rate exceeds 0.8, due to the vulnerability patterns of the 4-inch mesh nets. The 3.0-in mesh was the most effective and achieved the desired reduction at an exploitation rate of 0.65 (Figure 1-16). The 2.5-in mesh performance was intermediate between the 3.0 and 3.5-in mesh. The high compensation model indicated that only 2.5 and 3.0-in meshes fished every year at an exploitation rate of at least 0.75 could achieve a 75% biomass reduction (Figure 1-17). In summary, our models predicted that only a few gill net fishery scenarios would cause 75% biomass reduction in total gizzard shad biomass, and each of these require 1) fishing every year, 2) fishing with substantial fishing effort ($u > 0.65$ to 0.8), and 3) fishing with a smaller mesh size than is currently used (i.e., < 4 in).

For SPR, the low compensation model indicated that gizzard shad removals could reduce the SPR to below 0.35 with a two year harvest interval (all meshes) if exploitation rate exceeded 0.75 (Figure 1-18). A lower exploitation rate of 0.45 would be required if fishing took place each year. Harvesting every third and fourth year would not substantially reduce SPR values. Similar to the biomass simulations, the 3.0-in mesh performed best at reducing SPR. Results were similar for the high compensation model, but overall SPR values were slightly higher at a given mesh size and exploitation rate (Figure 1-19). Because the gill net fishery targets mainly large mature gizzard shad, SPR values can be reduced much more than population biomass as a result of the gill net fishery. Use of 3.0-in mesh at an exploitation rate greater than 0.5 could affect gizzard shad recruitment by substantially reducing the population fecundity (Figures 1-18, 1-19).

There are a few other things worth noting about these simulations. First, our modeling represented equilibrium conditions rather than a dynamic population with variable recruitment, and the simulations should be interpreted as the long-term average response to the fishing scenarios. Second, model predictions should be interpreted with caution with more emphasis on

the relative performance of different harvest scenarios rather than on the particular biomass or SPR value achieved. Third, it is clear that fishing every year will likely be required because the gizzard shad populations would be expected to rebound rapidly if not reduced annually. Finally, reducing the mesh size from 4.0 to 3.0 inch resulted in substantial decreases in biomass and SPR across all scenarios. Conversely, moving to an even smaller mesh size of 2.5 inch resulted in a slight increase in the equilibrium biomass and SPR, except at an exploitation rate near 1.0 (Figures 1-18, 1-19). Thus, the optimal mesh size for biomanipulation was 3.0 inch.

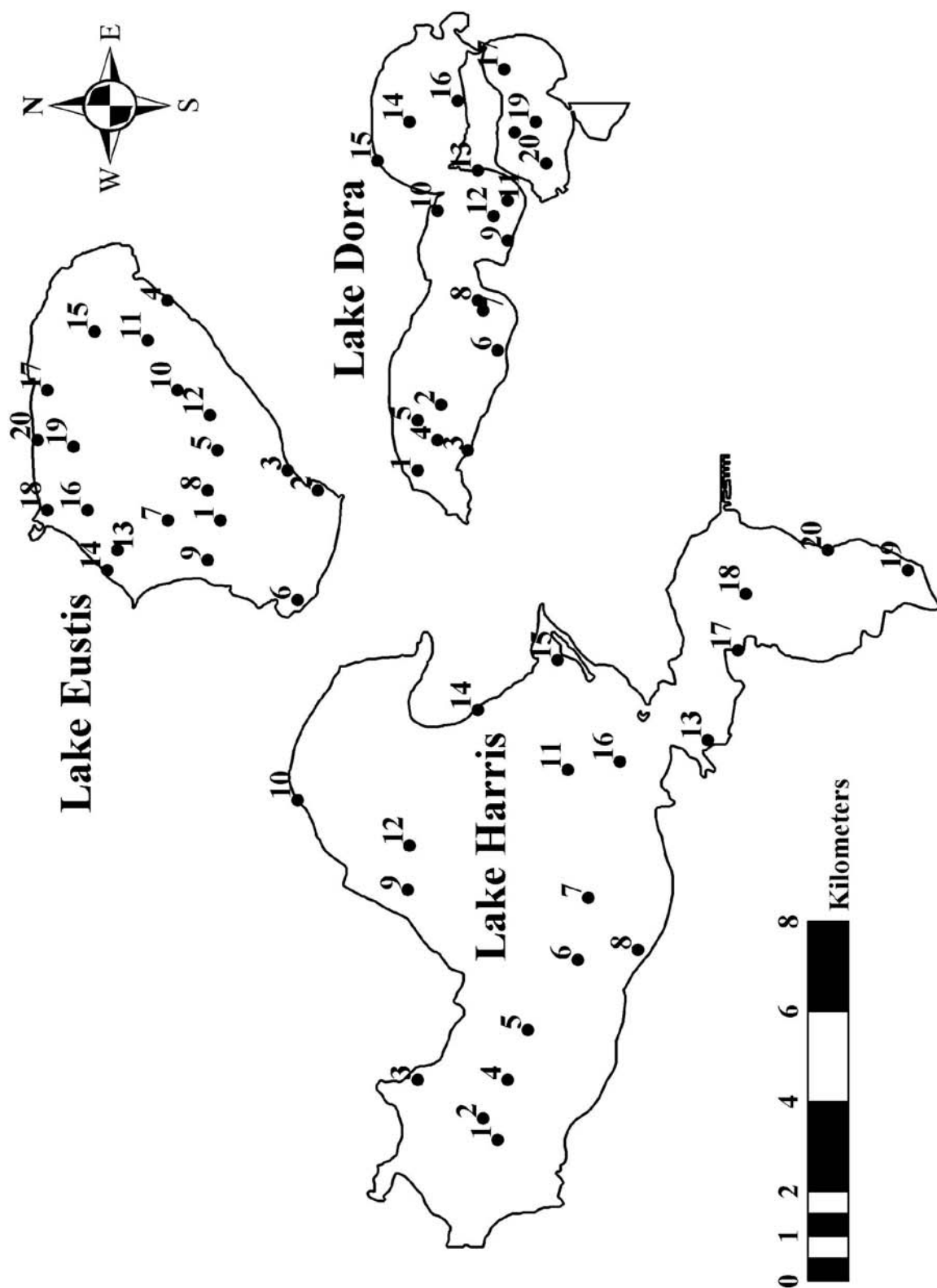


Figure 1-1. Gill net sample sites at Lakes Dora, Eustis, and Harris. Sites are numbered from one to 20 at each lake. Sites were randomly selected from a systematic grid of latitude and longitude coordinates. Site-specific lat/long coordinates and sampling activities are shown in Appendix A.

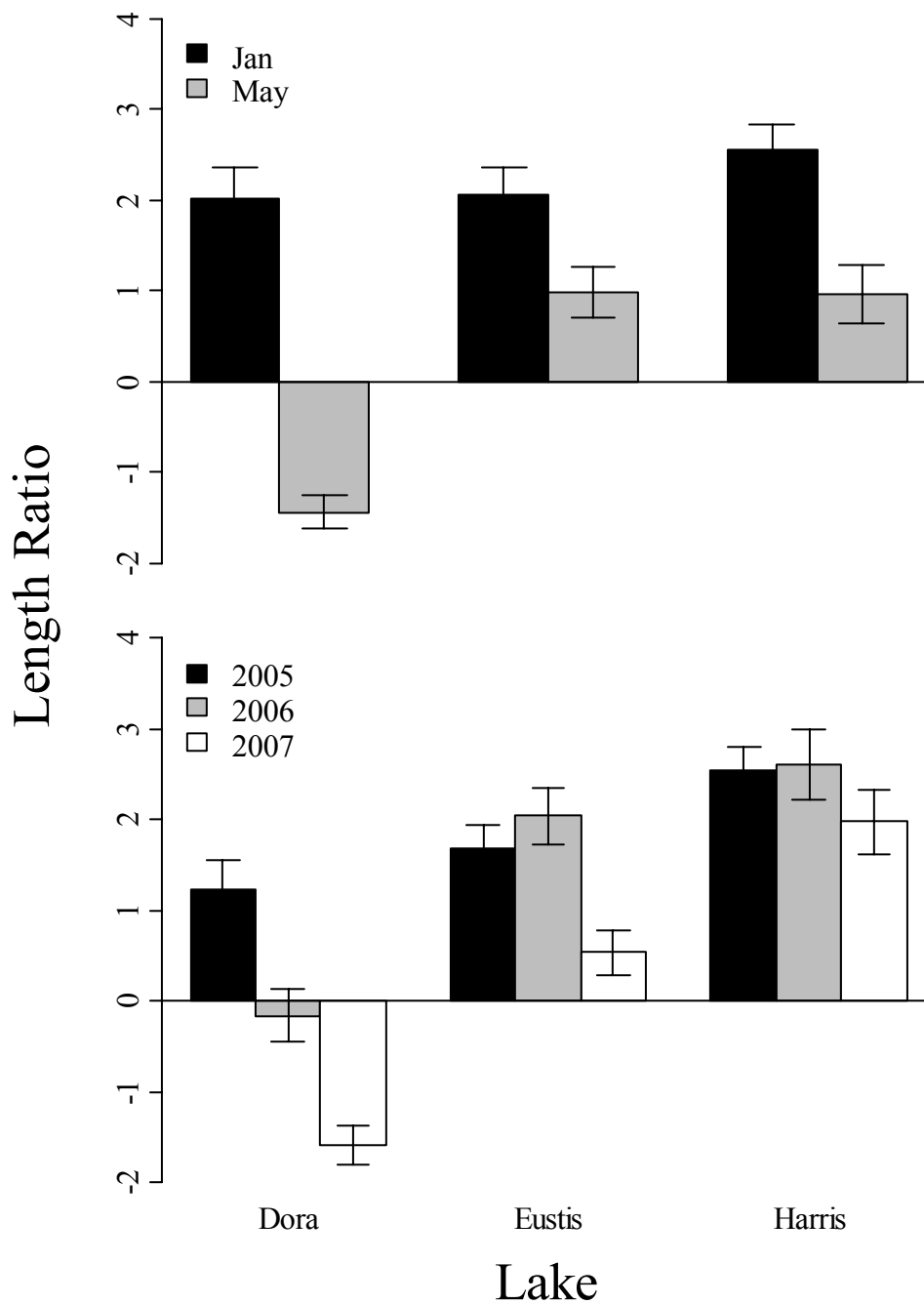


Figure 1-2. Mean length ratio (fish > 330 mm:fish < 330 mm) for January/February (before gizzard shad removal) vs. May (after gizzard shad removal) for 2005 (upper panel). The bottom panel represents the length ratio for January/February samples across all years at Lakes Dora, Eustis, and Harris. Ratios were calculated from 20 gill nets set during each month at each lake. Error bars represent one standard error.

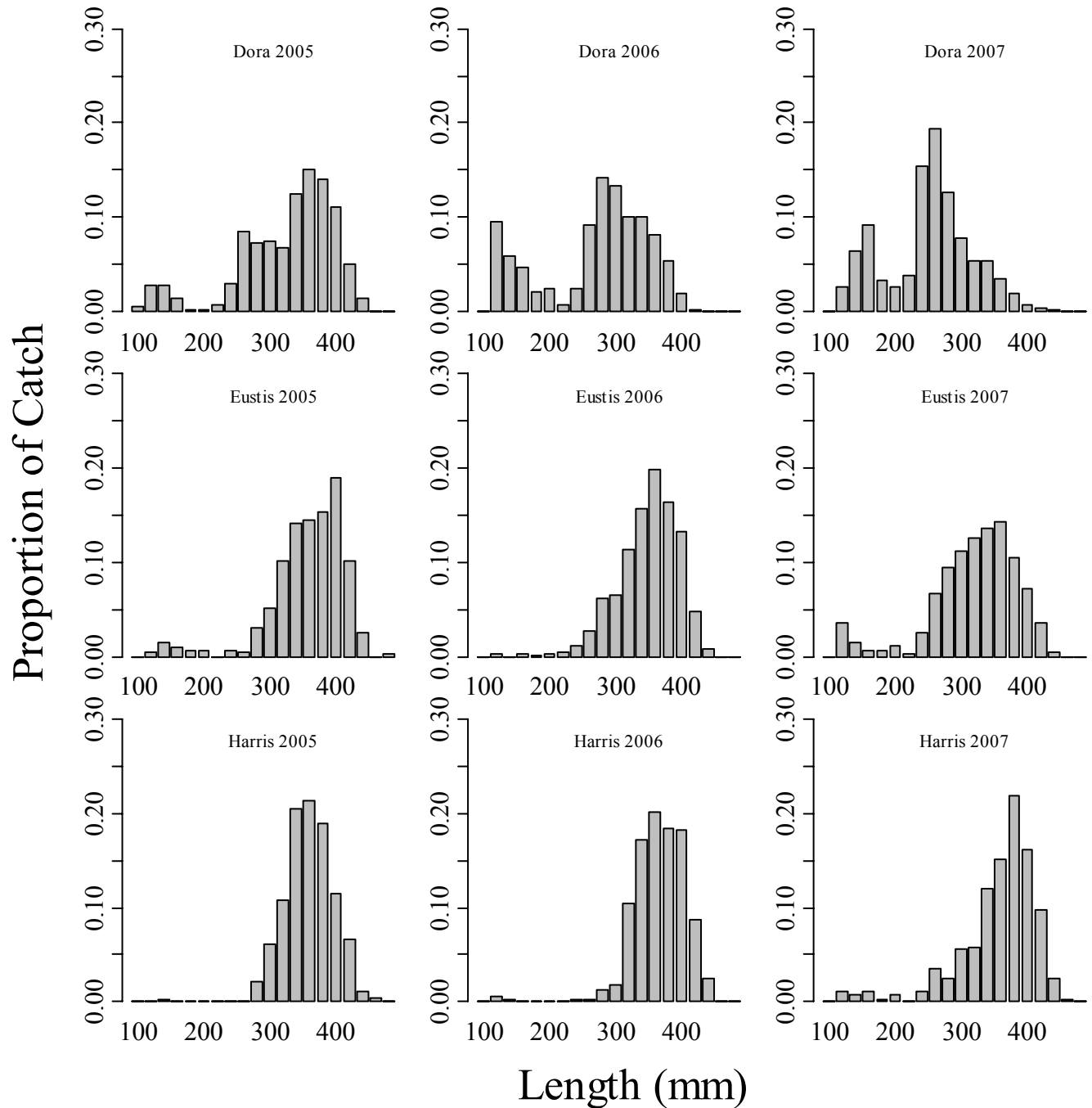


Figure 1-3. Relative length frequency histograms for gizzard shad at Lakes Dora, Eustis, and Harris. Data were collected using 20 gill net sets at fixed sites at each lake 2005 to 2007. Samples were from January/February collections for each lake/year.

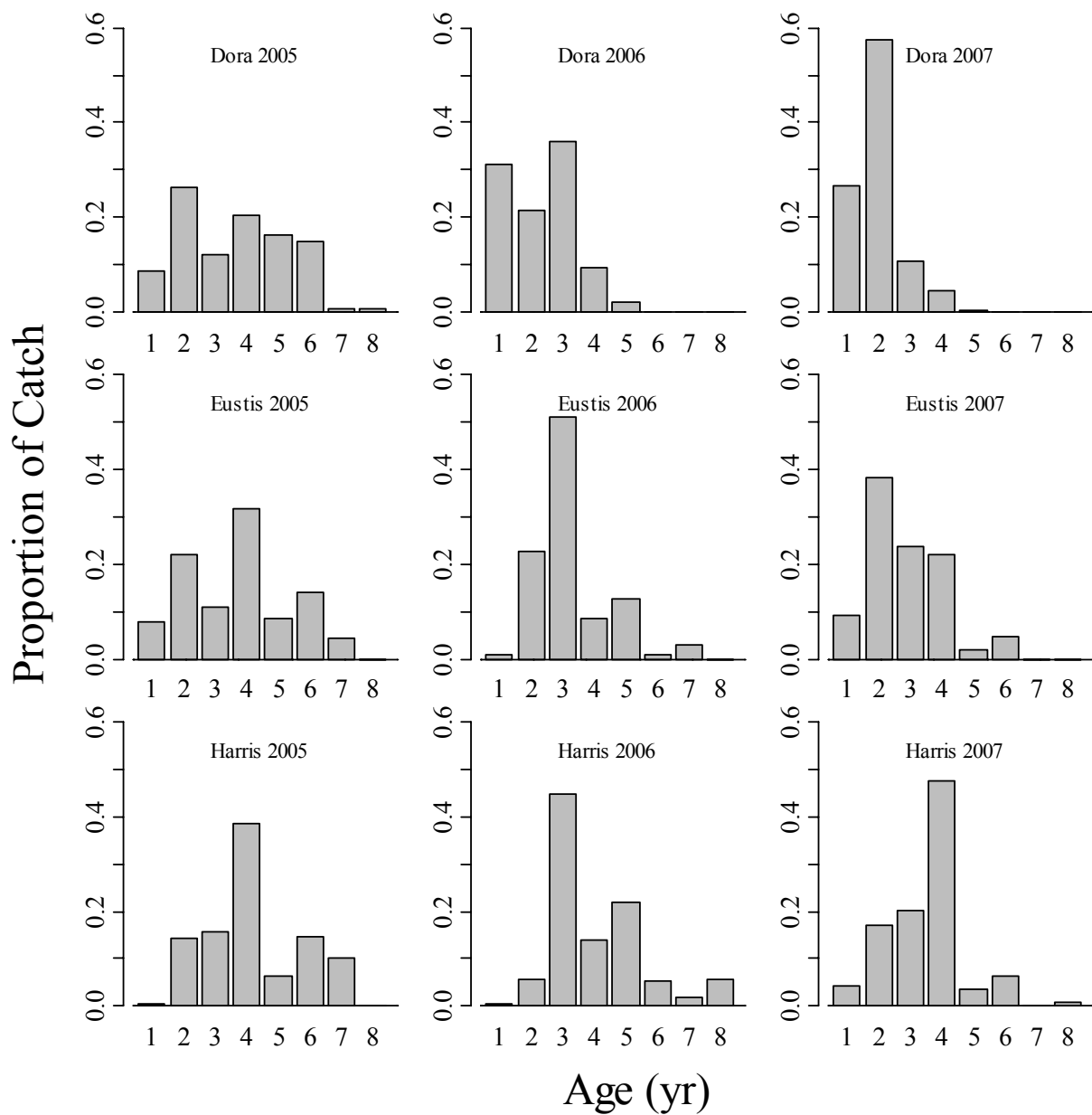


Figure 1-4. Gizzard shad age structure (proportion of fish in each age class) for Lakes Dora, Eustis, and Harris. Data were collected in January and February using 20 gill nets at fixed sites from 2005 to 2007.

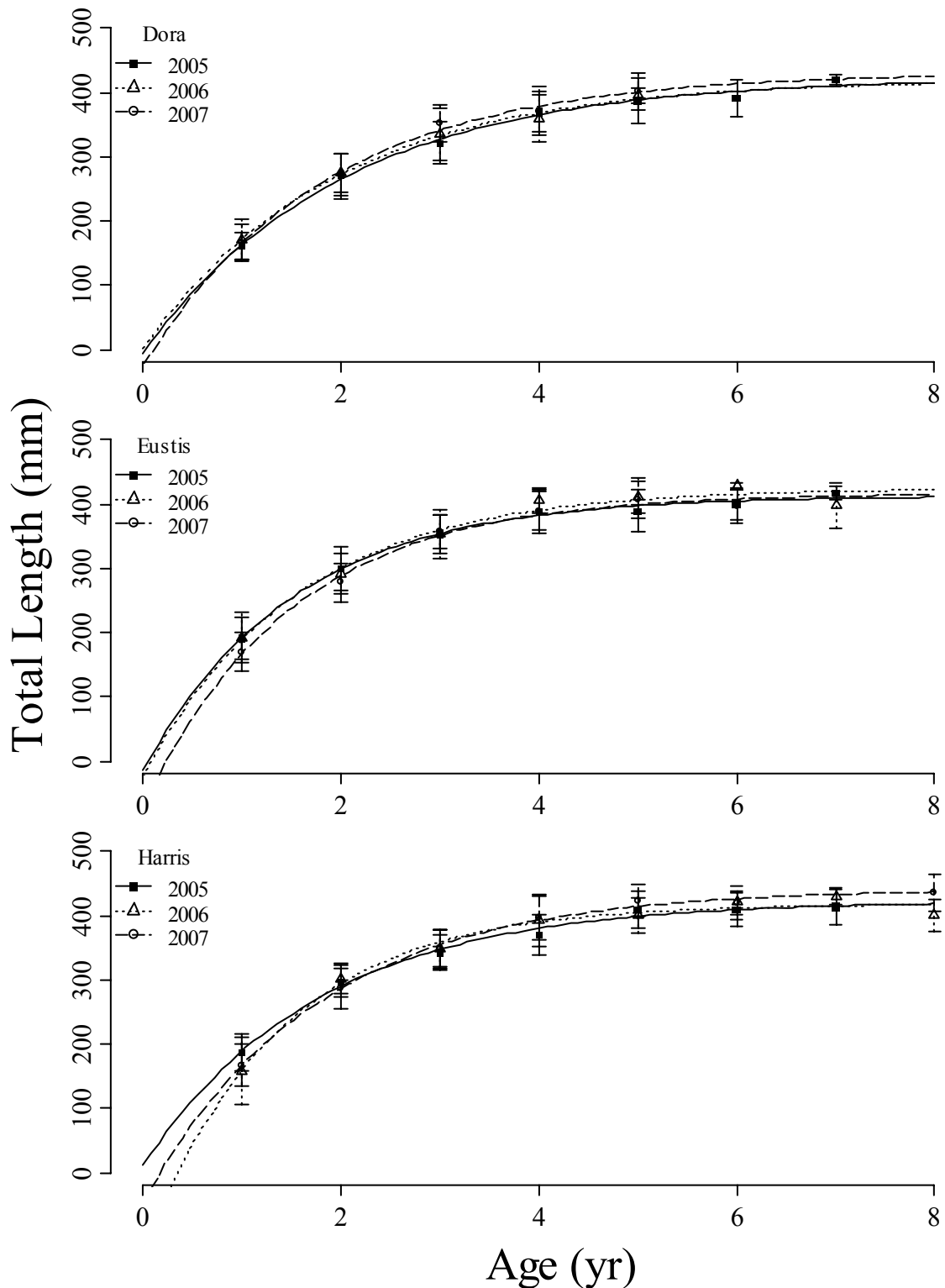


Figure 1-5. Gizzard shad length-at-age data for Lakes Dora, Eustis, and Harris from 2005 to 2007. Curves represent best-fit von Bertalanffy growth models for each lake/year using maximum likelihood estimation assuming a log-normal error structure. Error bars represent one standard error.

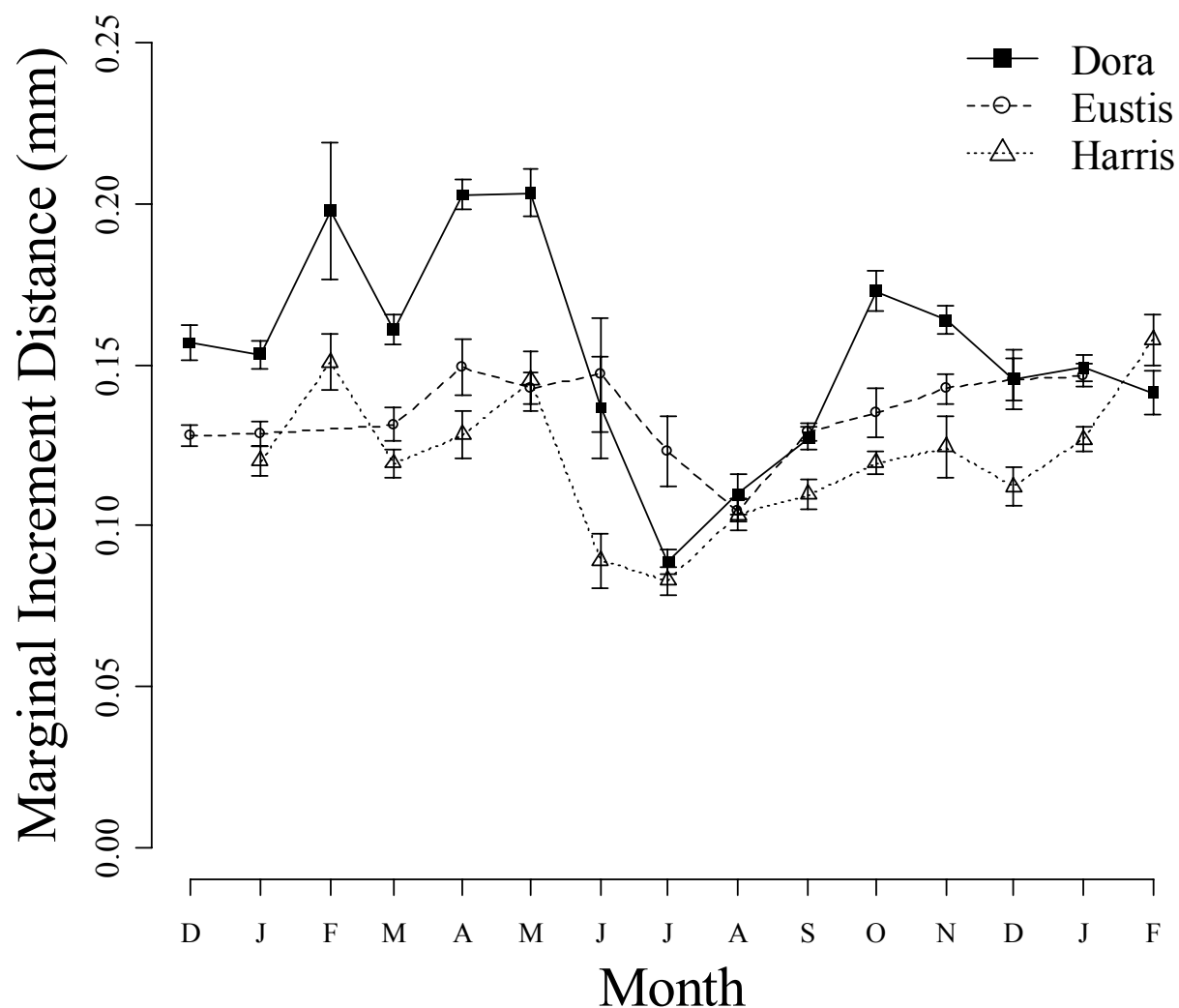


Figure 1-6. Mean monthly marginal increment distance for gizzard shad collected at Lakes Dora, Eustis, and Harris from December 2004 to February 2006. Marginal increment distance was measured as the width of the hyaline zone beyond the outer edge of the last opaque band on the otoliths. The timing of annulus formation is evident from the decrease in the mean increment from June to August. Error bars represent one standard error.

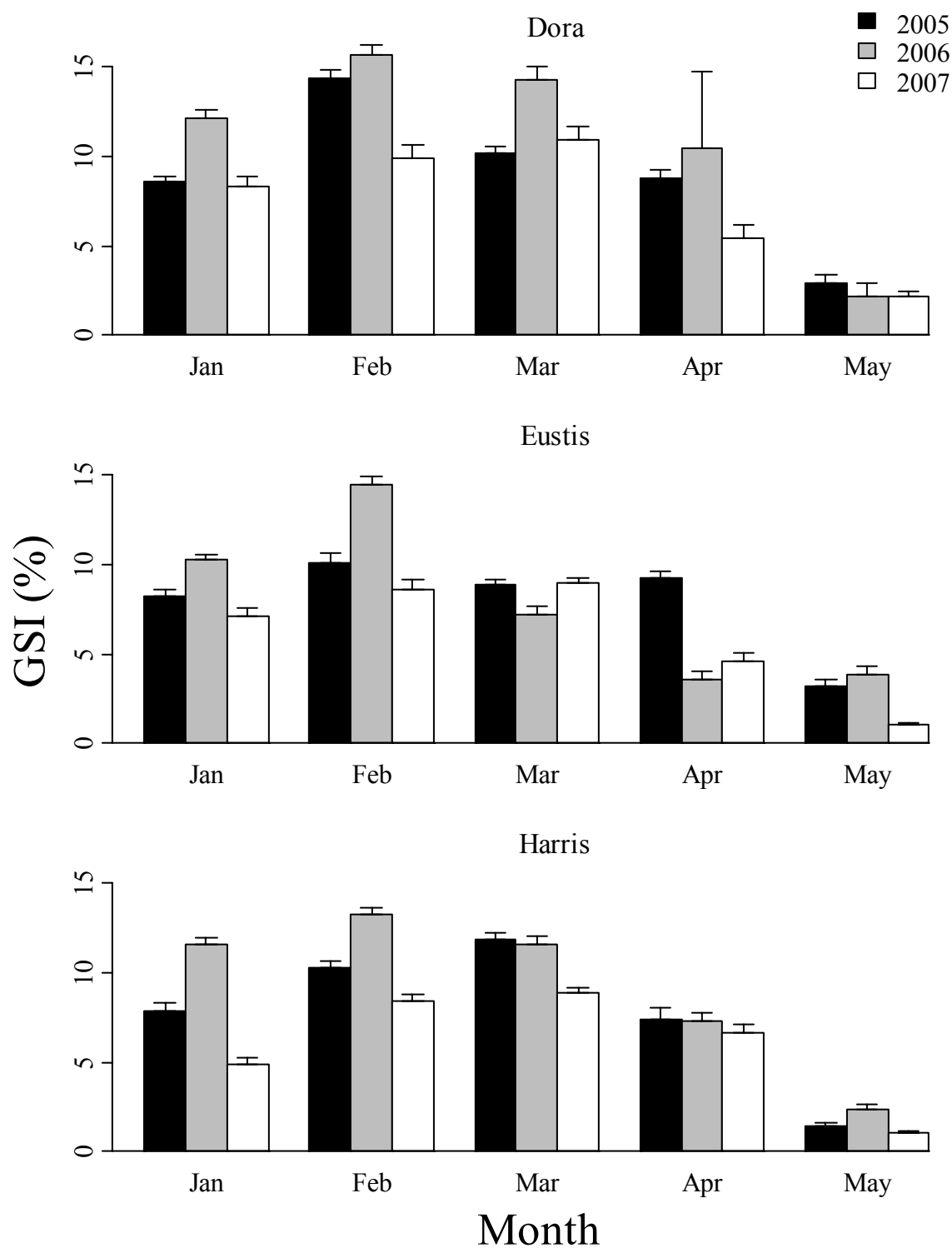


Figure 1-7. Mean gonadosomatic index (GSI) values for females from each lake from January-May in 2005-2007. GSI was calculated as the ovary weight divided by the ovary-free whole fish weight. Error bars represent one standard error.

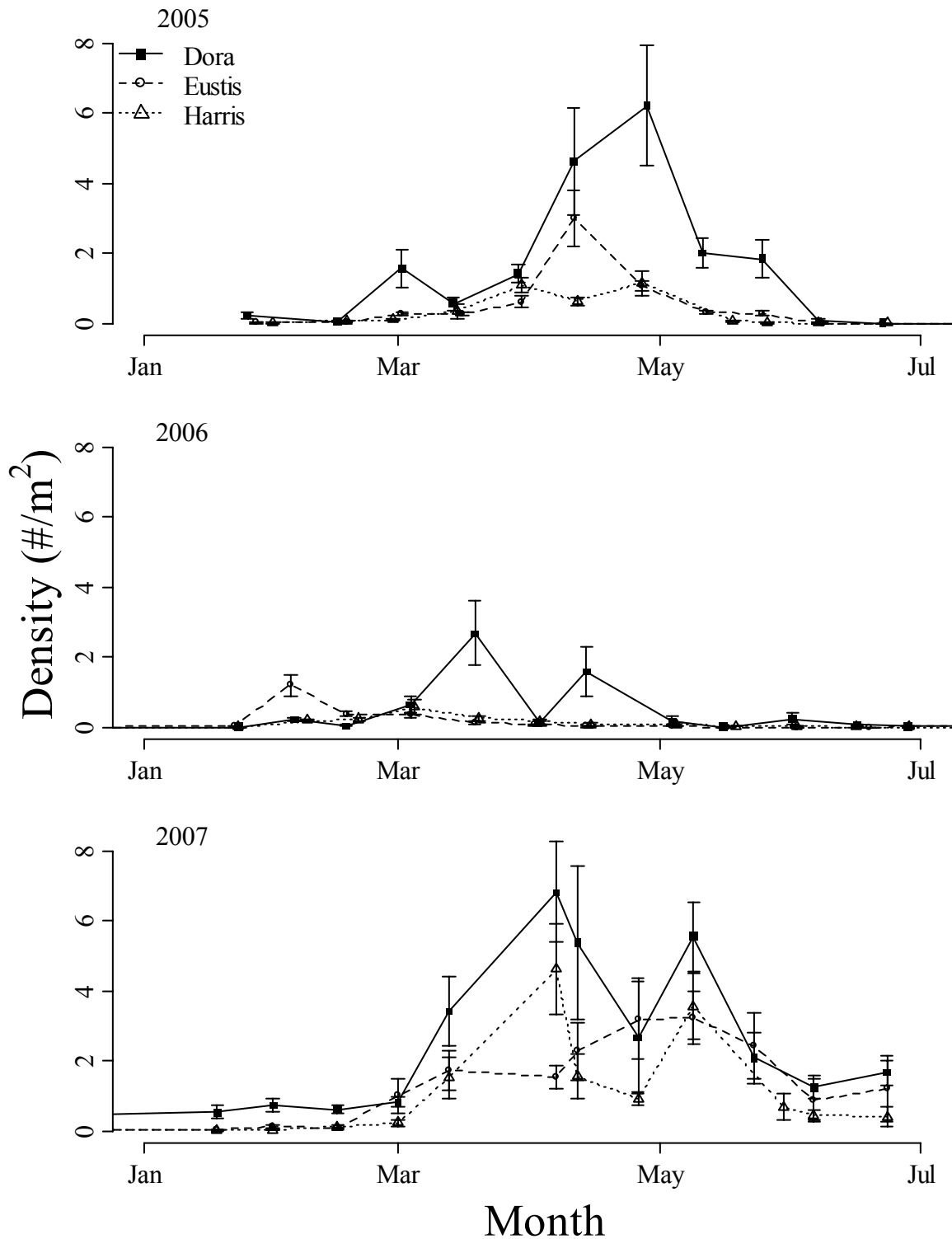


Figure 1-8. Larval gizzard shad abundance for Lakes Dora, Eustis, and Harris from January-June 2005, 2006, and 2007. Larval density was estimated from semi-monthly ichthyoplankton tows at 10 fixed sites for each lake. Error bars represent one standard error.

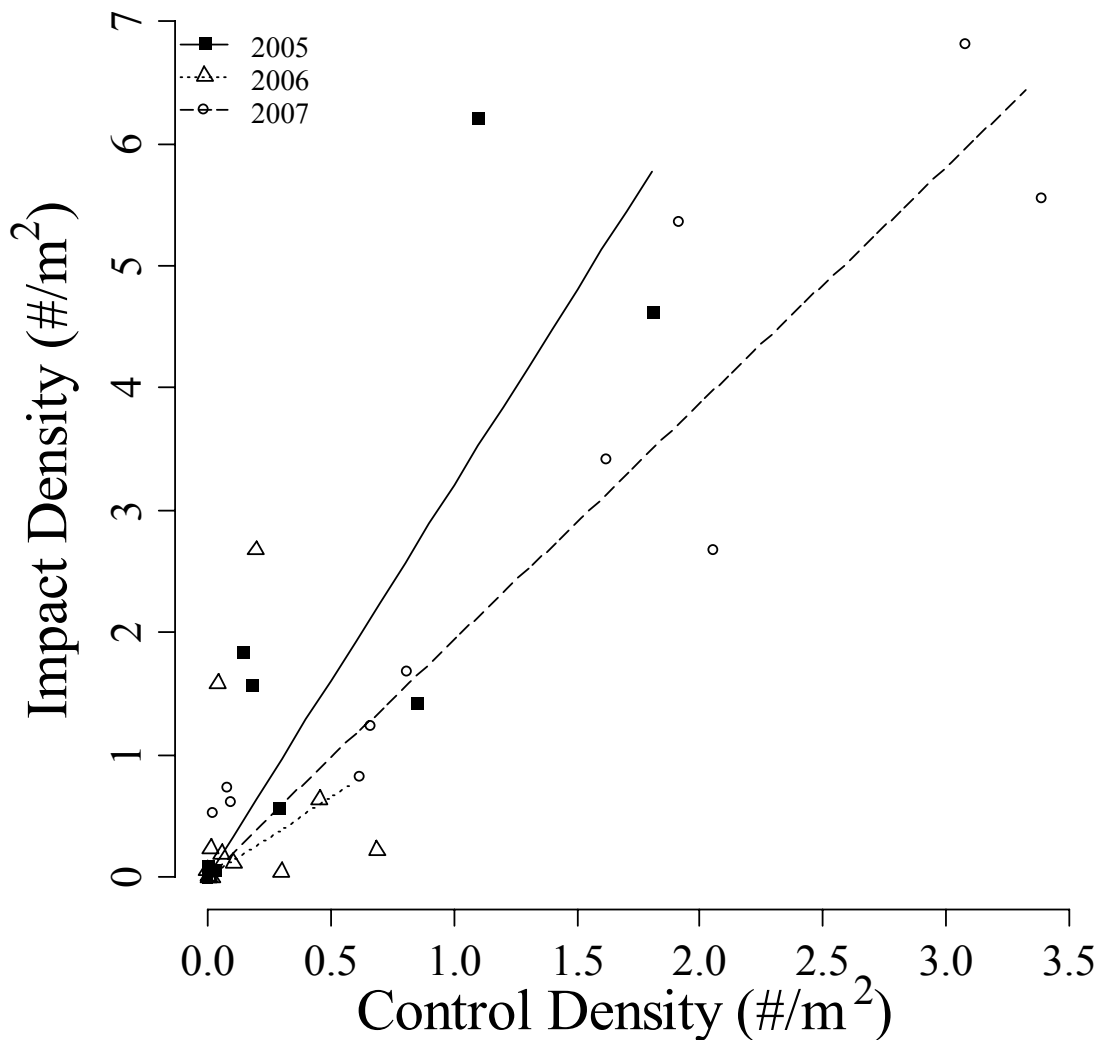


Figure 1-9. Scatterplot of larval gizzard shad density at Lake Dora (impact density; y-axis) vs. the average Lake Eustis/Harris density (control density; x-axis) during 2005, 2006, and 2007. Lines represent zero-intercept regression models for each year. The effect size (i.e., change in the between-lake difference between time periods) was calculated for each value of the control as the difference between model-predicted impact values.

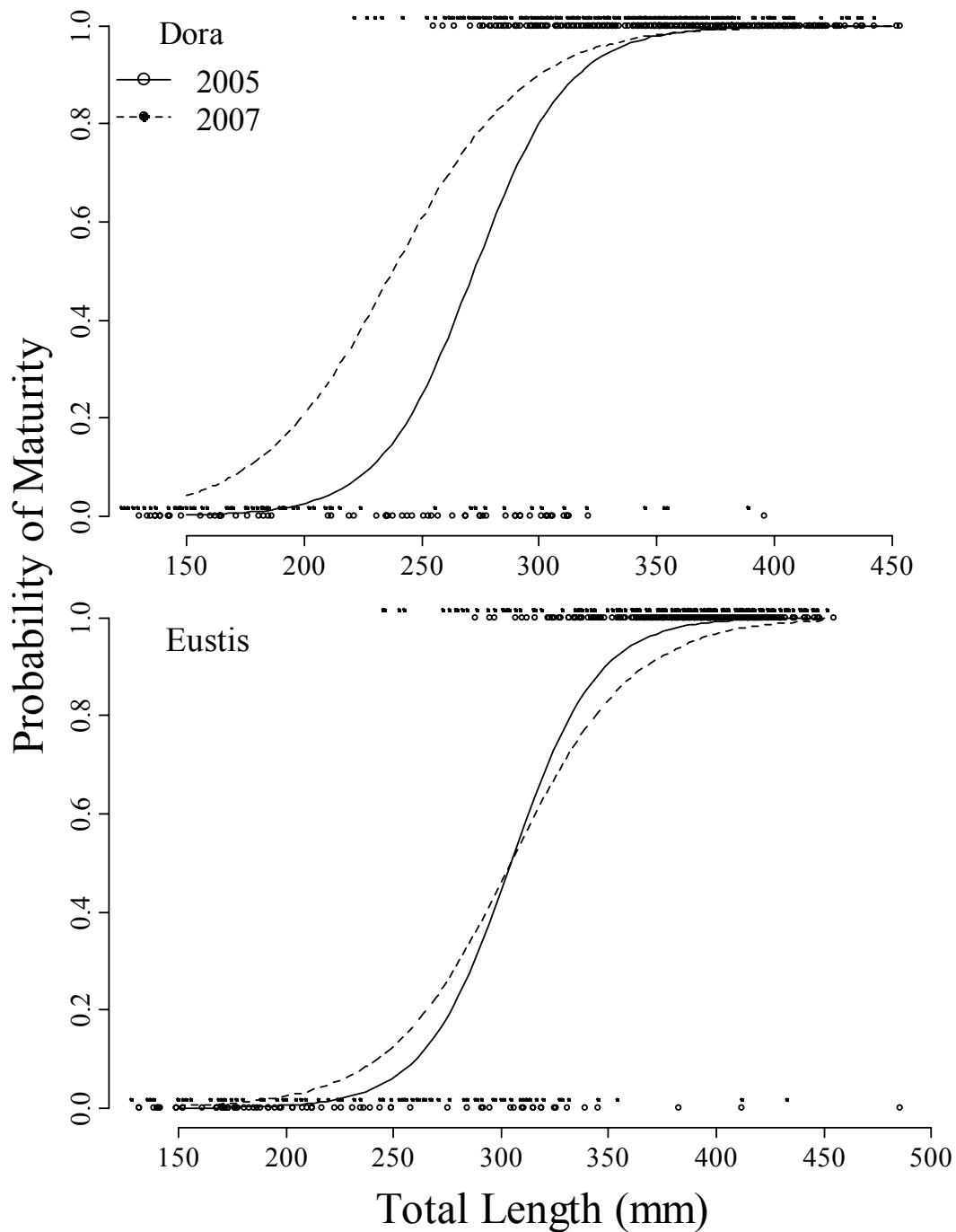


Figure 1-10. Length at maturity in 2005 and 2007 at Lake Dora (upper) and Lake Eustis (lower). Lines indicate the best-fitting logistic model based on AIC. Maturity was estimated from a maturity classification based on GSI values and histological ovary cross sections from females collected in 2007.

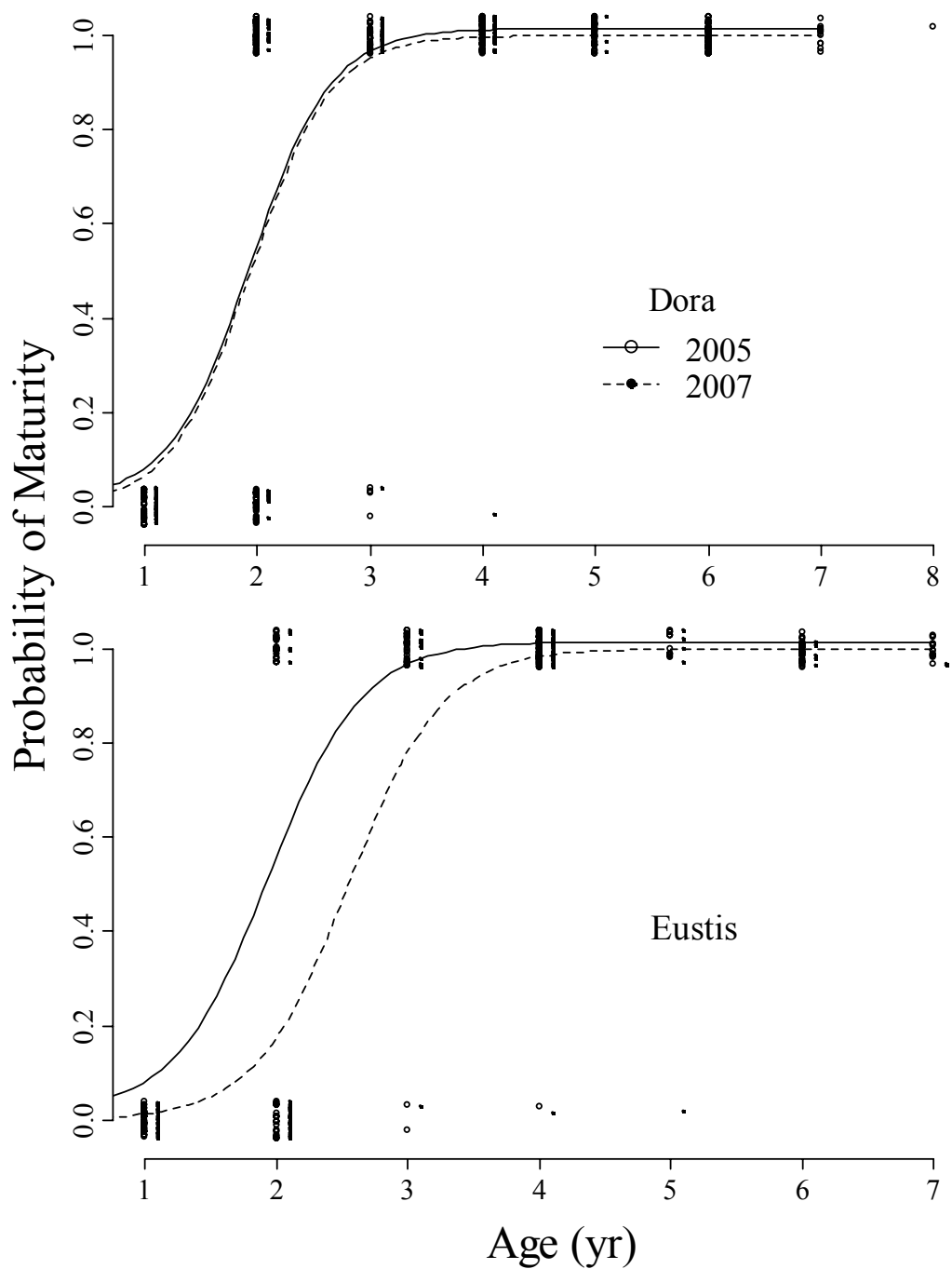


Figure 1-11. Age at maturity in 2005 and 2007 at Lake Dora (upper) and Lake Eustis (lower). Lines indicate the best-fitting logistic model based on AIC. Maturity was determined from a maturity classification based on GSI values and histological ovary cross sections from females collected in 2007.

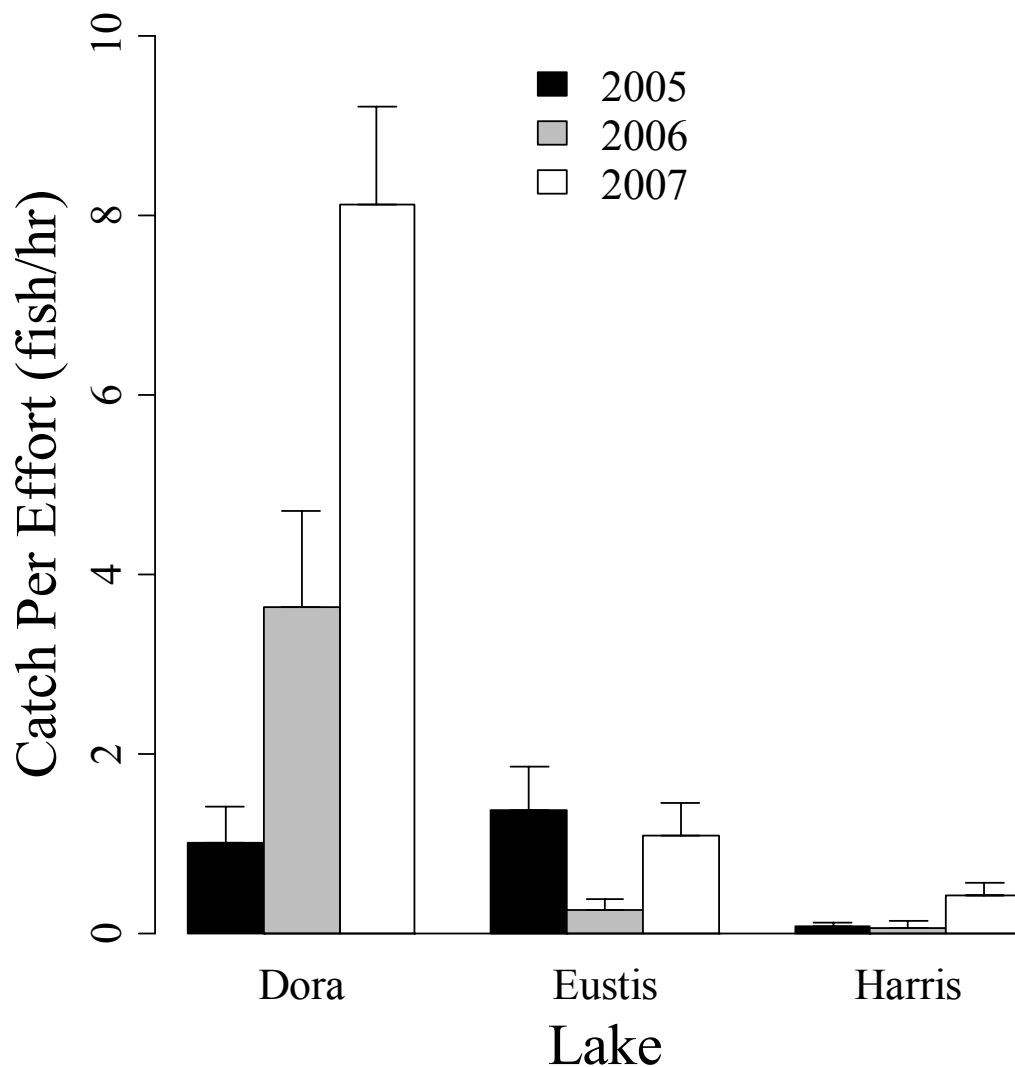


Figure 1-12. Catch per effort (CPE) of age-1 gizzard shad during January/February at each lake as an index of recruitment for the 2004, 2005, and 2006 cohorts when they were sampled in 2005, 2006, and 2007, respectively. Error bars represent one standard error.

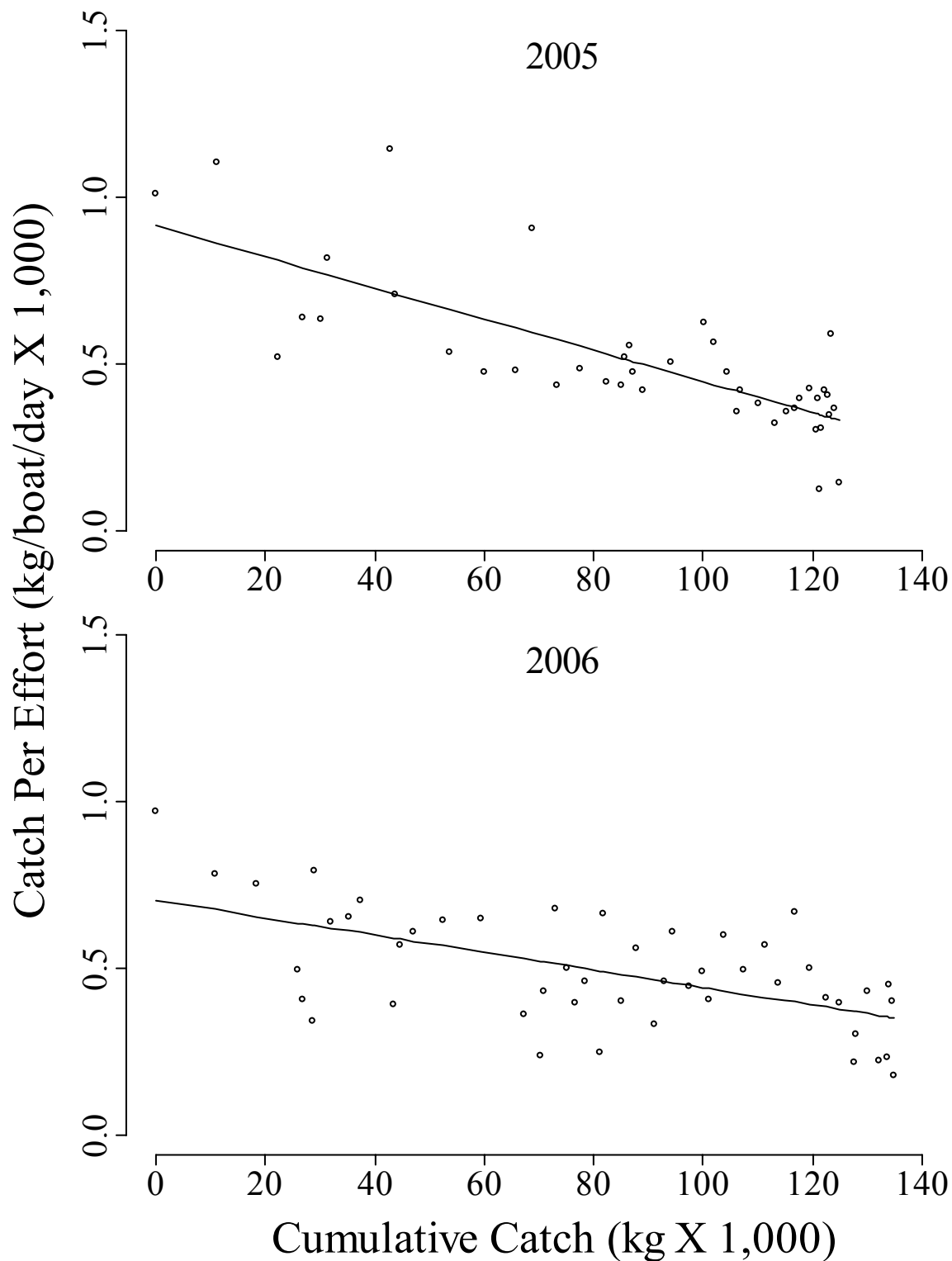


Figure 1-13. Catch per effort (kg/day) vs. cumulative catch (kg) of gizzard shad from commercial vessels in 2005 (upper) and 2006 (lower). Lines indicate linear regression models used in Leslie depletion analysis to estimate the annual exploitation rate on vulnerable-sized gizzard shad.

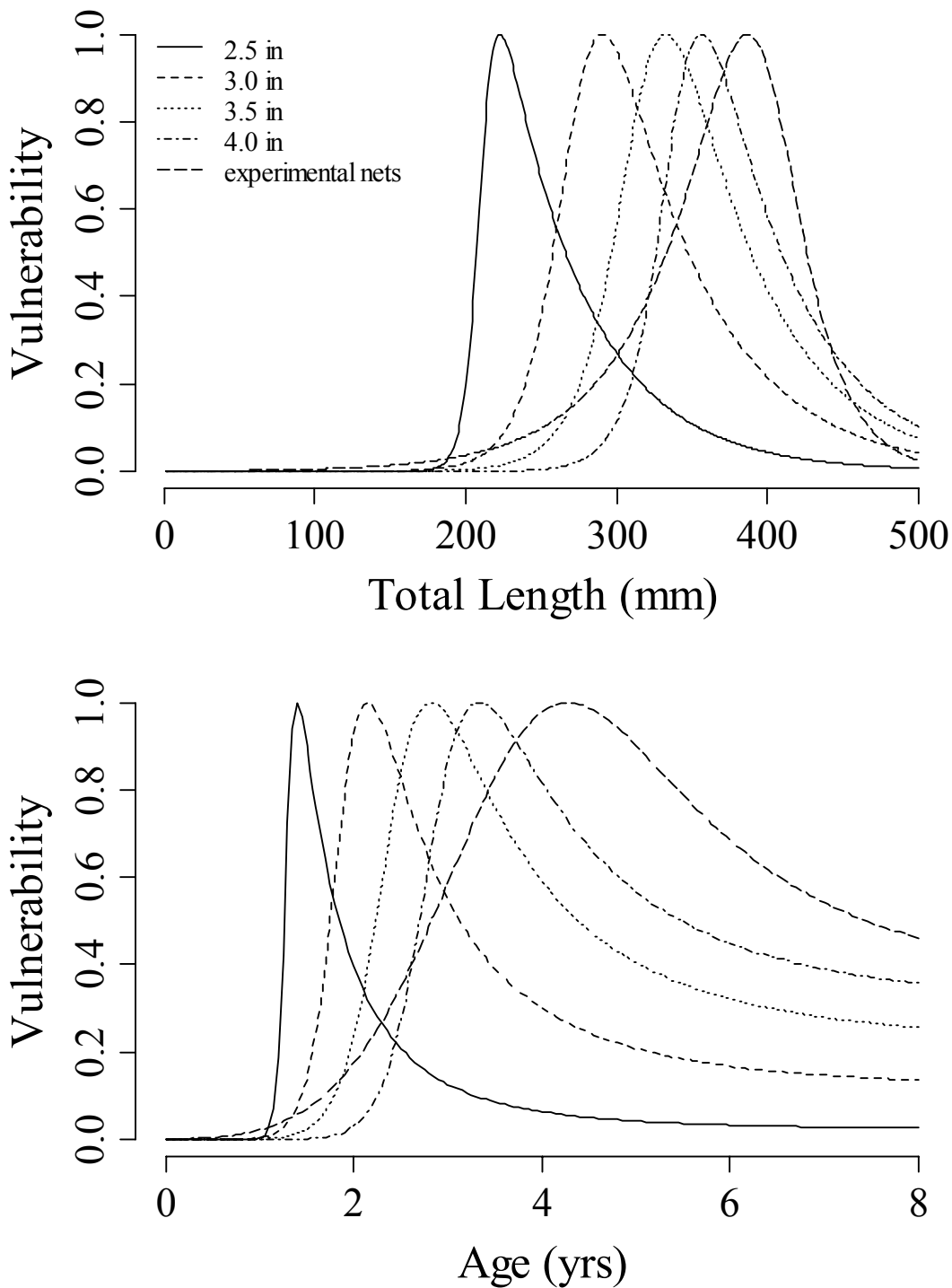


Figure 1-14. Vulnerability schedules with respect to total length (upper) and age (lower) for each of the four commercial gill net mesh sizes and the experimental gill nets. Vulnerabilities were estimated simultaneously along with natural mortality and growth parameters from unfished length-age data using an age and length structured model by Taylor et al. (2005; model 1).

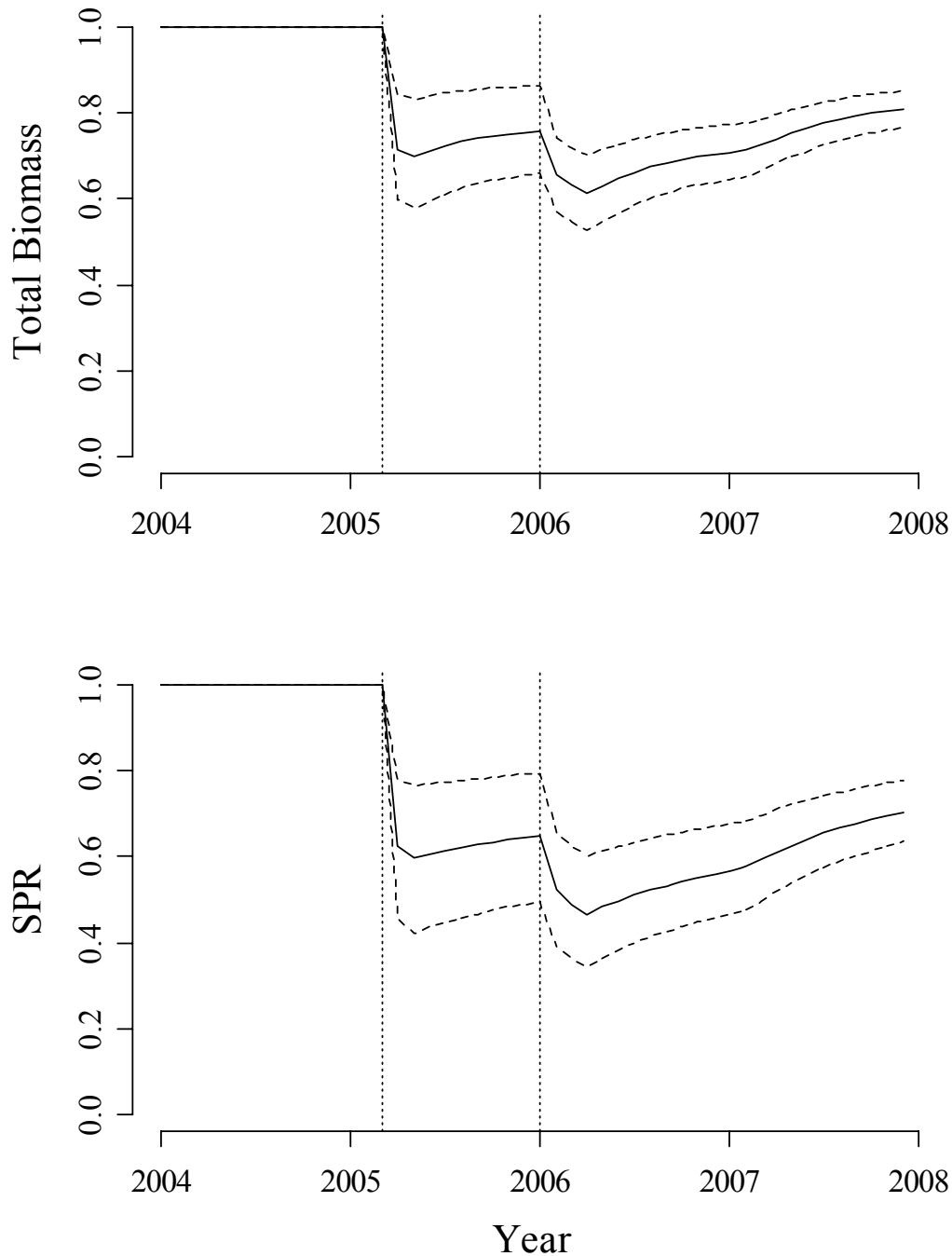


Figure 1-15. Total gizzard shad population biomass (upper) and weighted transitional spawning potential ratio (SPR; lower) from 2004 to 2008 at Lake Dora as a proportion of the unfished condition assuming stable recruitment. The solid line indicates the average biomass from 1,000 parametric bootstrap iterations of an age-structured population model that operated on monthly time steps. Each bootstrap iteration generated random exploitation rates drawn from a normal distribution with mean and variance estimated from Leslie depletion. Dashed lines represent 95% bootstrap confidence intervals. Vertical dashed lines show the timing of gizzard shad removals.

Low Compensation (CR = 10)

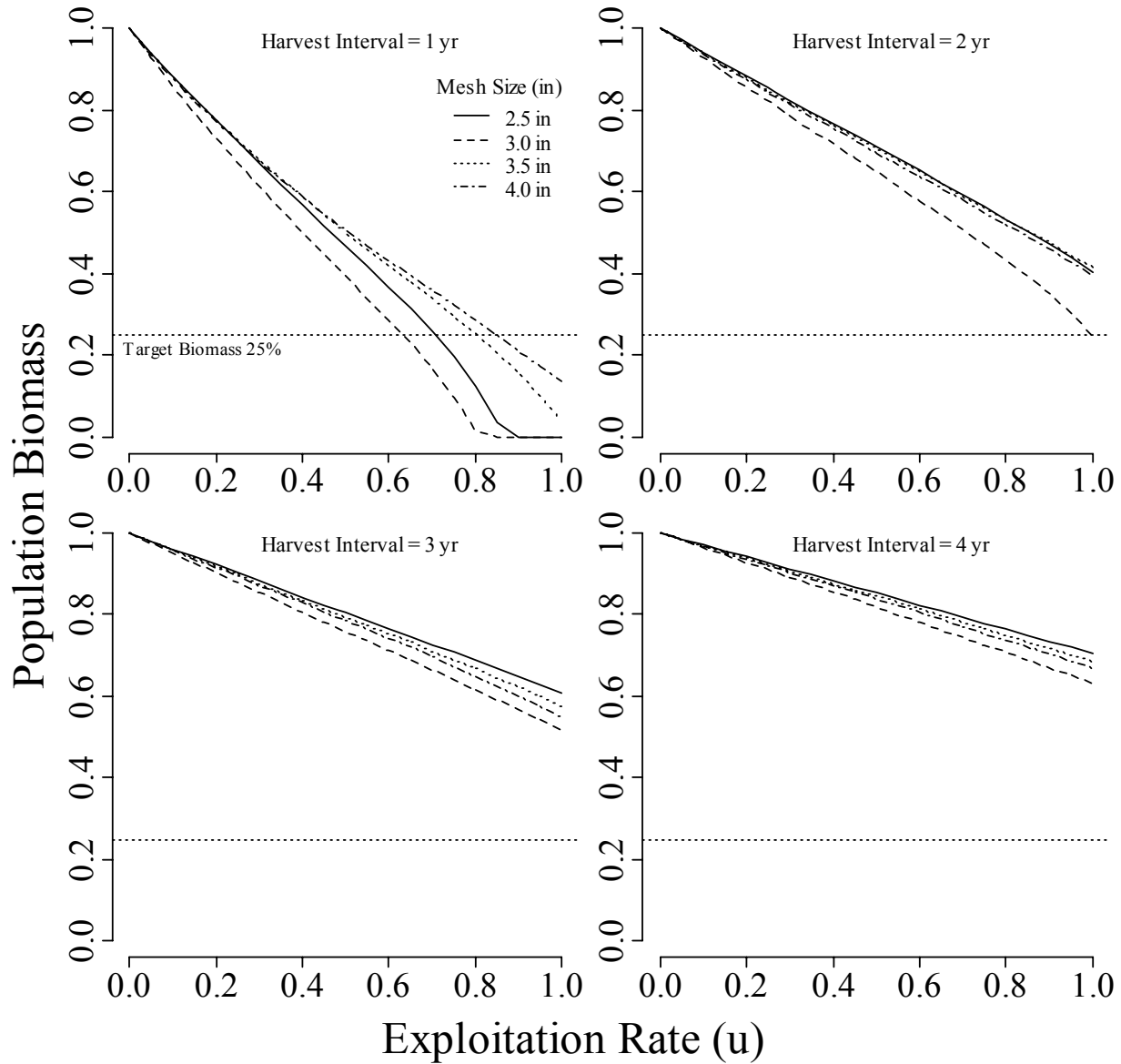


Figure 1-16. Equilibrium total population biomass as a proportion of the unfished biomass for a gizzard shad population with a low compensation ratio. Biomass was calculated across four harvest intervals (panels 1-4), four mesh sizes (lines; 2.5-4 in stretch), and a range of exploitation rates (x-axis), as the average equilibrium biomass for 50 model years after a 150-yr burn in period.

High Compensation (CR = 25)

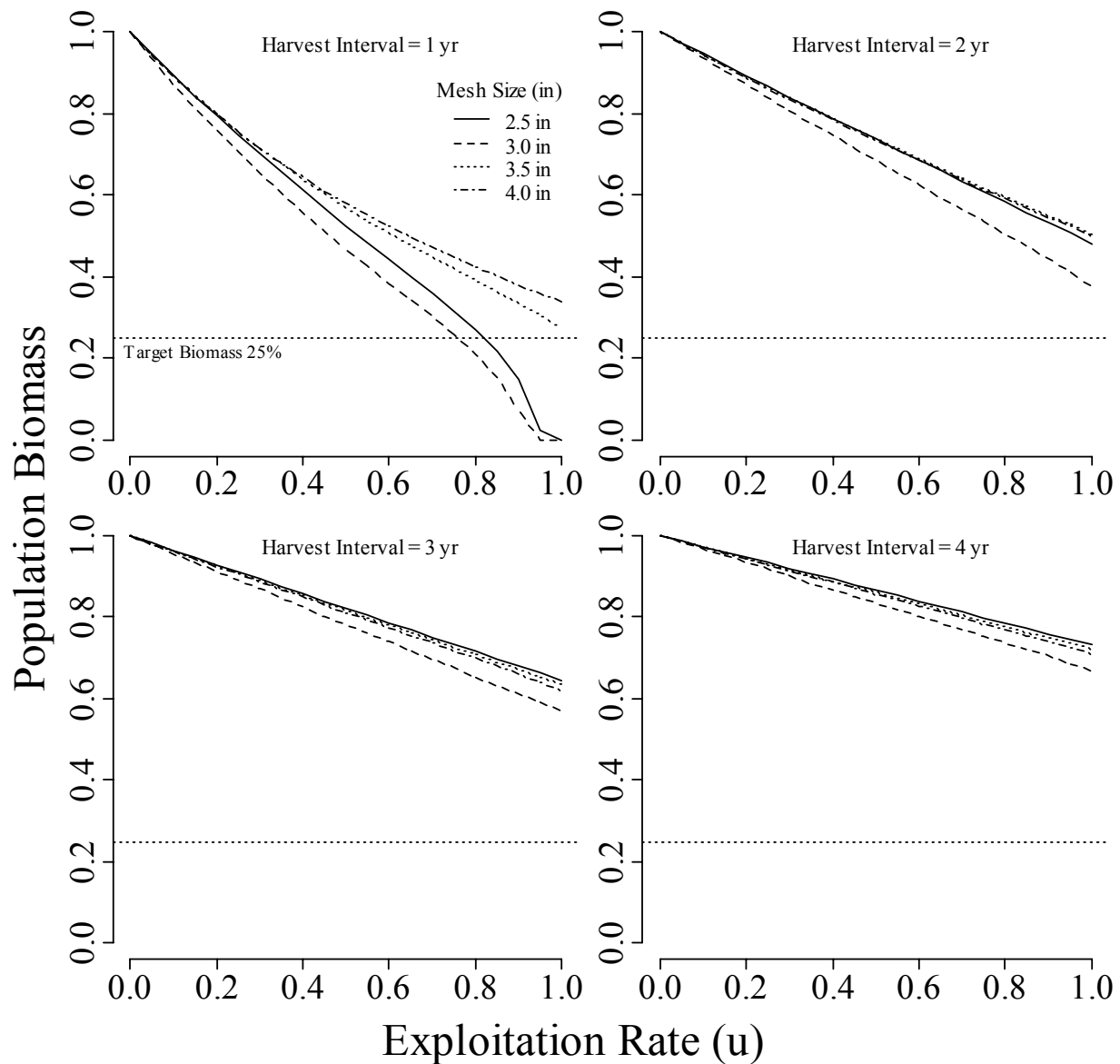


Figure 1-17. Equilibrium total population biomass as a proportion of the unfished biomass for a gizzard shad population with a high compensation ratio. Biomass was calculated across four harvest intervals (panels 1-4), four mesh sizes (lines; 2.5-4 in stretch), and a range of exploitation rates (x-axis), as the average equilibrium biomass for 50 model years after a 150-yr burn in period.

Low Compensation (CR = 10)

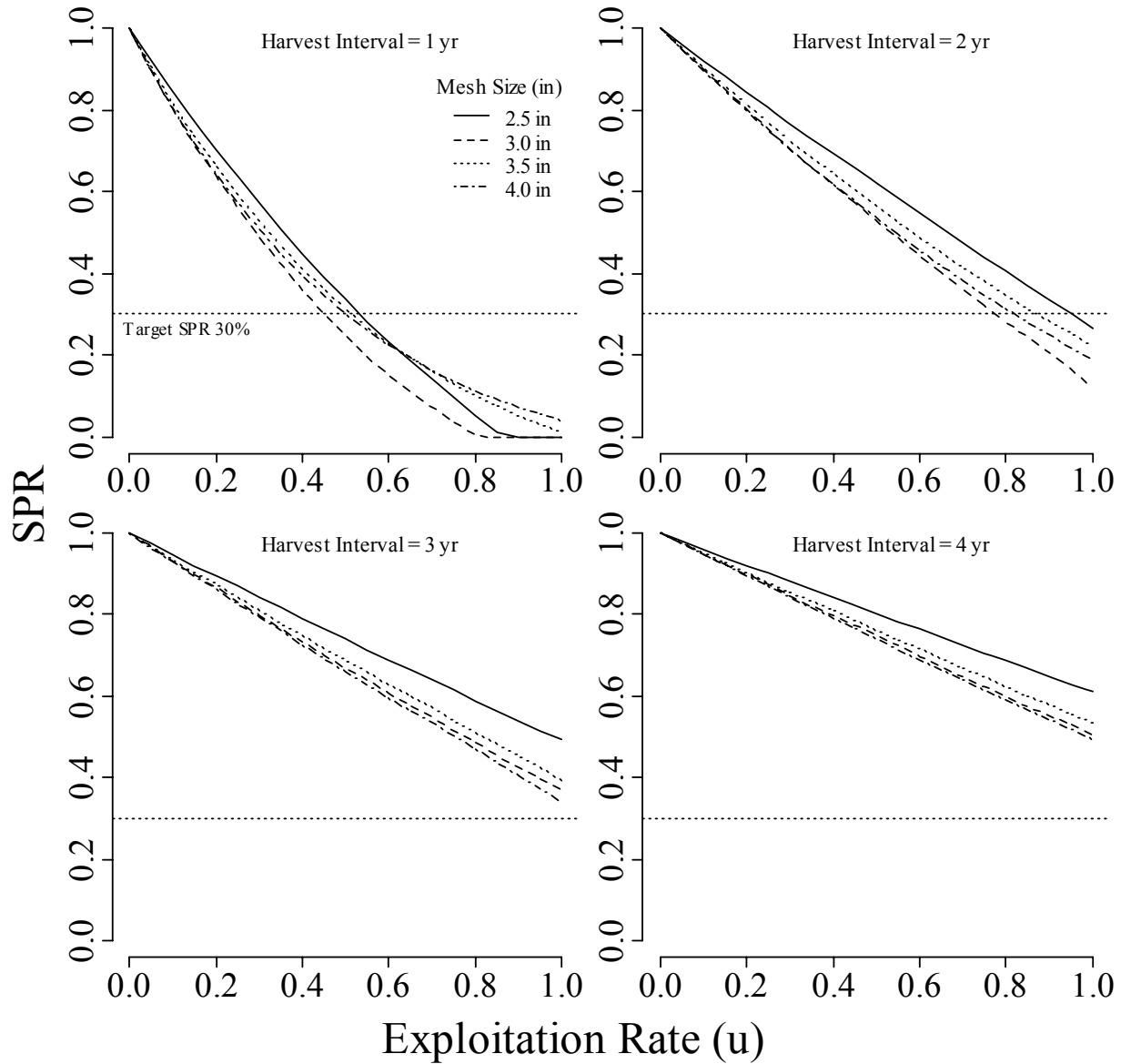


Figure 1-18. Equilibrium weighted transitional spawning potential ratio (SPR) as a proportion of the unfished biomass for a gizzard shad population with a low compensation ratio. Biomass was calculated across four harvest intervals (panels 1-4), four mesh sizes (lines; 2.5-4 in stretch), and a range of exploitation rates (x-axis), as the average equilibrium biomass for 50 model years after a 150-yr burn in period.

High Compensation (CR = 25)

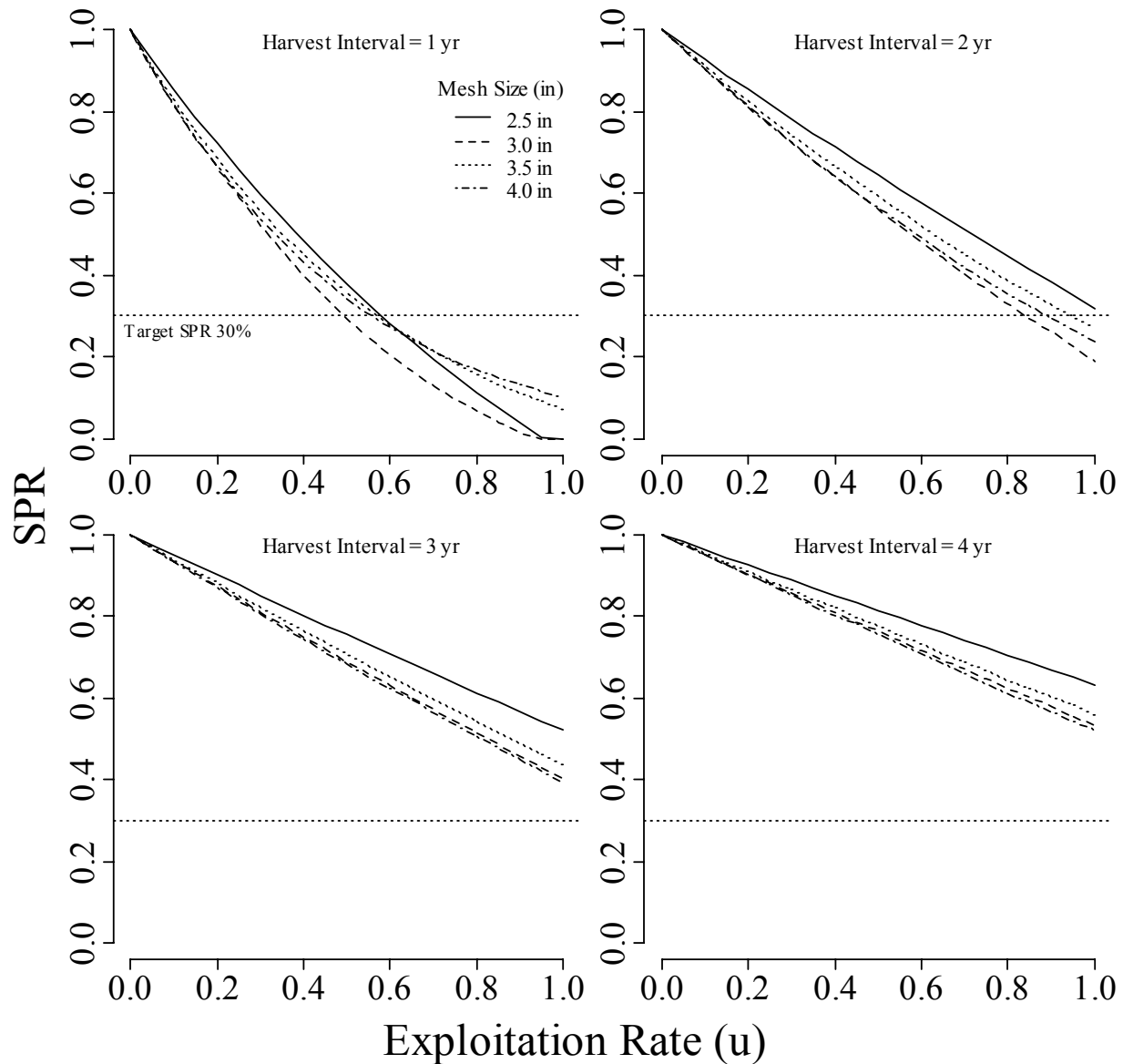


Figure 1-19. Equilibrium weighted transitional spawning potential ratio (SPR) as a proportion of the unfished biomass for a gizzard shad population with a high compensation ratio. Biomass was calculated across four harvest intervals (panels 1-4), four mesh sizes (lines; 2.5-4 in stretch), and a range of exploitation rates (x-axis), as the average equilibrium biomass for 50 model years after a 150-yr burn in period.

DISCUSSION AND MANAGEMENT RECOMMENDATIONS

Commercial fishing substantially reduced the age and size structure of the gizzard shad population at Lake Dora relative to Lakes Eustis and Harris. We estimated about a 40% reduction in total gizzard shad biomass via commercial fishing, with about a 50% exploitation rate on vulnerable fish. Gizzard shad were fully vulnerable to commercial gill nets at around age 4, but our age-structured model indicated that vulnerability declined after age 4 for the largest fish. Such dome-shaped selectivity patterns are not unexpected because the range of mesh sizes used by commercial fishers was relatively small (mostly 4.5 inch in 2005 and 4 inch in 2006), and fish vulnerability to gill net mesh is highly size specific (Hubert 1996). Thus, it is not surprising that vulnerability for the largest fish is lower than the peak vulnerabilities from the commercial gill nets.

Our depletion estimates of fishing mortality assumed that there was no change in catchability (q) throughout each fishing season. This assumption was reasonable for the short 2005 fishing season, but q could have changed through time during the long fishing season in 2006. If adult gizzard shad move inshore to spawn around vegetation (as per Heidinger 1983), we would expect catchability to be high in offshore areas prior to the spawn and decline as fish moved inshore and away from the gill net fishing areas during spawning. Decreasing q in 2006 would reduce our estimates of exploitation by predicting a higher vulnerable population size, resulting in an even lower estimate of biomass reduction. Thus, the 2006 exploitation rate could be viewed as biased high and the total biomass reduction of 40% should be viewed as the maximum level achieved at Lake Dora. The SCA model also corroborated our depletion estimates of the fishing mortality rate, albeit with a high level of uncertainty.

Growth is potentially an important mechanism for density dependence in fish populations. This occurs mainly through increases in size-at-age, which affects individual fecundity via a positive linear relation with fish weight. Lorenzen and Enberg (2002) showed that density dependent growth alone could explain population regulation in nine of 16 species fish populations they analyzed. Gizzard shad removal experiments to date have indicated strong density-dependent growth. Kim and Devries (2000) reported substantial increases in age-0 gizzard shad growth

following chemical density reduction at Walker County Lake, Alabama. Strong density-dependent growth led to early maturation and increased population fecundity, which resulted in rapid return to pre-removal biomass (Irwin et al. 2003). Thus, we expected substantial increases in gizzard shad growth following removal at Lake Dora. However, we detected no such changes.

This finding highlights an important point regarding the use of control lakes in whole-lake experiments. The control lakes are covariates that should behave as the manipulated lake would in the absence of manipulation. Thus, the temporal change in the between-lake differences becomes the variable of interest in these analyses. Our length-at-age analyses detected decreased growth at a control lake with no change at the manipulated lake. Would length-at-age at Lake Dora have decreased similar to Lake Eustis had the gizzard shad removal not taken place? This is unknown, but if true we would conclude that growth increased at Lake Dora relative to Lake Eustis after gizzard shad removal. However, there is no formal way to statistically test for change in between-lake differences for a variable that is measured once in each system in each time period, such as mean length-at-age, length/age-at-maturity, mean age-1 CPE, and length ratio analyses. Traditional BACIPS analyses cannot be employed in these cases and manipulation effects remain unclear relative to fish growth rates.

However, even if mean length-at-age did increase at Lake Dora relative to Lake Eustis after gizzard shad removal, the magnitude of these changes was small (approximately 20 mm) when compared to density-dependent changes in growth in other gizzard shad populations. Irwin et al. (2003) reported 80 to 120-mm increases in mean length at age 1 following gizzard shad removal at Walker County Lake relative to years with high population biomass. Furthermore, Schaus et al. (2002) reported three to four-fold increases in age-0 individual wet mass during a year of low shad biomass (<15 kg/ha) when compared with other years (>35 kg/ha). Clearly, we did not detect strong density-dependent changes in fish growth at Lake Dora that could contribute substantially to population regulation.

Changes in fecundity and age or length-at-maturity are also mechanisms that can underlie population regulation in fishes (Trippel 1995). Increased fecundity at a given length can result from an increased condition factor due to improved feeding conditions (Henderson et al. 1996;

Marshall and Frank 1999; Oskarsson and Taggart 2006). Fecundity at a given age can change substantially due to changes in growth and age or size-at-maturity, which can influence population fecundity and subsequent recruitment (Trippel 1995). We detected no changes in mean GSI (our index of individual fecundity at a given length) at Lake Dora following gizzard shad removal. Although the GSI may be a reasonable proxy for fecundity, factors such as egg size, maturation stage, and the number of batches spawned could affect the efficacy of GSI as a fecundity index. Jons and Miranda (1997) found that ovary weight and related indices such as the GSI could be confounded by egg size distributions and egg maturity. However, we partially controlled for these effects by limiting our evaluations to a six week period each year during which GSI values were highest. Another potential problem with using the GSI as an index of fecundity is that gizzard shad are batch spawners, and the number of batches spawned may increase with improved feeding conditions (Townsend and Wootton 1984). Consequently, increased population fecundity due to greater number of batches spawned would be undetectable with the GSI. Despite these issues, we feel the GSI was a reasonable metric of length-specific individual reproductive investment.

Although GSI did not differ after gizzard shad removal, we observed a substantially smaller length-at-maturity in 2007 than in 2005 at Lake Dora. This change could buffer the losses of large harvested individuals by increasing fecundity-at-age of smaller invulnerable-sized gizzard shad, which could help maintain recruitment in the face of the removal. However, we did not detect a decrease in the age-at-maturity, which was expected because length-at-maturity decreased and mean length-at-age did not change. This is most likely an artifact of the data selected for the analyses. We had a much smaller sample size for the age-at-maturity analysis than for the length-at-maturity analysis because we only aged a subsample of the fish from which we collected ovaries. Thus, we had few fish from the lower tail of the length distribution for age-2 fish. It was these smaller than average age-2 gizzard shad that were more likely to be mature in 2007 than in 2005 based on our length-at-maturity analyses. Thus, our data showed that most female gizzard shad matured at age 2 in both 2005 and in 2007, but that slow growing fish matured at age 2 in 2007 instead of waiting another year before maturation as they did in 2005.

Age-1 gizzard shad CPE increased at Lake Dora in each year of this study, indicating higher recruitment levels despite reduced population fecundity from removal of large fish. We detected recruitment compensation at Lake Dora because catch rates of age-1 fish increased despite slight decreases in larval abundance. Nevertheless, the ratio of age-1 catch relative to larval density did not vary among the lakes, and thus, we were unable to detect stronger compensation at Lake Dora relative to the other two lakes. Higher recruitment after fishing would be expected for Ricker type (i.e., dome shaped) stock recruitment curves. Gizzard shad life history would not lead us to expect a Ricker type curve, because cannibalism or extreme competition between adults and juveniles are the most frequent causes of this type of curve (Ricker 1975). It is more likely that gizzard shad exhibit a Beverton and Holt (i.e., asymptotic) stock recruitment curve, which is more common among fish species (Walters et al. 2006). We suggest that higher CPE of age-1 fish after fishing was due to interannual variation around a Beverton and Holt stock recruitment curve rather than a Ricker-type relationship. However, no previous studies have estimated stock recruitment relationships for gizzard shad, and identifying the underlying stock recruitment relationship will be important for future gizzard shad biomanipulation studies. If gizzard shad exhibit Ricker-type stock recruitment curves, then moderate levels of fishing would increase average recruitment and potentially counteract any positive effects of gizzard shad harvest on lake trophic dynamics.

Age-1 recruitment estimates were uncertain due to low vulnerability of these small fish to experimental gill nets, and should be viewed with caution. Further sampling in 2008 and 2009 will track these cohorts as they become more vulnerable to the gear at age 2. If future samples confirm preliminary conclusions from age-1 recruitment estimates, then we would conclude that the population compensated through increased reproduction and maintained constant or possibly increased recruitment in the face of a 40% biomass reduction. This finding would have important implications for biomanipulation efforts because compensatory reproduction may dampen biomass reductions by maintaining or increasing the numbers of age-0 gizzard shad, even if the mechanisms for compensation are difficult to detect in field data.

Understanding compensation is the key to predicting the limits for harvest of fish populations. The compensation ratio (*recK*) is a useful way to conceptualize compensation and describes the

ratio of juvenile survival at very low population size to juvenile survival in an unfished population. For example, a compensation ratio of 10 means that juvenile survival is capable of increasing by a factor of ten when a population is fished down to a very low level. This increase in juvenile survival buffers annual recruitment against reductions in population fecundity due to harvest. Recent meta-analyses by Myers et al. (1999) and Goodwin et al. (2006) of many fish populations have indicated that short-lived early-maturing pelagic fishes such as clupeids (mean *recK* = 18) have relatively weak compensation compared with large, long-lived benthic species such as cod (family Gadidae; mean *recK* = 39). Our simulations used *recK* values of 10 and 25, which represented roughly the upper and low bounds for clupeids assuming a mean value of 18 (Myers et al. 1999). Although these values are relatively low compared to those of species such as cod, a *recK* of 18 constitutes a substantial ability to withstand harvest for a short-lived, fast-growing species such as the gizzard shad. For example, average annual recruitment in our gizzard shad population would decrease by only 10% if the population fecundity were reduced by 50%, if a *recK* of 18 was assumed. The increase in recruits per spawner at low population sizes described above occurs mainly through changes in juvenile survival (Walters and Martell 2004). However, changes in growth, condition, and maturation may also contribute to increases in recruits per spawner at low population sizes.

Total biomass reduction of around 40% is likely within the range on natural interannual variation in gizzard shad populations, but still should induce density-dependent changes in vital rates. Size at maturity was the only life history metric that differed at Lake Dora after harvest compared to the control lakes. Decreased size-at-maturity appeared to allow the more abundant small fish to produce enough eggs to compensate for the reduction in large fish at Lake Dora. Larval gizzard shad densities showed only modest declines after fishing, suggesting that reproductive output was not substantially reduced after fishing. For species like gizzard shad with relatively low capacity to change juvenile survival under reduced densities (i.e., the compensation ratio), our results suggest that size-at-maturity can be a key factor for population compensation.

However, it is also possible that the degree of manipulation at Lake Dora was not strong enough to elicit detectable changes in fish growth rates, larval abundance, and compensation. Two years

of fishing at Lake Dora reduced total fish biomass by a maximum of about 40%, and a stronger manipulation could be required to cause changes in fish growth rates and juvenile survival rates. Future studies should quantify gizzard shad population responses to more intensive biomanipulation efforts.

Gill net fisheries for gizzard shad are unlikely to cause large total biomass reductions (i.e., 75% declines) under current gear and fishery configurations. Our simulations showed that 75% reductions in total shad biomass could only be achieved by 1) use of smaller mesh sizes, especially 3-inch mesh, 2) very high fishing mortality rates, and 3) fishing every year. If one of these three conditions were not met, our results predict that attaining a 75% reduction in total gizzard shad biomass would not be achieved. We chose a 75% biomass reduction target from the literature based on empirical data from many biomanipulation studies. The biomass reduction level that would reduce phytoplankton biomass at Lake Dora is unknown. The true value may be higher or lower than 75%, and our data do not address the applicability of this value to Lake Dora. However, our data suggest that long-term total gizzard shad biomass reductions are unlikely to exceed 40-50% at Lake Dora or similar lakes without substantial increases in the exploitation rate and decreases in gill net mesh size.

Gill net catch rates declined greatly through the season in both sample years, and fishers probably reach a point within 1-2 years where their low catches make fishing unprofitable. It is likely that sustaining very high exploitation rates for gizzard shad would require paying fishers for the number of angler days, or total net sets, rather than paying them based on biomass of the catch. Another option could be to increase the gizzard shad price subsidy as a function of the cumulative catch so that fishers can attain nearly constant income as catch rates decline. Use of smaller gill net mesh sizes would substantially increase bycatch impacts to recreational fisheries, and thus, attempts to use gill netting to incur high fishing mortality on gizzard shad could reduce value of recreational fisheries (see Chapter 4).

Our simulated biomanipulation strategies would be applicable to any gizzard shad population with similar growth rates and age structures to those found at Lake Dora, and the scenarios revealed here would apply to other hypereutrophic Florida lakes. The biomanipulation scenarios

were not strongly influenced by the compensation level of the simulated populations, but they were predicated on the assumption that a 75% reduction in total gizzard shad biomass is required for lake water chemistry improvements. Reviews of biomanipulation studies have usually identified this target as the minimum reduction in omnivorous fish biomass to alter lake trophic dynamics (Hansson et al. 1998; Meijer et al. 1999; Sondergaard et al. 2000). Thus, resource managers in Florida should consider alternate fishery configurations such as different pay schemes for fishers or different fishing gears that are less size selective for future biomanipulation projects.

CHAPTER 2: BENTHIC AND PELAGIC FOOD SOURCES IN THE DIET OF GIZZARD SHAD

INTRODUCTION

Increasing nutrient inputs and consequent eutrophication of Florida lakes has led to a proliferation of algae and cyanobacteria (Riedinger-Whitmore et al. 2005). Reversing the effects of eutrophication can be challenging and requires the reduction of external nutrient sources and internal nutrient loading (Carpenter 2005; Schindler 2006). Decreasing the rate of nutrient (phosphorus) recycling from the sediments is an important step in lake restoration (Carpenter 2005).

Detritivorous fish such as gizzard shad can facilitate the exchange of sediment-borne nutrients by stirring up sediments as a consequence of their foraging activity at the sediment-water interface and subsequent excretion of nutrients in the water column (Schaus and Vanni 2000; Vanni et al. 2006; Higgings et al. 2006). As gizzard shad tend to dominate fish biomass in eutrophic and hypereutrophic lakes in Florida (Bachmann et al. 1996), they may contribute considerably to the release of nutrients from the sediments. Gizzard shad have the potential to enhance production of cyanobacteria by excreting relatively high levels of phosphorous (Schaus et al. 1997; Torres and Vanni 2007), which could lower the N:P ratio of lake nutrients, and release sediment ammonium as a consequence of their foraging activities. Low N:P ratios and the release of ammonium from the sediment favor cyanobacterial production over other phytoplankton taxa (Ferber et al. 2004).

Although gizzard shad are assumed to be primarily detritivorous, this species will consume also phytoplankton and zooplankton (Baker and Schmitz 1971). Yako et al. (1996) showed that gizzard shad at Kokosing Lake, Ohio were facultative detritivores because zooplankton consumption increased with increases in zooplankton abundance (Yako et al. 1996). Schaus et al. (2002) found that gizzard shad markedly increased their consumption of zooplankton following an increase in zooplankton biomass at Acton Lake, Ohio. The increase in zooplankton biomass was a direct consequence of a decrease in grazing pressure by gizzard shad during a period of low ($< 15 \text{ kg} \cdot \text{ha}^{-1}$) gizzard shad biomass (Schaus et al. 2002).

In general, gizzard shad regulate food webs via ‘middle-out’ processes, an interaction of top-down and bottom-up processes (DeVries and Stein 1992). Gizzard shad can suppress zooplankton biomass (Dettmers and Stein 1992, 1996; Schaus and Vanni 2000) which can enhance phytoplankton production via a reduction of the grazing pressure (Schaus et al. 2002), with largest effects expected in lakes dominated by large zooplankton species such as *Daphnia* spp. and with abundant edible algae (Dettmers and Stein 1996). Alternatively, juvenile and adult gizzard shad can negatively affect phytoplankton production by consuming zooplankton species with low escapabilities and enhancing populations of more evasive herbivorous zooplankton species (Drenner et al. 1982).

To evaluate the role of gizzard shad in the presence and persistence of high algal and cyanobacterial biomass in eutrophic lakes, it is important to know the relative importance of benthic versus pelagic food sources of gizzard shad. We used stable isotope techniques to assess the contribution of different food sources in the diet of gizzard shad. Stable isotopes have the advantage over gut content analyses in that they reflect feeding behavior over a time frame of tissue turnover, whereas gut content analyses provide snapshot data of feeding behavior up to a few hours before capture. Diet studies generally compare the stable isotopic compositions of carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) to study trophic dependencies. However, a preliminary study of the stable C and N isotope distribution in fish, zooplankton and mud of Lake Dora revealed no differences in $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$ isotope signature between these groups (Allen et al. 2004). Stable sulfur isotope compositions of organic matter, however, are known to differ between benthic and pelagic compartments because of the activity of sulfur reducing bacteria which preferentially convert $^{32}\text{SO}_4^{2-}$ to sulfide, which is subsequently incorporated in benthic microorganisms and macrofauna (Fry 1986; Yamanaka et al. 2003; Grey and Deines 2005). Stable sulfur isotope ratios ($\delta^{34}\text{S}$) have been useful for investigating the relative importance of food sources in fish diets (Peterson and Howarth 1987; Hesslein et al. 1991; Weinstein et al. 2000). This technique is based on the assumption that the $\delta^{34}\text{S}$ composition of a consumer is similar to that of its food source because of the small change in isotopic composition (“isotope fractionation”) during sulfur assimilation (Fry and Sherr 1984). When a consumer relies on a mixture of different food sources, the final consumer $\delta^{34}\text{S}$ value will reflect the relative contribution and sulfur content of the food sources (Fry and Sherr 1984; Phillips and Koch 2002; Phillips and Gregg 2003). The stable isotopic composition of sulfur can thus be used to investigate the relative

proportion of benthic versus pelagic food items if there is a difference in $\delta^{34}\text{S}$ value between the food sources.

This chapter describes feeding behavior of gizzard shad from Lake Dora. The main objectives were to investigate the seasonal and size-specific changes in relative importance of benthivory and planktivory in gizzard shad. Sulfur isotope analyses were combined with foregut content analyses to check the validity of the isotope data.

METHODS

Study site

The study was conducted at Lake Dora, Florida. See Chapter 1 - *Study Site*, above, for a description of the lake.

Sampling collection and processing of gizzard shad

Gizzard shad were captured four times a year, once per season, for foregut content and sulfur isotope analyses. All potential food items (lake bottom mud, benthic invertebrates, zooplankton, cyanobacteria, aquatic macrophytes) were sampled in the same season as the gizzard shad sampling event (except fall 2006), in order to compare the $\delta^{34}\text{S}$ values of gizzard shad with the $\delta^{34}\text{S}$ of their potential food sources and to investigate the variability in the $\delta^{34}\text{S}$ composition of the food sources.

Gizzard shad were collected from Lake Dora in August and November 2006 and January and May 2007 with gill nets placed at 20 randomly selected locations. Captured fish were placed on ice and transported to the laboratory where they were measured for total length (to the nearest mm) and weighed (to the nearest 0.1 g). Fish were sorted by length and placed into size classes of 100 mm. Because of the large amounts of fish caught in the gill nets, the complete gastro-intestinal system and a subsample of the dorsal muscle of only 40 fish per size class were kept for later stomach and sulfur isotope analyses, but not all 40 fish per size class would ultimately be analyzed (see below). Muscle tissue and gastro-intestinal organs were stored frozen prior to analyses (see below). Because the gill nets selectively capture fish > 100 mm, several additional field trips were made to sample gizzard shad

< 100 mm. In late July and early August 2006, juvenile gizzard shad were sampled by electrofishing. In April 2007, gizzard shad larvae were collected with a 0.75-m ichthyoplankton net (500- μ m mesh size) using 3-minute tows. In all cases, larvae and juvenile gizzard shad were transported to the laboratory on ice and subsequently identified; larvae were sorted by size with the aid of a dissecting microscope and grouped into size classes of 15-20 mm, 20-25 mm and 25-30 mm. Per size class, the entire body of 10-15 larvae were stored frozen for further analysis.

Sampling collection and processing of potential food sources

Lake bottom sediment was sampled in summer (July 2006), winter (January 2007) and spring (May 2007) at three sites in the eastern (site 14), middle (site 12) and western (site 2) part of Lake Dora using an Eckman grab sampler (see Figure 1-1 for site locations). A subsample of the upper (fluid) mud layer was transferred into a 150-ml plastic container and immediately stored on ice and transported to the laboratory. At the laboratory, mud samples were first frozen to stop all microbial activity. Subsequently, samples were thawed and homogenized. Subsamples were dried at 60°C (24h) in preparation for $\delta^{34}\text{S}$ analyses.

Benthic invertebrates were sampled in winter (February 2007) and spring (May 2007) at sites 2, 12 and 14 using an Eckman grab sampler. At each site, four mud samples were taken of which the upper liquid mud layer (5 – 10 cm) was pipetted into a 1-L poly-ethylene bottle and stored on ice. Mud samples were strained over a 212 μ m sieve to remove excess organic matter and the resulting sample frozen prior to further processing. Later, benthic invertebrates were hand-picked from the thawed sample under a dissecting microscope, transferred to a pre-weighed vial and dried to a constant weight at 60°C. Vials were subsequently re-weighed to determine the mass of the invertebrate sample. In spring 2007, benthic invertebrates from the three sites had to be pooled to get a net weight of minimum 3 mg, the minimum weight required for reliable analyses.

Zooplankton and cyanobacteria (*Microcystis* sp.) were collected in summer (August 2006), winter (December 2006) and spring (May 2007) at the three sites 2, 12 and 14. In winter, zooplankton was collected with a Wisconsin plankton net (mesh size = 80 μ m) in 3 to 5-minute tows. However, in

spring, the sampling efficiency of this plankton net was considerably lowered due to clogging by *Microcystis*. Thus, a zooplankton net with larger mesh size, i.e. 202 μm , had to be used to ensure collection of sufficient material for the $\delta^{34}\text{S}$ analyses. Zooplankton and cyanobacteria were sampled both at the surface (ca. 0.5-m depth) and in the lower water column (ca. 2 m to 2.5 m). Samples were placed on ice and transported to the laboratory. In the laboratory, samples were centrifuged to separate *Microcystis* from zooplankton, after which the samples were frozen. In summer 2006 and winter 2007, the supernatant containing *Microcystis* was filtered onto a precombusted Whatman glassfiber filter and dried to constant weight at 60°C. In spring, however, the *Microcystis* sample was first frozen and subsequently freeze-dried. The thawed zooplankton sample was strained over a 202- μm sieve and zooplankton were hand-picked under a dissecting microscope. Per sample, a total amount of 1,500 to 3,000 copepods were hand-picked from the sample, equaling 3 to 10 mg copepod dry weight. No attempt was made to isolate phytoplankton or microzooplankton (such as rotifers) from the samples because of the difficulty of isolating them from the suspended matter mixture and the large amounts of material (15 $\mu\text{g S}$) needed for the $\delta^{34}\text{S}$ analyses.

Macrophytes growing in the shallow littoral zones of Lake Dora were collected in May 2007. One specimen each of *Vallisneria americana*, *Salvinia sp.*, *P. geminatum*, *Scirpus sp.* and *Typha sp.* were collected by hand, placed on ice in plastic bags and transported to the laboratory. In the laboratory, above- and below-ground tissue was separated and the above-ground material retained and dried for subsequent analysis of $\delta^{34}\text{S}$.

Stable isotope analyses

Gizzard shad muscle tissue, whole gizzard shad larvae, zooplankton, benthic invertebrates, macrophyte and sediment samples were dried at 60°C and ground to a fine powder. The filtered *Microcystis* sample was dried at 60°C and peeled from the filter to reduce the amount of glassfiber in the sample, while the freeze-dried *Microcystis* samples were ground to a powder. $\delta^{34}\text{S}$ analyses were performed by continuous flow isotope mass spectrometry at the Marine Science Institute, University of California at Santa Barbara. The analytical precision of the $\delta^{34}\text{S}$ measurements, based on replicate analyses of multiple standards, was typically 0.3‰. However, the precision of *Microcystis* sampled in winter was 3‰ because of the presence of glassfiber filter in the sample.

Diet analyses

To quantify diets, ten gizzard shad (>100mm), distributed evenly across the full size range of fish caught in the gill nets were selected for analysis of the foregut. In general, about 50% of the fish had empty foreguts, especially in the larger size classes, which was probably partly due to the time lag (< 2h) between the moment they were caught in the gill nets and the moment gill nets were pulled out of the water. In November 2006, only nine fish could be analyzed because of the many fish with empty foreguts in the upper size classes. Only the fish for which the foregut was analyzed were ultimately also analyzed for muscle $\delta^{34}\text{S}$.

The contents of the foregut were transferred to a beaker filled with tap water to loosen the tightly packed food items. Three separate, 1 ml subsamples of the slurry were transferred to a Rafter counting cell to enumerate the most dominant prey items (rotifers, nauplii, copepods, cladocerans, ostracods and chironomid and *Chaoborus* larvae) under a microscope. Percent by number of various prey items in the diet were inspected to evaluate how gizzard shad diets varied with fish size and across the seasons.

RESULTS

$\delta^{34}\text{S}$ composition of gizzard shad

During the summer of 2006, gizzard shad $\delta^{34}\text{S}$ signatures showed clear evidence of an ontogenetic shift in assimilated food items. The $\delta^{34}\text{S}$ values of young gizzard shad (TL > 60 mm) were initially high (9-10‰), but declined rapidly to values between 0.1‰ and 2.4‰ once a TL size of 100-200 mm was reached (Figure 2-1). The $\delta^{34}\text{S}$ values of larger fish increased steadily to a value of 9-10‰. In the fall of 2006, $\delta^{34}\text{S}$ values of gizzard shad (TL >100 mm) showed a slight, but consistent increase from 5-6‰ to 9-10‰. Similar patterns were observed in winter and spring of 2007. Gizzard shad larvae (15-30 mm) collected in spring 2007 exhibited a mean $\delta^{34}\text{S}$ value of $10.8 \pm 0.3\text{‰}$. Thus, gizzard shad >200 mm TL showed a consistent increase with size during the different seasons and their $\delta^{34}\text{S}$ values did not show major changes across seasons. Conversely, smaller gizzard shad (100 – 200 mm TL) $\delta^{34}\text{S}$ values were lower in summer than during the other seasons, during which their values did not change considerably.

$\delta^{34}\text{S}$ composition of potential food sources

Zooplankton $\delta^{34}\text{S}$ values, in general, did not differ significantly between the upper ($9.4 \pm 0.4\text{‰}$) and lower ($9.0 \pm 1.1\text{‰}$) water column (paired t-Test, $P = 0.38$) and were therefore combined for analyses. Zooplankton were not manually removed from the net tow samples during the summer sampling event, thus a precise $\delta^{34}\text{S}$ value was not available. However, zooplankton $\delta^{34}\text{S}$ values can be estimated by subtracting the trophic fractionation factor for sulfur assimilation from the $\delta^{34}\text{S}$ of the obligate planktivore threadfin shad which were available as a bycatch from the gizzard shad sampling effort. The $\delta^{34}\text{S}$ values of threadfin shad averaged $10.2 \pm 0.5\text{‰}$ ($N = 11$, size range 22 – 114 mm). The trophic fractionation factor ($+0.8 \pm 0.4\text{‰}$) was calculated from the difference between spring gizzard shad larvae and zooplankton, their presumed food source (Dettmers and Stein, 1992). Correcting for this trophic fractionation factor provides a corresponding zooplankton $\delta^{34}\text{S}$ value of $9.3 \pm 0.6\text{‰}$. This value could be slightly overestimated if cyanobacteria are part of the diet of threadfin shad, as this species feeds on a mixture of zooplankton and phytoplankton (Miller 1967). A comparison between the zooplankton $\delta^{34}\text{S}$ values of the different seasons showed that there was little variation across the seasons (Figure 2-2; Table 2-1).

In contrast to zooplankton $\delta^{34}\text{S}$ values, cyanobacterial $\delta^{34}\text{S}$ values varied across seasons and in winter 2007 also between the upper and lower water column. Cyanobacteria $\delta^{34}\text{S}$ values from the upper water column were highest during summer 2006 ($14.0 \pm 1.3\text{‰}$) and lowest in winter 2007 (3.2‰). In fact, this winter $\delta^{34}\text{S}$ value seemed unusually low compared to the other $\delta^{34}\text{S}$ values of cyanobacteria from the upper and lower water column in the different seasons. The origin of such low value is unclear and merits further investigation. Winter $\delta^{34}\text{S}$ values of cyanobacteria from the lower water column were much higher, i.e. 12.9‰ . In spring, cyanobacteria collected from surface water had a value of 9.7‰ which was very similar to the $\delta^{34}\text{S}$ value of cyanobacteria from the lower water column (10.0‰).

The benthic invertebrates found in the upper mud layer of Lake Dora sediments consisted mainly of ostracods, nematods, oligochetes, chironomids, *Chaoborus* larvae and gastropoda. The $\delta^{34}\text{S}$ values of benthic invertebrates ranged between $4.6 \pm 1.7\text{‰}$ and 5.1‰ while the upper mud layer

$\delta^{34}\text{S}$ values varied between $9.8 \pm 2.0\text{‰}$ and $12.2 \pm 2.3\text{‰}$. Both benthic invertebrates and mud $\delta^{34}\text{S}$ values varied little across the seasons (Figure 2-2; Table 2-1).

Macrophyte leaves were only sampled in spring. Submerged species (*Vallisneria americana* and *Salvinia* sp.) had $\delta^{34}\text{S}$ values (7.5‰ and 9.3‰, respectively) that were slightly lower than those of cyanobacteria ($10.8 \pm 1.2\text{‰}$). Emergent macrophyte leaf $\delta^{34}\text{S}$ values ranged from -1.2‰ (*P. geminatum*) to 11.8‰ (*Typha* sp.). The $\delta^{34}\text{S}$ value for *Scirpus* sp. was intermediate at 2.8‰.

Overall, potential food sources showed little (cyanobacteria) or no (zooplankton, benthic invertebrates and mud) significant variation in $\delta^{34}\text{S}$ across the seasons. This agrees with the lack of seasonal variation in $\delta^{34}\text{S}$ values for gizzard shad >200 mm (Figure 2-1) and suggests that the distinct drop in $\delta^{34}\text{S}$ of gizzard shad of 100 – 200 mm TL in summer might be linked to a change in feeding behavior rather than a change in the $\delta^{34}\text{S}$ composition of the food source.

The $\delta^{34}\text{S}$ values of gizzard shad are shown for comparison with the signatures of their potential food sources (Figure 2-2). All gizzard shad $\delta^{34}\text{S}$ values presented in Figure 2 are corrected for the fractionation factor of $0.8 \pm 0.4\text{‰}$. Corrected gizzard shad $\delta^{34}\text{S}$ values were mostly lower than the $\delta^{34}\text{S}$ values of zooplankton, cyanobacteria and upper mud. Only in winter were the $\delta^{34}\text{S}$ values of some gizzard shad similar to the $\delta^{34}\text{S}$ of zooplankton. Conversely, winter and spring gizzard shad $\delta^{34}\text{S}$ values were similar or higher than the $\delta^{34}\text{S}$ of the benthic invertebrates. The low summer $\delta^{34}\text{S}$ values of gizzard shad in the 100-200 mm size range could not be related to any of the collected potential food items, warranting future investigation.

Foregut content analyses

Gizzard shad foregut contents suggested an omnivorous feeding pattern as all fish foreguts contained a mixture of plant detritus, detrital and fresh microcystis, phytoplankton, zooplankton and benthic organisms. No attempt was made to quantify the relative biomass contribution of the different food items in the diet because most organisms were fragmented, making it difficult to

measure length that would be needed for subsequent conversion to biomass. Instead, the proportion by number of selected diet components was used to assess temporal and ontogenetic changes in foraging behavior. Presenting the diet composition as percentages by number of selective diet components does not provide information about the relative importance of the different diet component. However, it is assumed that studying the change in the relative amounts of benthic organisms (ostracods, gastropoda, chironomids and *Chaoborus* larvae) versus pelagic and hyperbenthic fauna (nauplii, copepod, cladocerans and rotifers) provides information about a change in feeding strategy. In other words, if gizzard shad do not show changes in feeding behavior, they would show equal proportions of benthic versus hyperbenthic and pelagic food sources at all fish sizes or between seasons.

Foregut contents showed some seasonal variation in both the 100 – 200 mm and > 200 mm size range, which is in contrast to the $\delta^{34}\text{S}$ data that did not show seasonal variation in the >200 mm size range (Figure 2-3). Gizzard shad in the 100 -200 mm size range consumed more rotifers during summer 2006 than during the other seasons. Gizzard shad > 200 mm consumed the fewest cladocerans during summer 2006 and most during spring 2007. Benthic organisms, and in particular chironomids and *Chaoborus*, were more often consumed during spring 2007 than during the other seasons.

The relative proportion of rotifers was higher in fish < 300mm, especially in summer when rotifers comprised 20-90% of the organisms observed in the diet (Figure 2-3). In larger fish, copepods and cladocerans were the numerically dominant prey items in the diet, suggesting that these fish feed in the water column. In summer, fall and winter, copepods were consumed in higher percentages than cladocerans (Figure 2-3). The opposite was true in spring when cladocerans were relatively more abundant than copepods in the diet. In spring, chironomids and *Chaoborus* were more frequently observed in the foreguts than during the other seasons (Figure 2-3). However, nearly all gizzard shad stomachs contained evidence of both hyperbenthic/pelagic and benthic organisms.

Table 2-1. The $\delta^{34}\text{S}$ (‰) average ($\pm$ standard deviation) of potential food sources of gizzard shad at Lake Dora 2006-2007.

	Zooplankton	Cyanobacteria	Benthic Invert.	macrophytes	Upper Sediment
Summer	9.3 (± 0.6) [§]	14.0 (± 1.3)	n.d.	n.d.	12.2 (± 2.3)
Winter	8.6 (± 0.7)	12.9	4.6 (± 1.7)	n.d.	9.8 (± 2.0)
Spring	9.8 (± 0.3)	9.7 (± 0.2)	5.1	6.1 (± 5.2)	10.8 (± 1.2)

[§] This value was calculated based on the average $\delta^{34}\text{S}$ of planktivorous threadfin shad ($10.2 \pm 0.5\text{‰}$) and the estimated fractionation factor $0.8 \pm 0.4\text{‰}$.

n.d. = no data

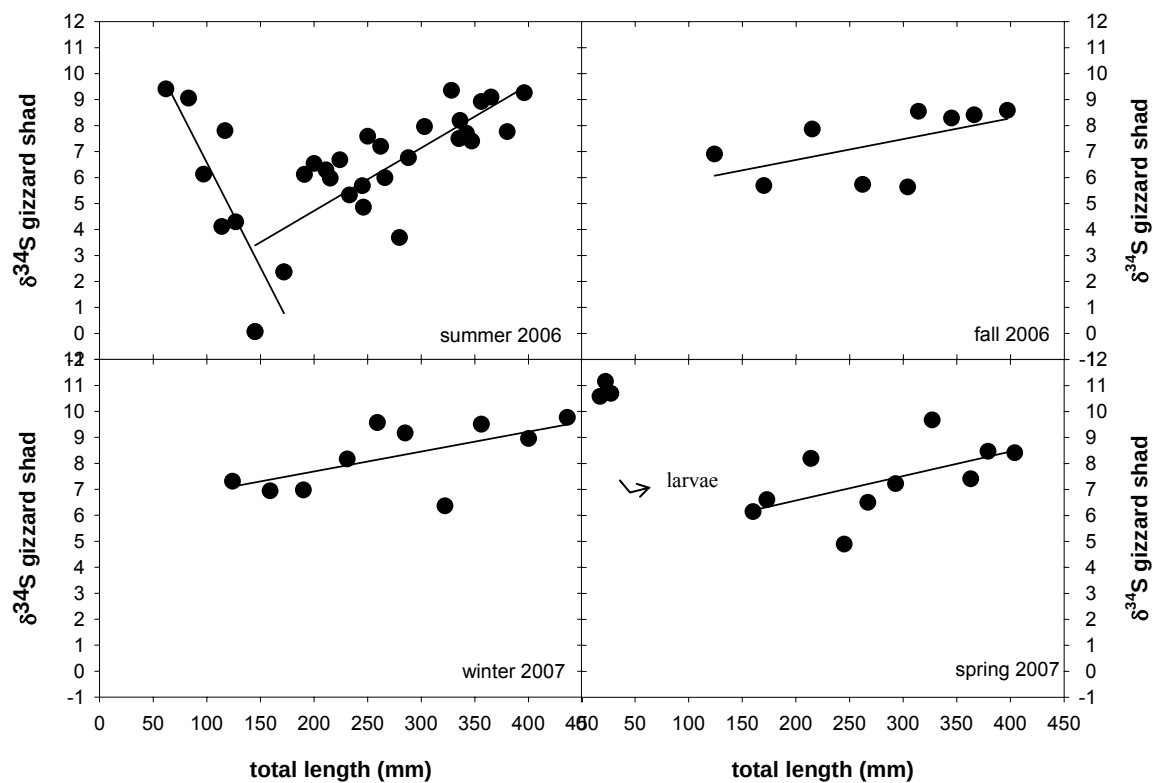


Figure 2-1. Seasonal and size-specific variation of gizzard shad $\delta^{34}\text{S}$ at Lake Dora 2006-2007. Standard deviation of $\delta^{34}\text{S}$ measurements was 0.3‰ .

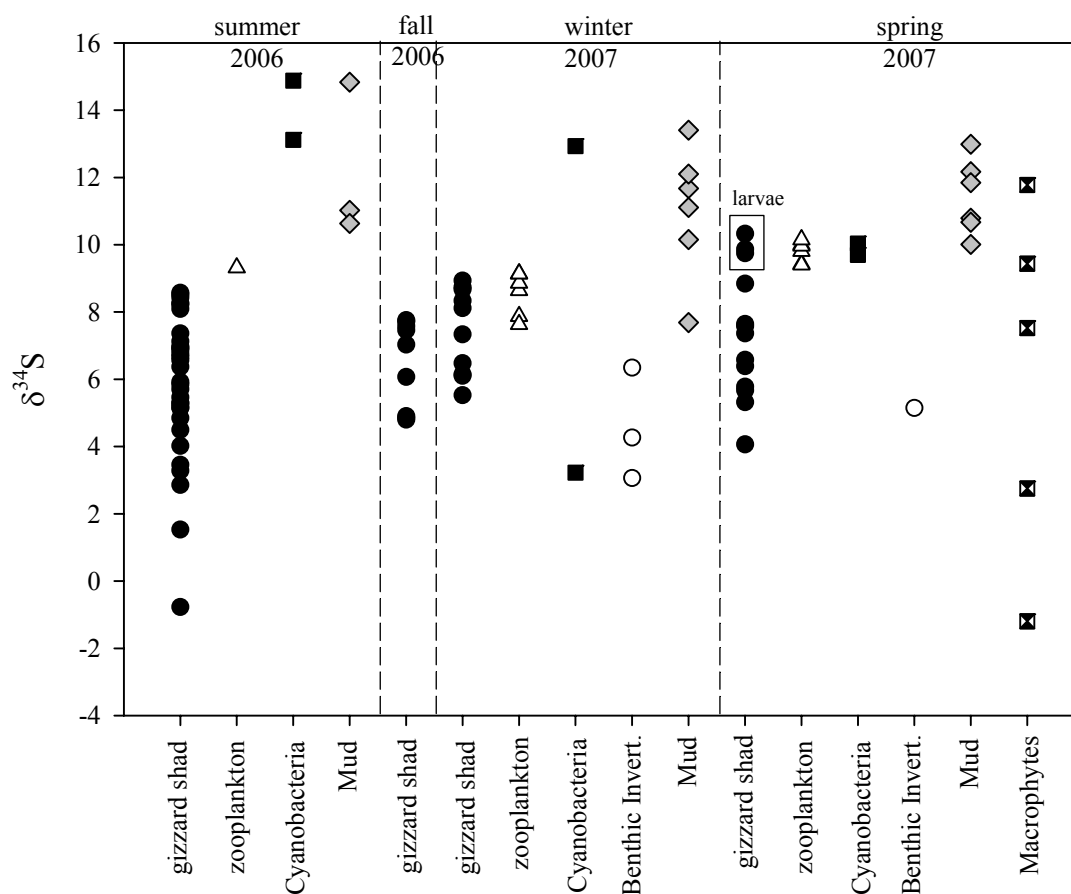


Figure 2-2. Seasonal variation of sulfur isotope signatures for gizzard shad (black circles), zooplankton (white triangles), cyanobacteria (black squares), benthic invertebrates (white circles), upper mud (grey diamonds) and macrophyte leaves (black/white square) for Lake Dora 2006-2007. Gizzard shad $\delta^{34}\text{S}$ were corrected for fractionation using a value of $0.8 \pm 0.4\text{‰}$. The summer zooplankton $\delta^{34}\text{S}$ value was estimated by subtracting the fractionation factor (0.8‰) from the average $\delta^{34}\text{S}$ value of threadfin shad (10.2‰). The reproducibility of the $\delta^{34}\text{S}$ measurements was 0.3‰ for all samples except for winter cyanobacteria where the reproducibility was 3.0‰ .

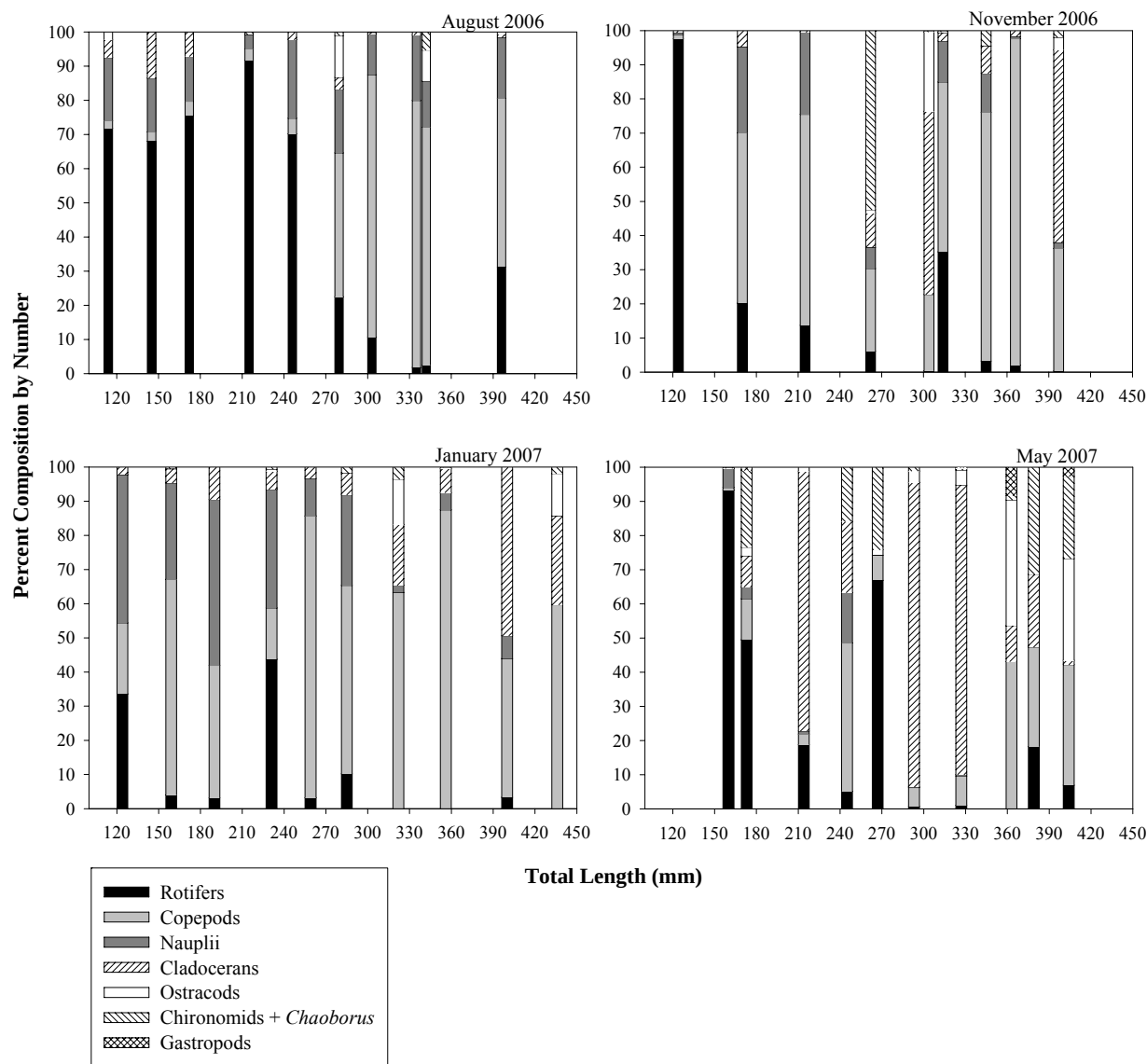


Figure 2-3. Seasonal and ontogenetic variation in percent composition by number of various prey items in foregut (dominant animal taxa only) of gizzard shad from Lake Dora 2006-2007. In November 2006, only nine fish could be analyzed because of the many fish with empty foreguts in the upper size classes.

DISCUSSION

Food preferences and ontogenetic shifts in the diet composition of gizzard shad have been well documented in both field and laboratory studies (e.g., Baker and Schmitz 1971; Heinrichs 1982; Mundahl and Wissing 1988; Dettmers and Stein 1992; Yako et al. 1996). Young gizzard shad (<25-30mm) are obligate planktivores (Heinrichs 1982; Dettmers and Stein 1992), but adopt a bottom-feeding mode when the mouth changes from a supra-terminal to a sub-terminal position and a series of anatomical and histological changes of the digestive system create the option for young shad to feed on benthos (Heinrichs 1982). This probably induces a change in their feeding mechanism as they change from particle feeders to pump filter feeders (Baker and Schmitz, 1971; Drenner et al. 1982). The anatomical change coincides with a diet shift in which zooplankton are replaced by detritus as the major food item (Yako et al. 1996; Schaus et al. 2002). When gizzard shad reach a length of ~60 mm, the diet consists almost entirely of detritus with zooplankton and phytoplankton comprising only a minor fraction (Mundahl 1988; Yako et al. 1996). Such increases in the detrital contribution are more likely to occur when zooplankton abundance is low (Yako et al. 1996).

Our $\delta^{34}\text{S}$ data clearly reflected these ontogenetic changes in the diet of gizzard shad. Larval gizzard shad (spring, Figures 2-2, 2-3) had $\delta^{34}\text{S}$ values that were close to those of zooplankton. After gizzard shad reached a length of 25-30 mm, at which time the mouth position and the digestive system's anatomy and histology change, gizzard shad showed a steep decline in $\delta^{34}\text{S}$ (minimum $\delta^{34}\text{S} = 0.1\text{‰}$), which coincided with the sharp increase in the percentage of detritus (minimum 90%) in the foreguts as reported in literature (Yako et al. 1996).

If detritus is the major sulfur source for gizzard shad in the size range of 100-200 mm, then the sulfur assimilated from the detritus must have a low $\delta^{34}\text{S}$ value. Potential detritus sources in Lake Dora are decaying leaves from riparian macrophytes and organic mud detritus, the latter consisting of a mixture of settled phytoplankton and cyanobacteria and fragmented plant material (Bachmann et al. 2005, Schelske 2006). Riparian macrophytes occasionally had low $\delta^{34}\text{S}$ values (e.g., *P. geminatum*: -1.2‰) suggesting that macrophyte detritus could be an important S source

for gizzard shad. The $\delta^{34}\text{S}$ values of the upper mud in Lake Dora ranged from 9.8‰ to 12.2‰, suggesting that it is an unlikely sulfur source for small gizzard shad. However, the source of light sulfur might come from the microflora associated with mud organic matter. Microflora $\delta^{34}\text{S}$ values have not been measured separately, but indirect evidence of low $\delta^{34}\text{S}$ values exists from the benthic invertebrate $\delta^{34}\text{S}$ values. Indeed, benthic invertebrates can acquire low $\delta^{34}\text{S}$ values when feeding on bacteria that coat the detritus particles (Grey and Deines 2005). Bacterial organic sulfur has low $\delta^{34}\text{S}$ values as a result of the biogenic incorporation of sulfides produced during the dissimilatory sulfate reduction process (Fry 1986; Yamanaka et al. 2003), which typically occurs under anoxic conditions as observed in the bottom mud layer in Lake Dora (personal observation). Benthic invertebrate $\delta^{34}\text{S}$ values in Lake Dora varied between 4.6‰ and 5.1‰. Mud microflora should thus have maximum $\delta^{34}\text{S}$ values of about 5‰, making them a likely contributor to the sulfur assimilated by gizzard shad in the size range of 100-200 mm. Benthic invertebrates are a less likely sulfur source for these gizzard shad. Although the lowest $\delta^{34}\text{S}$ values were observed in August for gizzard shad between 100-200 mm TL, foregut content analyses showed that benthic invertebrates were not an important diet item for gizzard shad in this size range during August (Figure 2-3). The foregut contents also showed a higher content of rotifers in the fish smaller than 300 mm. Most of the rotifers were actually rotifer skeletons from the genus *Keratella* sp. and *Brachionus* sp. which could have been present in the mud detritus.

Gizzard shad showed a gradual increase in $\delta^{34}\text{S}$ with size (Figure 2-1) suggesting a shift in diet composition with an increasing contribution of sulfur assimilated from food sources enriched in ^{34}S . The potential food sources that have high $\delta^{34}\text{S}$ values were mud organic matter, some macrophytes such as *Typha* sp., *Microcystis* and zooplankton (Table 2-1). Phytoplankton (other than *Microcystis*) was occasionally observed in the foreguts, but the $\delta^{34}\text{S}$ value of this potential food source was not determined. The phytoplankton $\delta^{34}\text{S}$ composition is, however, probably similar to that of cyanobacteria and floating macrophytes in Lake Dora (range 7.5‰ - 14‰) because they all use dissolved sulfate (SO_4^{2-}) as a sulfur source.

It is unlikely that an increase in sulfur assimilated from mud organic matter (and not the associated microflora) would cause such a substantial increase in $\delta^{34}\text{S}$, because gizzard shad probably assimilate sulfur mostly from the associated microflora (see above). Indeed, gizzard shad selectively ingest the more nutritious components of the detritus (Mundahl and Wissing 1988). In addition, adult gizzard shad are equally efficient as young gizzard shad in digesting the detritus components (Mundahl and Wissing 1988).

Fresh *Microcystis* (observed as bright green colonies in the foreguts) and phytoplankton were not quantified during the foregut analyses, but did not appear to be a major dietary component for gizzard shad (pers. obs.). Therefore, the increase in $\delta^{34}\text{S}$ with fish size is probably the result of an increase in zooplankton in the diet. Several lines of evidence support this hypothesis. First, sulfur incorporated in the muscle tissue of gizzard shad is most likely derived from animal proteins (McCutchan et al. 2003). Because zooplankton represents a protein rich food source, it is reasonable to assume that zooplankton will have the largest effect on the $\delta^{34}\text{S}$ value of fish muscle tissue. Second, larval gizzard shad were $0.8 \pm 0.3\text{‰}$ enriched relative to zooplankton. Consumers feeding on protein rich food sources tend to discriminate against ^{34}S (positive fractionation factor) during sulfur assimilation (McCutchan et al. 2003). Third, larger gizzard shad showed an increase in the relative proportion of copepods and cladocerans in their diets compared to smaller fish. Zooplankton is preferred as a food source, as indicated by an increase in gizzard shad zooplankton consumption with increasing zooplankton biomass (Schaus et al. 2002). When gizzard shad biomass is high, as in Lake Dora, competition for zooplankton is very likely to exist (Schaus et al. 2002), which could explain why gizzard shad in the size range of 100 – 200 mm rely more heavily on mud detritus as their main sulfur source. Finally, gizzard shad, in the size range of 40-380 mm, showed an increasing dependence on zooplankton in a nearby hypereutrophic and *Microcystis* dominated lake (Lake Apopka, Florida), as evidenced by a gradual increase in $\delta^{15}\text{N}$ with fish size (Gu et al. 1996). Although the $\delta^{34}\text{S}$ data suggest that zooplankton become increasingly important in the diet of larger fish, they do not necessarily imply that large gizzard shad spend more time feeding in the water column. Some zooplankton taxa such as cladocerans of the genus *Alona* sp., which were frequently observed in the stomachs, principally inhabit the littoral zones (Tremel et al. 2000) and zooplankton might migrate up and down the water column during the day. An increase in zooplankton

consumption only suggests that large gizzard shad might spend relatively less time feeding on benthic organisms and therefore contribute less to nutrient release to the water column.

Increased feeding on macrophyte material enriched in ^{34}S (e.g., *Typha* sp.) could also increase the $\delta^{34}\text{S}$ of large gizzard shad. Large plant fragments were more often observed in large gizzard shad than in small ones, but it seems unlikely that the increase in $\delta^{34}\text{S}$ is solely due to an increase in *Typha* consumption. Although *Typha* is one of the most dominant macrophytes along the fringe of Lake Dora, macrophyte biomass is very low at this lake and confined to a narrow and shallow riparian zone. Zooplankton, in contrast, represent a more available source of sulfur because it is more readily digested, has a higher sulfur weight ($0.9 \pm 0.0\%$ versus $0.3 \pm 0.1\%$) and because sulfur is provided as proteins (see above).

Benthic invertebrates (ostracods, chironomid and *Chaoborus larvae* and gastropods) were more often observed in the foreguts of large gizzard shad than in the ones of smaller shad. This suggests that, although large gizzard shad probably consume an increasing amount of zooplankton as they grow larger, they still spend some time feeding directly in the sediments. Although gizzard shad $\delta^{34}\text{S}$ values most likely reflect a diet consisting of a mixture of benthic organisms and mud microflora with low $\delta^{34}\text{S}$ value and zooplankton with high $\delta^{34}\text{S}$ value, they might derive most of their sulfur from zooplankton since the $\delta^{34}\text{S}$ values are closer to those of zooplankton than to those of benthic invertebrates.

Conclusions

Gizzard shad $\delta^{34}\text{S}$ values confirm the ontogenetic changes in the diet composition reported in literature. Larval gizzard shad feed on zooplankton but change to a diet rich in detritus as they grow. In summer, gizzard shad in the 100-200 mm length class probably derive most of their food from the microflora associated with sediment detritus, while larger fish likely spend more time foraging on zooplankton (nauplii, copepods and cladocerans), although their foreguts still contained mainly plant and mud detritus. The size relationship with $\delta^{34}\text{S}$ suggest some size-dependent diet shifts to zooplankton in gizzard shad populations.

Reduction of the gizzard shad biomass can induce a change in feeding behavior in the remaining gizzard shad population from predominantly feeding on detritus to predominantly feeding on zooplankton (Schaus et al. 2002). The harvesting of large gizzard shad (> 200 mm), however does not appear to have induced a switch toward a diet dominated by zooplankton as observed by Schaus et al. (2002). This is most likely because the gizzard shad biomass in lake Dora was only reduced to about 150 kg/ha, which is much higher than the 15 kg/ha reported by Schaus et al. (2002) at which the shift to primarily zooplanktivory should occur. Findings from the present study suggest that competition for zooplankton may still exist, forcing smaller gizzard shad to feed primarily in the benthos. Consequently, gizzard shad in Lake Dora are likely to play an important role in the transfer of nutrients from the sediment to the water column.

CHAPTER 3: A TEST FOR CHANGES IN WATER QUALITY AND MACROZOOPLANKTON FOLLOWING GIZZARD SHAD BIOMANIPULATION

INTRODUCTION

Many studies have documented reductions in phytoplankton biomass following fish removals (Drenner and Hambright 1999) although considerable uncertainty remains regarding the generality of the approach and its mechanisms (DeMelo et al. 1992). Fish biomanipulation typically targets planktivore or benthivore species, and hypothesized mechanisms for changes in phytoplankton may depend on the feeding ecology of target species. Planktivore removals are thought to operate through top-down cascading trophic interactions that increase grazing pressure on phytoplankton due to increased zooplankton biomass following decreased fish predation (Carpenter et al. 1987). Benthivore removals may reduce internal phosphorus loading by decreasing sediment bioturbation and reducing excretion of soluble sediment-derived phosphorus into the water column (Horppila et al. 1998; Vanni et al. 2006).

The utility of fish biomanipulation projects is not well understood for tropical and sub-tropical lakes. The literature suggests that it may be less effective at eliciting changes in phytoplankton via cascading trophic interactions than in temperate lakes (Jeppesen et al. 2005). There are several reasons for this including (1) greater fish richness and niche overlap, (2) predominance of omnivores that can switch to herbivorous or benthivorous feeding after zooplankton are grazed to low levels, (3) smaller size and lower biomass of piscivores, (4) high fish density, particularly of small juvenile fishes, leading to intense, nearly constant grazing pressure on zooplankton, and (5) lack of large zooplankton grazers such as cladocerans due to predation by fish and high densities of invertebrate predators such as *Chaoborus* (Lazzaro et al. 2003; Jeppesen et al. 2005; Jeppesen et al. 2007). Cascading effects on phytoplankton, if achieved, may be short-lived due to the aforementioned compensatory processes (Nagdali and Gupta 2002). However, experimental studies on fish biomanipulation in the tropics and sub-tropics are sparse. Consequently, the efficacy of biomanipulation in these systems remains up for debate.

Here we used a Before-After-Control-Impacts Paired Series (BACIPS) study design to examine four years (2003-2007) of data on water quality and macrozooplankton during the gizzard shad removal at Lake Dora. Gizzard shad can maintain high biomasses (>90% of total fish biomass) in eutrophic lakes during most years by consuming zooplankton when zooplankton are abundant then becoming detritivorous after zooplankton are grazed to low levels (Schaus et al. 2002). This feeding strategy is hypothesized to control food webs through “middle-out” processes whereby overgrazing of zooplankton simultaneously facilitates high phytoplankton biomass and reduces piscivore recruitment via competition for zooplankton (DeVries and Stein 1992). Detritivorous feeding of gizzard shad may also contribute substantially to internal phosphorus loading via bioturbation and translocation of sediment-derived phosphorus and nitrogen to the water column where it is available for phytoplankton (Schaus et al. 1997; Vanni et al. 2006). We tested the hypothesis that gizzard shad removal results in decreased phytoplankton biomass and increased water transparency. We also evaluated macrozooplankton and total phosphorus data to investigate whether changes in phytoplankton, if detected, resulted from changes in macrozooplankton biomass via cascading trophic interactions or from reductions in phosphorus concentrations via reduced bioturbation/phosphorus translocation from the sediments.

METHODS

Study Lakes

We evaluated water quality and macrozooplankton at Lake Dora (impact lake) and Lake Harris (control; Figure 3-1). Eustis was not used because of poor overlap of site locations between SJRWMD and UF sites and the fact that Eustis receives upstream nutrient inputs from Lake Dora. Lake stage is similar between lakes and is controlled at a downstream lock and dam. Stage peaked following several hurricanes in fall 2004 then declined through 2007 during a period of below-average precipitation (Figure 3-2).

Water Quality

Monthly water samples were collected for two years before and two years after biomanipulation (April 2003 to March 2007) at two pelagic locations at each lake (Figure 3-1). Water samples

were analyzed for chlorophyll *a* concentration, Secchi depth, and total phosphorus by the SJRWMD using standard operating procedures of the Florida Department of Environmental Protection (FDEP 2004). Chlorophyll *a* samples were obtained by passing a known volume of water through a 0.7- μm Whatman glass fiber filter, and the concentration ($\mu\text{g L}^{-1}$) was measured with a fluorometer following acetone extraction. Secchi depth was measured at each site to the nearest 0.01 m. Total phosphorus ($\mu\text{g L}^{-1}$) was determined using an Alpkem Flow Solution 3000 analyzer after acid digestion in mercuric sulfate and potassium sulfate and reaction with molybdenum and antimony.

Macrozooplankton

Macrozooplankton samples were collected monthly from April 2003 to March 2007 at two pelagic locations at each lake (Figure 3-1). Macrozooplankton samples from 2003–2004 were collected using a 75- μm mesh Wisconsin-style plankton net. Macrozooplankton samples from 2005–2006 were collected using an 83- μm mesh Wisconsin-style plankton net. The net was towed vertically from ~0.25 m above the sediment-water interface to the surface and depth was recorded. Samples were preserved in 5% buffered formalin solution. Sample preparation and enumeration followed methods described in Tugend and Allen (2000). Macrozooplankton were counted with a compound microscope at 100X magnification and were identified usually to the genus level. Macrozooplankton biomass estimates (dry weight; $\text{dw } \mu\text{g L}^{-1}$) were calculated using published length-weight relationships (McCauley 1984; Culver et al. 1985). Rotifers and nauplii were excluded from all calculations because of the large mesh size. For analyses, macrozooplankton were divided into three groups representing gross divisions in ecological function and taxonomic group: calanoid copepods, cladocerans, and cyclopoid copepods.

Statistical analyses

We evaluated the effects of omnivore removal on phytoplankton biomass (as estimated from Chlorophyll *a* concentration), water transparency (Secchi depth), total phosphorus, and macrozooplankton biomass, using a Before-After-Control-Impact Paired Series (BACIPS) analysis, which tests whether differences between a control and impact site change after an intervention (Stewart-Oaten et al. 1986). Data were divided into two time periods corresponding

to the timing of the initial shad removal: before and including March 2005, and after March 2005. We used the mean of the two sites in each lake to calculate monthly differences (referred to hereafter as deltas) between Lake Dora (impact) and Lake Harris (control). The standard BACIPS analysis uses a *t*-test to evaluate whether the deltas differ between time periods (Stewart-Oaten et al. 1986). We conducted six BACIPS analyses: chlorophyll *a* concentration, Secchi depth, total phosphorus concentration, calanoid copepod biomass, cladoceran biomass, and cyclopoid copepod biomass.

The BACIPS analysis requires that data satisfy four assumptions: additivity of control and impact values, normality of error terms, minimal serial autocorrelation, and homogeneity of variance of control-impact differences between time periods. Cyclopoid copepod biomass and total phosphorus data were $\log_e$ transformed to achieve additivity and the standard BACIPS analysis was carried out on these two variables using Welch's *t*-test to adjust for non-homogeneity of variance. The $\log_e$ transformation also satisfied normality and autocorrelation assumptions. The average effect size was calculated as the difference between mean delta values before and after biomanipulation.

For calanoid copepods, chlorophyll *a*, and Secchi depth, no transformation achieved additivity. Consequently we used the predictive BACIPS approach, which models the impact site as a function of the control site for each time period and requires no additivity assumption (Bence et al. 1996; Osenberg et al. 2006). Akaike's information criterion determined that a linear model with a non-zero intercept would best describe this relationship. Effect size for the predictive BACIPS was calculated for each control value as the difference between before and after model-predicted impact values, and the average effect size was calculated by averaging these differences (Bence et al. 1996). We evaluated statistical significance by determining whether 95% confidence intervals for effect size included zero. Cladoceran biomass was not statistically analyzed because of a lack of temporal variation in Lake Dora densities due to a high proportion of zero biomass values.

RESULTS

Biomanipulation

Commercial fishers removed an estimated 125,000 kg (54 kg/ha) of gizzard shad in 2005 and 135,000 kg (58 kg/ha) in 2006. Depletion analysis estimated an exploitation rate on vulnerable-sized fish of 0.61 (95% confidence interval = 0.42-0.73) in 2005 and 0.46 (95% confidence interval: 0.3-0.63) in 2006. Our age-structured population model estimated a maximum biomass reduction relative to the unfished population of 40% (95% confidence interval: 31-48%) in April 2006, just after the second removal. The average biomass reduction over the entire post-removal time period was 28% (95% confidence interval: 20-37% (see Chapter 1 – *Strength of Biomanipulation*)).

Water Quality

We detected no changes in water quality following biomanipulation and effect sizes were small relative to the magnitude of variation in these variables across months. Chlorophyll *a* ranged from 51.8 to 157.2 $\mu\text{g L}^{-1}$ at Lake Dora and from 19.7 to 92.7 $\mu\text{g L}^{-1}$ at Lake Harris (Figure 3-3). The average effect size was 5.2 $\mu\text{g L}^{-1}$ and the 95% confidence interval included zero across the range of control values (Figure 3-5 and 3-6). Secchi depth ranged from 0.28 to 0.53 m at Lake Dora and from 0.4 to 1.5 m at Lake Harris (Figure 3-3). The average effect size was -0.02 m and the 95% confidence interval included zero across the range of control values (Figure 3-5 and 3-6). Total phosphorus ranged from 36.5 to 88.8 $\mu\text{g L}^{-1}$ at Lake Dora and from 21.0 to 67.5 $\mu\text{g L}^{-1}$ at Lake Harris (Figure 3-3) and the average effect size was 0.03 $\mu\text{g L}^{-1}$ (Table 3-1; $P = 0.67$).

Macrozooplankton

We detected no changes in macrozooplankton biomass ($\text{dw } \mu\text{g L}^{-1}$) following biomanipulation and, similar to water quality variables, average effect sizes were small. Calanoid copepod biomass was highly variable and ranged from 0 to 10.6 $\text{dw } \mu\text{g L}^{-1}$ at Lake Dora and between 0 and 38.9 $\text{dw } \mu\text{g L}^{-1}$ at Lake Harris (Figure 3-4). Average effect size for Calanoid copepods was 13.4 $\text{dw } \mu\text{g L}^{-1}$ and zero was included in the 95% confidence interval across the entire range of control biomass (Table 3-1; Figures 3-5 and 3-6). Cyclopoid biomass ranged from 0.05 to 41.2

dw $\mu\text{g L}^{-1}$ at Lake Dora and from 0 to 30.2 dw $\mu\text{g L}^{-1}$ at Lake Harris (Figure 3-4) and the average effect size was 0.25 dw $\mu\text{g L}^{-1}$ (Table 3-1; $P = 0.38$). Cladoceran densities were near zero at Lake Dora during both time periods and showed no response to biomanipulation (Figure 3-4). Cladoceran densities at Lake Harris exhibited seasonal cycles with peak densities occurring from December to May (Figure 3-4).

Table 3-1. Average effect size for zooplankton and water quality variables collected at Lakes Dora (impact) and Harris (control) for two years before and two years after biomanipulation of gizzard shad. Units of measure, type of data transformation, and type of BACIPS model are given. Cladoceran densities were not statistically analyzed because densities lacked temporal contrast at the impact lake, which resulted in violations of model assumptions. Effect sizes for analyses on log transformed data were back transformed. No effect sizes were statistically significant at $\alpha = 0.05$.

Variable	Units	Data	BACIPS Model	Average Effect Size
calanoid copepod	dw $\mu\text{g L}^{-1}$	untransformed	predictive	13.4
cladoceran	dw $\mu\text{g L}^{-1}$	untransformed	NA	NA
cyclopoid copepod	dw $\mu\text{g L}^{-1}$	$\log_e$ transformed	standard	0.25
chlorophyll <i>a</i>	$\mu\text{g L}^{-1}$	untransformed	predictive	5.2
secchi	m	untransformed	predictive	-0.02
total phosphorus	$\mu\text{g L}^{-1}$	$\log_e$ transformed	standard	0.03

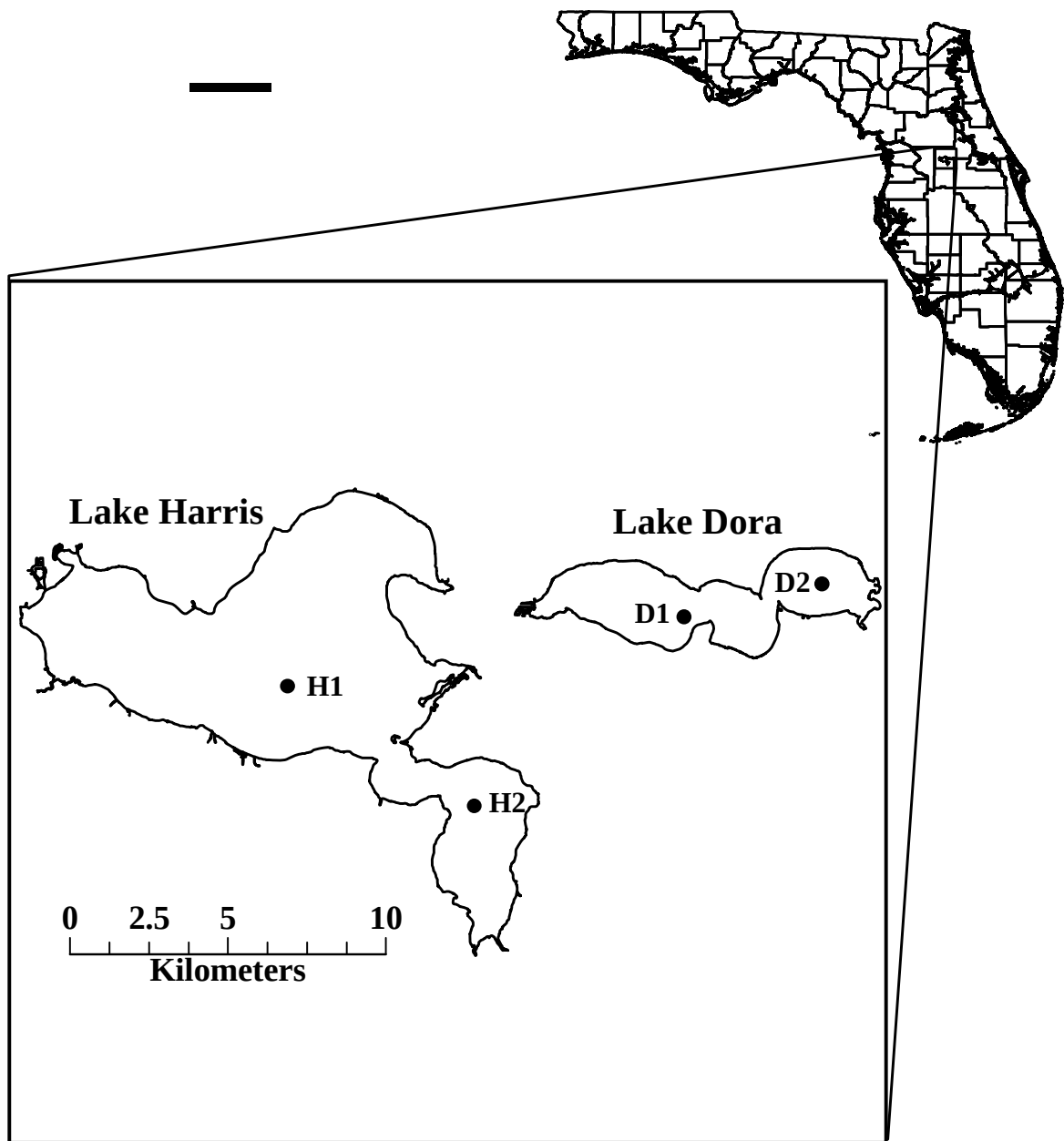


Figure 3-1. Map of the Harris-Chain-of-Lakes showing the locations of sampling sites at Lake Dora (experimental lake) and Lake Harris (control lake). The inset map shows the location of the Harris Chain in Florida, USA.

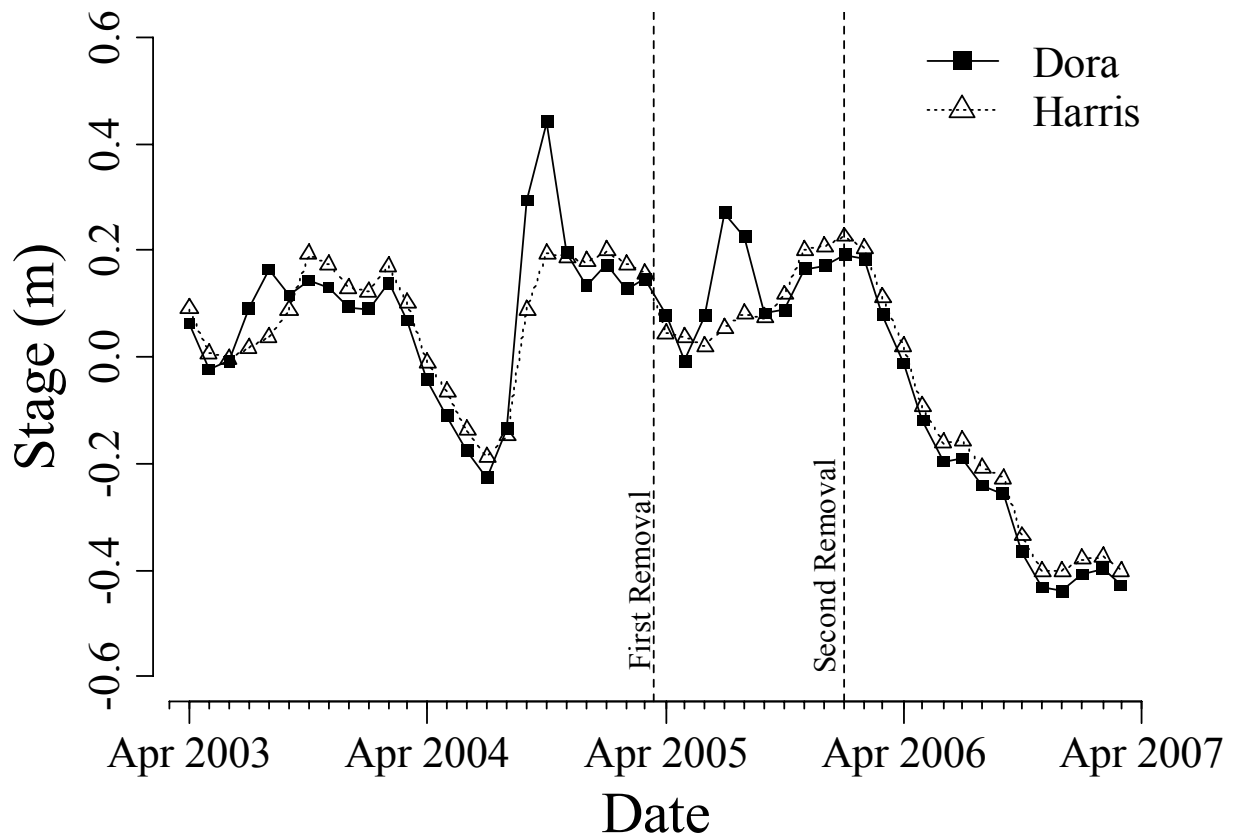


Figure 3-2. Seasonal patterns of lake stage relative to the average at Lake Dora (solid line) and Lake Harris (dashed line) from April 2003 to March 2007. Vertical dashed lines indicate the timing of gizzard shad removals.

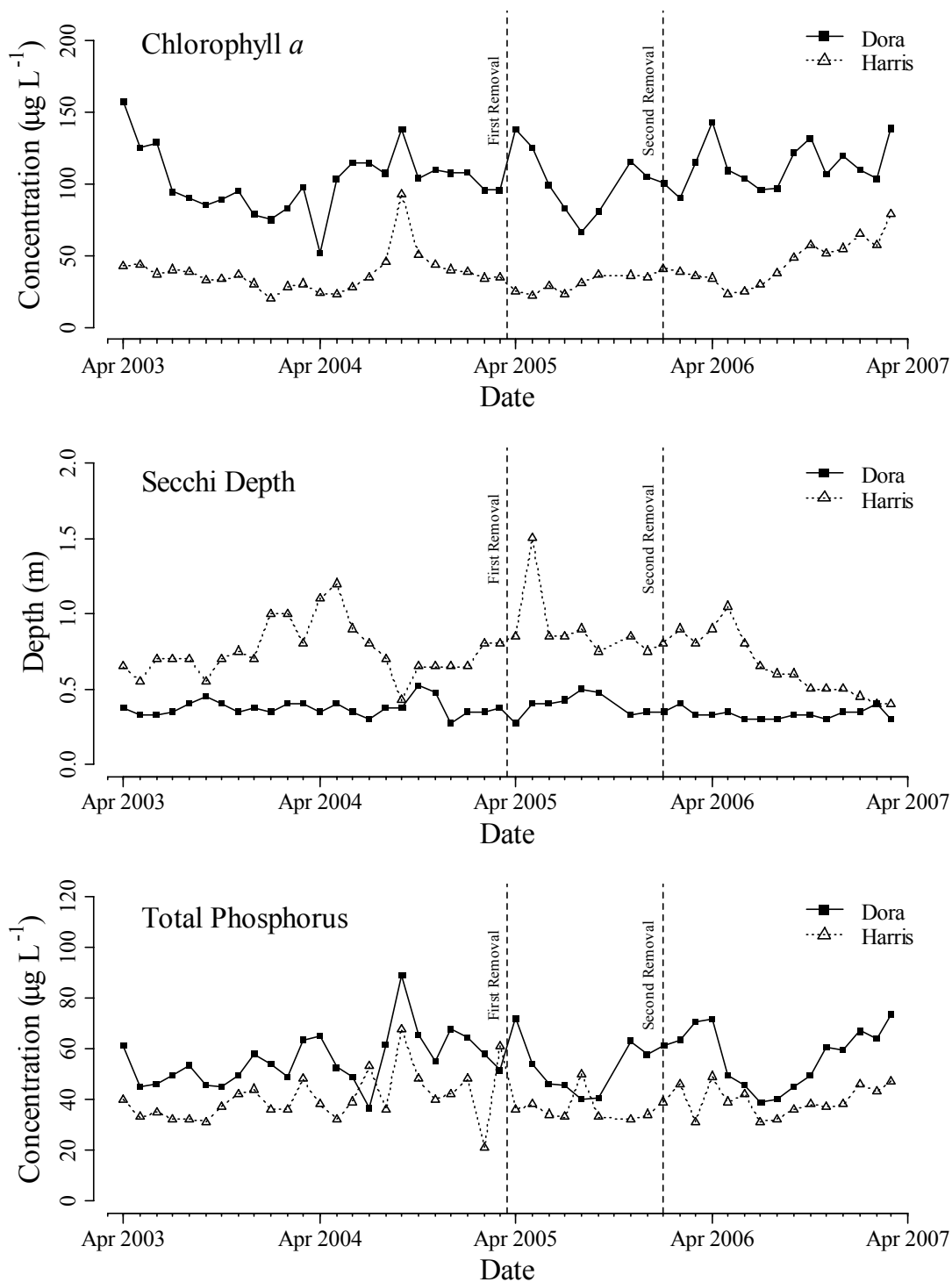


Figure 3-3. Mean monthly chlorophyll *a* concentration ($\mu\text{g L}^{-1}$; upper), Secchi depth (m; middle), and total phosphorus concentration ($\mu\text{g L}^{-1}$; lower) at Lake Dora (experimental lake; solid line) and Lake Harris (control lake; dashed line) from April 2003 to March 2007. Data represent average values from two sites per lake that were samples once per month by the St. Johns Water Management District, Palatka, Florida USA. Chlorophyll *a* and total phosphorus concentrations were analyzed according to standard laboratory procedures of the Florida Department of Environmental Protection (FDEP 2004). Vertical dashed lines indicate the timing of gizzard shad removals.

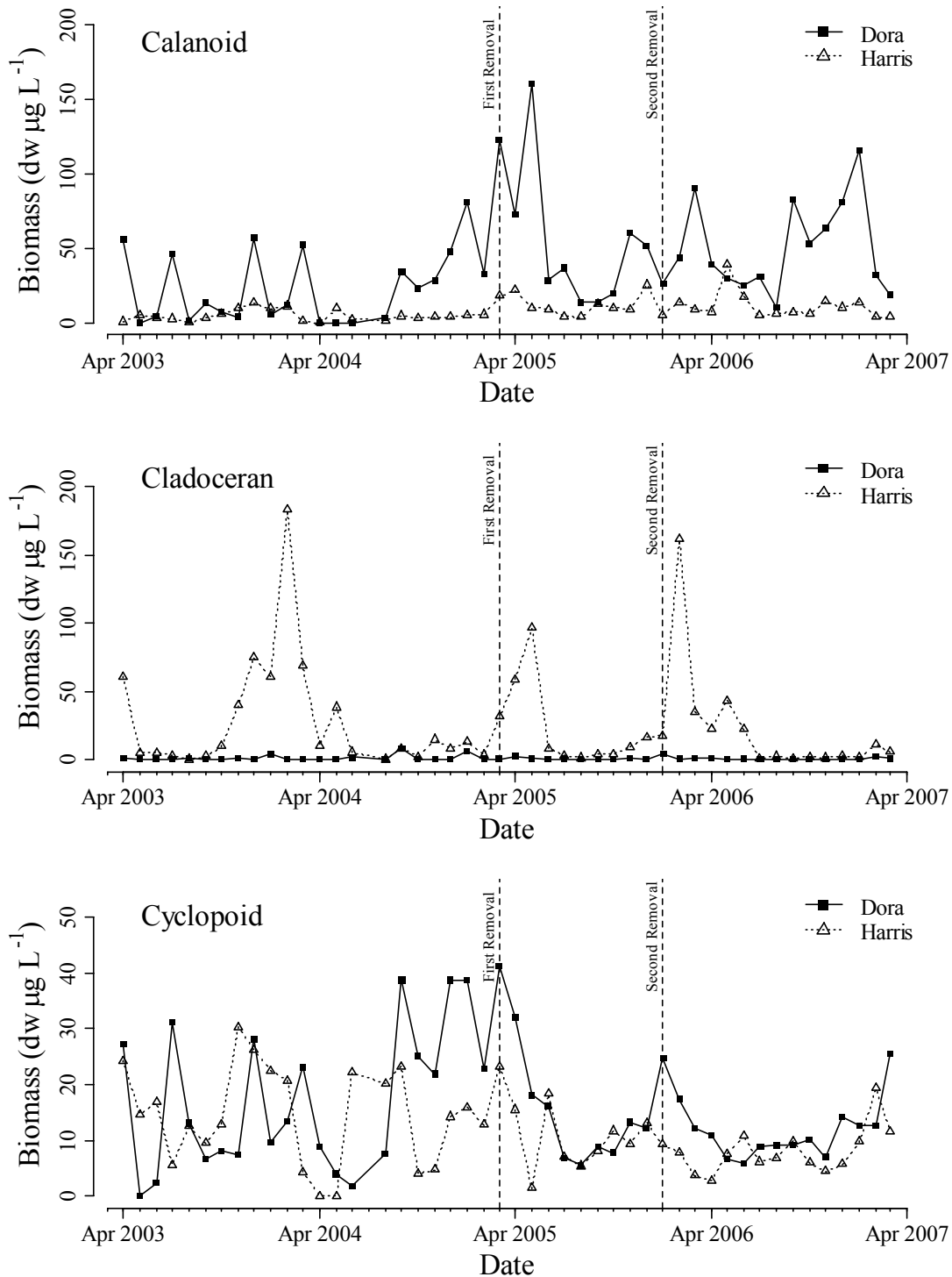


Figure 3-4. Mean monthly biomass (dw $\mu\text{g L}^{-1}$) of calanoid copepods (upper), cladocerans (middle), and cyclopoid copepods (lower) at Lake Dora (experimental lake; solid line) and Lake Harris (control lake; dashed line) from April 2003 to March 2007. Data represent average values from two sites per lake that were samples once per month by vertical tows with a 75 μm (2003-2004) and 83 μm (2005-2007) mesh net. Vertical dashed lines indicate the timing of gizzard shad removals.

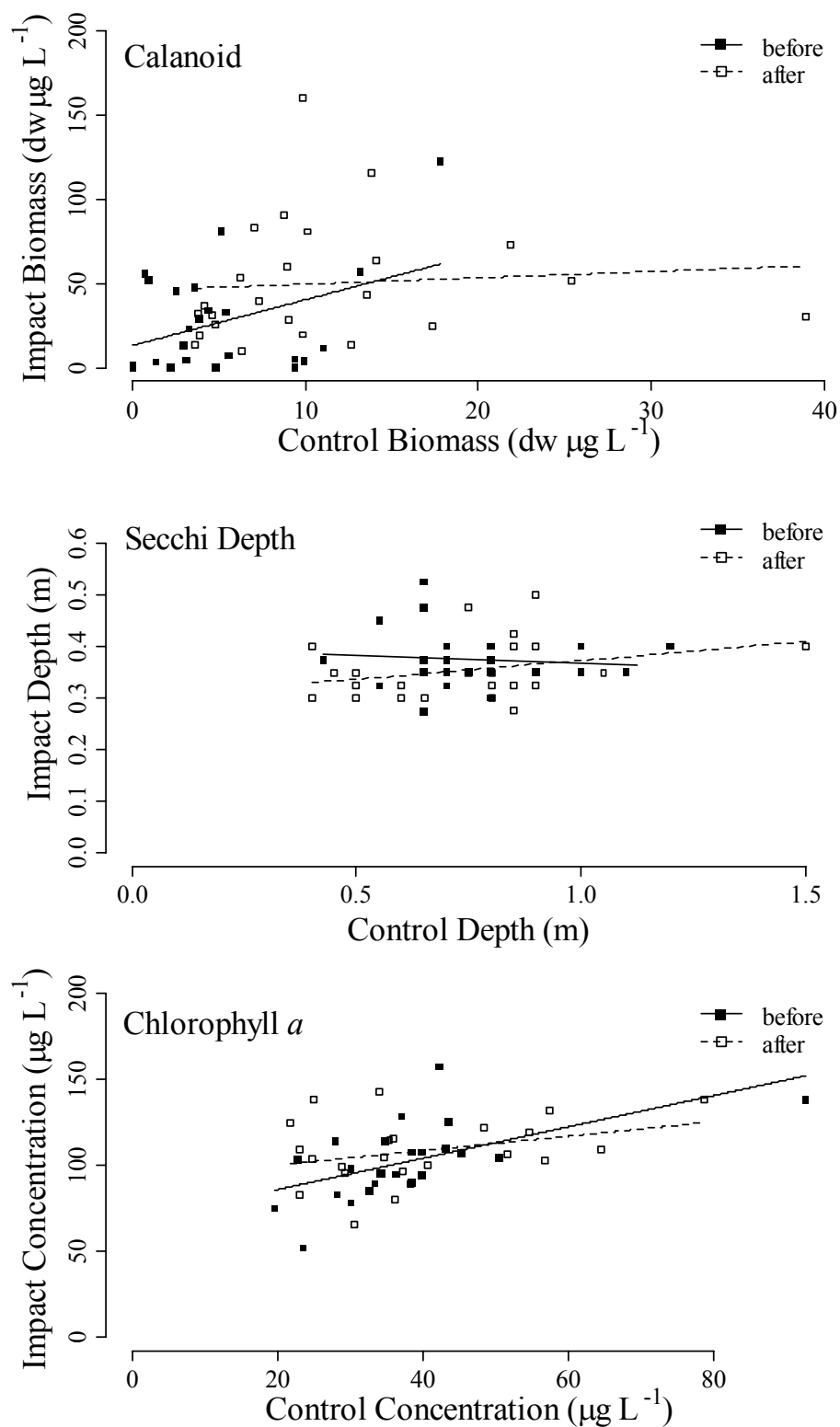


Figure 3-5. Scatterplots of monthly impact (Lake Dora) values as a function of control (Lake Harris) values for three variables analyzed with the predictive BACIPS model. The lines represent the least squares regression model fit to the data from before (solid line) and after (dashed line) gizzard shad removal.

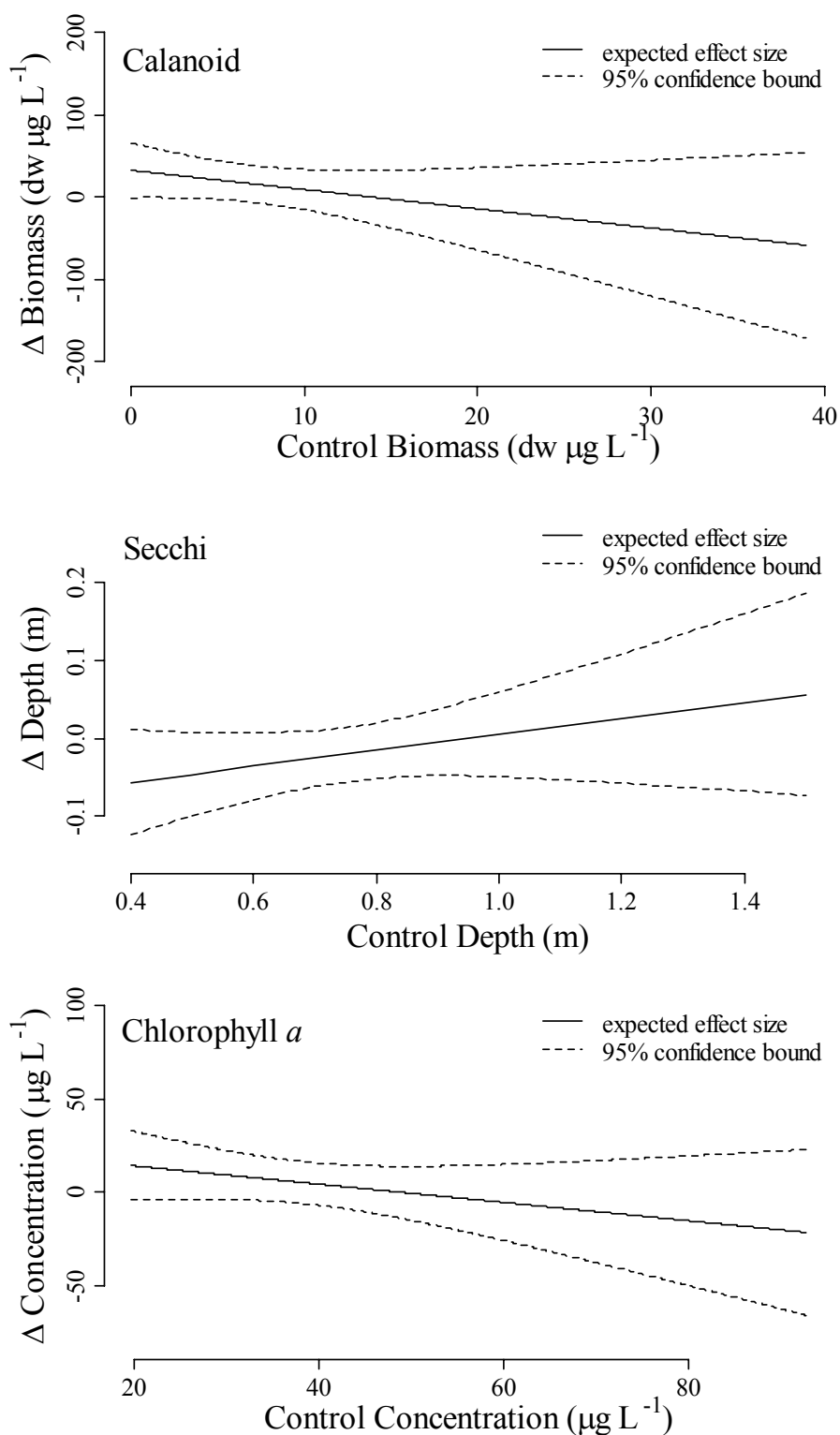


Figure 3-6. Effect sizes (delta; solid line) and 95% confidence intervals (dashed lines) from predictive BACIPS models for calanoid copepod biomass ($\text{dw } \mu\text{g L}^{-1}$; upper), Secchi depth (m; middle) and chlorophyll *a* concentration $\mu\text{g L}^{-1}$; lower) that predict the impact (Lake Dora) value as a function of the control (Lake Harris) value. Analyses were considered statistically significant if zero fell outside the 95% confidence intervals.

DISCUSSION

We detected no changes in water quality and macrozooplankton biomass following partial omnivore removal at Lake Dora. This finding differs from the many examples of reduced phytoplankton biomass following fish biomanipulation (Hansson et al. 1998; Drenner and Hambright 1999). However, Kim and DeVries (2000) evaluated a whole-lake removal of gizzard shad at Walker County Lake, USA, a shallow eutrophic south-temperate lake. They detected no changes in phytoplankton biomass following biomanipulation despite drastically reduced larval gizzard shad densities and increased zooplankton biomass. Kim and DeVries (2000) concluded that the classic trophic cascade paradigm of strong zooplankton-phytoplankton linkages did not apply due to high lake productivity and the absence of large herbivorous daphnids.

Studies of biomanipulations in subtropical lakes are rare, but there are a few notable examples. At Lake Denham, Florida, USA, a one time fish removal of approximately 85% of the total rough fish biomass left seasonal dynamics of zooplankton unchanged yet resulted in increased total abundances of three primary herbivorous zooplankton taxa (Beaver et al. unpublished report). Nagdali and Gupta (2002) reported decreased phytoplankton biomass and increased zooplankton biomass following mass-mortality of *G. affinis* at Lake Naini Tal, India. Their study indicates that trophic linkages among fish, zooplankton, and phytoplankton can be strong in some subtropical systems, but they also documented a rapid return to the pre-manipulation state within three months after the mortality event. Starling et al. (2002) reported reduced total phosphorus and chlorophyll *a* following mass mortality of omnivorous *Oreochromis niloticus* at Lago Paranoá, Brasil. They did not find changes in zooplankton biomass, suggesting that *O. niloticus* stimulated phytoplankton growth via bottom-up internal phosphorus loading and recycling. These two studies suggest that fish biomanipulation can reduce phytoplankton biomass through either top-down or bottom-up mechanisms in tropical lakes, but that the duration of the effect may be short due to compensatory processes.

Cascading trophic interactions are strongest in lakes with relatively simple trophic structure (Carpenter et al. 1987). Tropical and subtropical lakes, in contrast, have complex food webs

with omnivorous species, niche redundancy, and many organisms undergoing ontogenetic diet shifts (Blanco et al. 2003; Jeppesen et al. 2005; Jeppesen et al. 2007). These complexities may buffer top-down biomanipulation effects (Lazzaro et al. 2003; Jeppesen et al. 2005). Moreover, these systems have few large cladocerans that are capable of exerting top-down control on phytoplankton. Researchers have hypothesized that the lack of these species in subtropical lakes could be due to intense fish predation. Our data suggest that large adult gizzard shad are not likely to control macrozooplankton communities at Lake Dora. Rather, Lakes Dora and Harris have complex food webs containing a congeneric planktivore threadfin shad, which feeds primarily in the water column and has a protracted spawning period leading to sustained high larval and juvenile fish densities relative to gizzard shad (University of Florida, unpublished data). Moreover, larval and juvenile gizzard shad which were invulnerable to removal, feed on macrozooplankton and phytoplankton in the water column before undergoing an ontogenetic diet shift to benthivory. In such a system, zooplankton may be controlled by threadfin shad and larval/juvenile gizzard shad rather than by adult gizzard shad. Perhaps future biomanipulation studies in subtropical systems should consider trophic guilds as biomanipulation targets and should also understand the potential compensatory effects of ontogenetic diets shifts by target species.

Another possible explanation for weak top-down zooplankton control at Lake Dora is that macrozooplankton are controlled by some factor other than fish biomanipulation. For example, cladoceran grazing rates are strongly affected by phytoplankton species composition due to interference by inedible filamentous species (Gliwicz and Lampert 1990). Lakes of a higher trophic state tend to have higher densities of large inedible phytoplankton, which results in fewer cladoceran grazers and a higher abundance of copepods. Recall that cladocerans showed seasonal peaks in biomass at Lake Harris, but not at Lake Dora. Lake Dora has much higher nutrient and phytoplankton densities than Lake Harris, which could lead to less efficient cladoceran grazing due to interference by inedible phytoplankton particles. Thus, cladoceran populations at Lake Dora could be controlled by bottom-up effects of nutrient levels that affect phytoplankton biomass and species composition.

Gizzard shad contribute to internal phosphorus loading in eutrophic lakes through bioturbation and translocation of soluble sediment-derived phosphorus directly into the water column where it is highly available for phytoplankton (Drenner et al. 1996; Schaus et al. 1997; Vanni et al. 2006). This has been supported by mesocosm experiments and whole-lake studies (Schaus and Vanni 2000; Gido 2002). Thus we expected gizzard shad removal to reduce water column phosphorus and chlorophyll *a*. Our results suggest that either 1) these effects are not likely via gizzard shad removal in Florida lakes, or 2) the biomass reduction was not enough to elicit a response in the phytoplankton community or total phosphorus concentrations. Although gizzard shad clearly contribute to internal phosphorus loads in eutrophic lakes, the magnitude of this loading relative to external inputs, sediment fluxes, and wind resuspension is unknown. We suggest that these other phosphorus loads substantially exceeded those attributable to gizzard shad harvest at Lake Dora. Surficial sediments at Lake Dora are primarily unconsolidated flocculent organics that are easily resuspended during wind events and may contribute substantially to internal phosphorus loading via remineralization in the water column (Danek et al. 1991). Sediment fluxes may also likely contribute to water column total phosphorus concentrations in the presence of an anoxic sediment-water interface, high sulfur concentrations, and low flux of iron oxyhydroxides (Katsev et al. 2006).

The strength of the biomanipulation should be a key consideration in studies of fish biomass reductions. Planktivore biomass reductions must usually exceed 75% to achieve decreases in phytoplankton biomass through cascading trophic interactions because biomanipulation effects are often dampened at lower trophic levels (Hansson et al. 1998; Meijer et al. 1999). However, little information exists on reduction targets for benthivorous and omnivorous fish in subtropical lakes. Biomass reduction thresholds for these species may be less than for planktivores because benthivore/omnivores act as a bottom-up nutrient load that may affect phytoplankton biomass more directly than top down effects mediated by intermediary zooplankton grazing.

Nevertheless, biomass reductions for benthivores and omnivores should be substantial to elicit ecosystem responses. In our study, biomanipulation achieved a maximum biomass reduction of about 40%. Perhaps a greater biomass reduction would have elicited a phytoplankton response. Jeppesen et al. (2005) inferred that biomass reductions may need to be greater in tropical and subtropical lakes due to additional compensatory mechanisms not found in temperate lakes,

which suggests that the biomanipulation at Lake Dora may not have been strong enough. Another possibility is that the biomass reduction was of sufficient magnitude but was not carried out for enough years to elicit a phytoplankton response. However, the duration of the manipulation and the length of the post-manipulation period at Lake Dora was similar to many other published fish biomanipulation studies in which significant changes in phytoplankton biomass were detected (Drenner & Hambright, 1999).

This study was one of the first experimental evaluations of biomanipulation in subtropical lakes. Our results demonstrate that ~40% biomass reduction was not enough to cause cascading interactions that will reduce algae concentrations and improve water clarity. Future experiments should attempt to achieve higher biomass reductions when evaluating the potential impacts of biomanipulations on eutrophic subtropical lakes. Manipulating more than one species of zooplanktivore accompanied with large reductions in fish biomass should be explored to evaluate the potential value of biomanipulation as a management tool in subtropical systems.

CHAPTER 4: EFFECTS OF COMMERCIAL GILL NET BYCATCH ON THE BLACK CRAPPIE FISHERY AT LAKE DORA, FLORIDA

INTRODUCTION

Bycatch, the incidental catch of non-target species with fishing gear, occurs in almost all commercial fisheries, and has become a central resource management concern throughout the world (Diamond et al. 2000; Crowder and Murawski 1998; Pikitch et al. 1998). Many studies have attempted to assess total bycatch in commercial fisheries (Hale et al. 1981; Hale et al. 1983; Renfro et al. 1989; Hale et al. 1996; Clark and Hare 1998; Pikitch et al. 1998; Stein et al. 2004), assess mortality of incidental bycatch (Hale et al. 1981; Hale et al. 1983; Clark and Hare 1998; Belda and Sanchez 2001; Beerkircher et al. 2002; Stein et al. 2004), and ultimately address population-level effects (Crouse et al. 1987; Mangel 1993; Crowder et al. 1994; Caswell et al. 1998; Diamond et al. 1999; Diamond et al. 2000; Tuck et al. 2001; Majluf et al. 2002). Prior to 1998, hypotheses about population-level impacts rarely had been tested (Crowder and Murawski 1998) and Diamond et al. (2000) noted that population-level effects of bycatch have been difficult to quantify.

Observations made on commercial fishing vessels have estimated the proportion of total landings made up of bycatch and bycatch initial mortality rates (Hale et al. 1981; Hale et al. 1983; Hale et al. 1996; Clark and Hare 1998; Pikitch et al. 1998; Beerkircher et al. 2002; Stein et al. 2004). Hale et al. (1983) observed pound net fishing operations in the St. Johns River, Florida, and estimated game fish total bycatch and initial mortality with estimates of fishing effort, area fished, and game fish catch rate. Pikitch et al. (1998) used on-board observer data to estimate bycatch of Pacific halibut *Hippoglossus stenolepis* in Washington, Oregon, and California bottom trawl fisheries to test differences in catch rates of trawl types and time of year. Stein et al. (2004) tested for differences in total bycatch and mortality of Atlantic sturgeon *Acipenser oxyrinchus* among three gear types (trawl and two gill nets). Beerkircher et al. (2002) quantified shark bycatch by species and initial mortality rates in the Southeast United States pelagic longline fishery with nine years of fisheries observer data.

Onboard observations can provide useful information for measuring the proportion of total landings made up of bycatch and can provide estimates of initial mortality due to fishing.

Total bycatch mortality includes initial mortality occurring as part of the capture process and secondary mortality, which occurs following release from fishing gear. Initial mortality is most often calculated directly onboard as part of observer programs, whereas secondary mortality is estimated via pen studies or tagging programs. Total bycatch mortality is difficult to measure due to the long observation periods required after fish capture. Total mortality may result from chronic effects such as injury or infection, or increased vulnerability to predation (Crowder and Murawski 1998). Crowder and Murawski (1998) argued that secondary and total mortality should be considered in bycatch management, and appropriate survival studies should be conducted.

Total bycatch and bycatch mortality estimates provide useful information to aid in optimizing gear choice, fishing areas, and fishing seasons, but these estimates alone do not quantify population effects of bycatch. Catch of non-target species in fisheries can have implications at the population level (Crowder and Murawski 1998), and there are concerns about impacts to fish populations (Murray et al. 1992) and marine fauna such as sea turtles, seabirds, sharks, and mammals (Lewison et al. 2004). Methods to determine the population impacts of bycatch typically involve field estimates and population modeling. Age-and-stage-structured modeling techniques have been applied successfully to examine bycatch population implications for a variety of species including sea turtles (Crouse et al. 1987; Crowder et al. 1994), wandering albatross *Diomedea exulans* (Tuck et al. 2001), humpback penguins *Spheniscus humboldti* (Majluf et al. 2002), right whale dolphins *Lissodelphis borealis* (Mangel 1993), and harbor porpoises *Phocoena phocoena* (Caswell et al. 1998). Diamond et al. (1999) explored the population level effects of catch and bycatch on Atlantic croaker *Micropogonias undulatus* in the Gulf of Mexico and the Atlantic Ocean.

Lake Dora was recently selected by Florida resource management agencies for a whole-lake gizzard shad reduction experiment via intensive commercial fishing with gill nets. Gizzard shad are an omnivorous fish with the potential to influence lake nutrient cycling. Gizzard

shad can greatly reduce large crustacean zooplankton density (DeVries and Stein 1992; Stein et al. 1995) and can also consume benthic detritus when zooplankton resources are low (Stein et al. 1995; Irwin et al. 2003). Density and biomass of gizzard shad increase with trophic state, and gizzard shad often occupy the majority of total fish biomass in hypereutrophic systems (Bachmann et al. 1996; Allen et al. 2000). Because gizzard shad have the potential to influence zooplankton abundance and influence nutrient cycling between the sediment and the water column (Schaus and Vanni 2000; Schaus et al. 2002; Gido 2003), gizzard shad at Lake Dora were targeted for removal.

Gill nets are size selective and not species specific; thus, adult sport fish bycatch associated with the commercial gill net fishery for gizzard shad at Lake Dora is of concern to state agency scientists and anglers. Black crappie provide some of the most popular sport fisheries throughout North America (Hooe 1991; Allen and Miranda 1998) and represent the primary recreational fishery on Lake Dora, Florida (Benton 2005). Bycatch of black crappie is of concern to lake managers because significant bycatch mortality could have deleterious impacts on recreational fisheries. Thus, there is a need to evaluate whether bycatch could influence black crappie fisheries, which would elucidate policy trade-offs between potential benefits of gizzard shad removal and impacts of commercial gill net bycatch on recreational fisheries.

The objectives of this chapter were to (1) estimate total black crappie bycatch in commercial gill nets, (2) estimate bycatch mortality (initial and secondary) from commercial gill nets on black crappie, (3) assess recreational fishing effort and harvest of black crappie, and (4) address population-level effects that bycatch could have on the black crappie fishery at Lake Dora. We assessed the population-level impacts of black crappie bycatch from the gizzard shad gill net fishery at Lake Dora, Florida by investigating the potential for recruitment overfishing via a stock reduction analysis (SRA) model and evaluating the potential for growth overfishing with a yield-per-recruit model. Growth overfishing occurs when fish are being harvested at an average size that is less than the size that produces maximum yield per recruit, and usually results from excessive effort and a selectivity schedule where small fish are vulnerable to harvest and not allowed to reach their maximum growth potential.

Recruitment overfishing occurs when fishing mortality rates are so high that the adult population does not have the reproductive capacity to replace itself. Recruitment overfishing is less common than growth overfishing but is of serious concern because it can lead to stock depletion and collapse. If selectivity schedules are skewed towards larger fish that have passed the age at sexual maturity, recruitment overfishing may occur where growth overfishing is not a concern.

METHODS

Commercial Fishing

Permits were issued by the Florida Fish and Wildlife Conservation Commission (FWC) for 28 commercial fishers to remove gizzard shad from Lake Dora in 2005 and 2006. The fishery was regulated in an effort to minimize bycatch mortality as much as possible with the following restrictions. A maximum of two gill nets, not to total more than 1,097 meters could be used simultaneously by each boat, and gill net specifications were a minimum stretch mesh size of 10.2 cm (4.0 inches). The maximum allowable length of one net was 549 meters, and nets were allowed 2 hours maximum soak time. There was no restriction on the maximum number of nets fished daily, as long as all other guidelines were followed. Floating and sinking gill nets were used. Commercial fishing was allowed only during daylight hours in open water areas at least 90 meters from shore during open seasons. Commercial fishers harvested gizzard shad, Florida gar *Lepisosteus platyrhincus*, longnose gar *Lepisosteus osseus*, blue tilapia *Oreochromis aurea*, and the nonnative sailfin catfish *Liposarcus multiradiatus*. All other fish species caught in gill nets were required to be returned to the water immediately after removal from the nets.

Total Bycatch Assessment

Gill net operations during the gizzard shad removal were monitored by St. Johns River Water Management District (SJRWMD) observers. Monitoring was conducted at least twice per week during the commercial seasons and consisted of random observations of gill net fishing operations. Observers reported catch numbers, species composition, mesh size, net type (floating or sinking), and net length. An observation day consisted of at least six gill net sets. If there was no commercial gill net activity or weather prohibited observations, an attempt was made to

average 12 gill net set observations per week and two sampling days per week over a one-month period. Subsamples of crappie bycatch were measured for total length weekly until a maximum of 100 fish was recorded each month. The first four weeks of fishing in 2006 required increased monitoring as follows; observations were conducted at least three days per week, at least 18 gill net sets were observed per week, and all black crappie encountered were measured until a maximum of 200 were recorded. The SJRWMD was required to follow these methods set forth in the sampling permit for the shad removal project issued by FWC.

Bycatch Mortality

To evaluate bycatch mortality of black crappie we collected fish from commercial fishing vessels as gill nets were being retrieved in both years. After black crappie were removed from gill nets by commercial fishers, we transferred the fish to a research vessel where they were measured to the nearest mm TL and placed in a 190 liter cooler with aerators used to maintain dissolved oxygen levels over 5 mg/L. Dissolved oxygen levels were recorded in the cooler to assure that they exceeded 5 mg/L at all times. Any initial mortality of fish from gill nets was recorded. We considered a fish to be alive when the net was pulled if there was opercular movement (Kwak and Henry 1995). We recorded gill net mesh size and style (sinking or floating) for each sample fish were collected from.

We estimated secondary mortality of black crappie entangled in gill nets. Secondary mortality has been effectively measured for largemouth bass in live-release tournaments (Schramm et al. 1987; Kwak and Henry 1995; Weathers and Newman 1997; Neal and Lopez-Clayton 2001; Edwards et al. 2004) using pens to hold fish that were captured during hook-and-line tournaments. Holding time ranged from two to 21 days (Schramm et al. 1987; Kwak and Henry 1995; Weathers and Newman 1997; Neal and Lopez-Clayton 2001; Edwards et al. 2004), and Edwards et al. (2004) considered the three-day observation period adequate compared to other studies. Secondary mortality was measured using replicates of fish held in pens for 72 hours.

After fish were collected from the commercial fishers, they were transported to holding pens placed in the lake. The pens used were large hoop nets measuring 4.57 meters long, 1.22 meter

diameter, and 50.8 mm stretch mesh nylon. A total of four hoop nets were used, and the nets were placed in three meters of water on a hard sand substrate bottom and marked with University of Florida research buoys. All net replicates were performed in the same area of Lake Dora during both commercial seasons. A minimum of 10 and maximum of 20 fish were placed in each pen. If a minimum of 10 fish could not be collected within 30 minutes of net pull time with the fishers, any fish that had been collected were transported to the pens to avoid further stress. All fish exhibiting opercular movement were placed in the pens for measures of secondary mortality. After the 72 hour treatment all fish were released, and any dead fish were measured to the nearest mm TL. Consistent with Hale et al. (1981) and Hale et al. (1983), we considered a fish to be dead if it was unable to swim away after 72 hours.

Pollock and Pine (2007) recognized the need for control replications in assessing delayed mortality for catch and release studies. It is not possible to obtain an unbiased estimate of fish captured in gill nets alone unless one assumes that there is no handling mortality (Pollock and Pine 2007). This is most likely not a reasonable assumption, hence control fish are necessary to account for handling mortality. Control fish were collected via electrofishing and hoop net gear during the 2006 season. Replicates of control fish placed in pens were used to account for potential mortality effects from transporting and holding fish. The same methods were applied during replications of control fish as described for treatment replications.

Water temperature and dissolved oxygen are critical factors influencing secondary mortality of fishes (Schramm et al. 1987; Gallinat et al. 1997; Weathers and Newman 1997; Wilde et al. 2000; Edwards et al. 2004). A temperature logger was placed at our pen holding site to record temperature every four hours during the course of the experiment. Dissolved oxygen (mg/L) was also measured each time a pen was set and retrieved, and in 2006 a dissolved oxygen logger was placed at my pen holding site to record dissolved oxygen levels every four hours during the course of the experiment to measure oxygen levels throughout the 72-hour treatment period.

Recreational Fishing Effort and Harvest

Roving creel surveys were conducted by the FWC on Lake Dora from November 2004 to June 2005, November 2005 to May 2006, and November 2006 to March 2007, respectively (three fishing seasons) to measure angling effort, harvest, and catch rates. Each survey was conducted on ten randomly selected days (six weekdays and four weekend days) for each 28-day period (Benton 2005). Using a randomly selected time, lake section, and direction of travel on each sample day, a clerk completed a survey of the entire lake by taking an instantaneous count of all anglers actively fishing on the lake to determine fishing effort (man-hour) (Benton 2005). The clerk also interviewed anglers about their target species (if any species were specified by the angler), the number of each species caught, and how much time was spent fishing to determine fishing success (fish/hour) (Benton 2005). Catch from the angler interviews was extrapolated to angler effort estimates from the instantaneous counts to estimate total harvest at each lake in both years (Malvestuto et al. 1978; Malvestuto 1996; Benton 2005). Measurements of TL were recorded for a subsample of the black crappie catches during the three survey periods.

Tagging Study

A tagging study was conducted in 2006 for a direct estimate of exploitation from the recreational fishery (μ_{rec}). Lake Dora was divided into four areas and an approximately equal number of fish were tagged in each area. Fish were collected for tagging with a boat electrofisher, hoop nets, and an otter trawl. All fish captured were measured to the nearest mm TL, and fish 230 mm TL and greater were tagged and released into approximately the same area they were captured. Although there was no minimum size limit in place, we assumed that all fish 230 mm TL and greater had recruited to the fishery based on creel survey data.

All black crappie were tagged with dart tags with a yellow streamer containing information specifying the tag specific identification number, monetary reward value, and return address. Tags were inserted into the body of the fish below the dorsal fin rays using a hollow needle. When injected the streamer of each tag extended in a posterior direction at a 45° angle to the body. All black crappie were tagged from November 2005 to January 2006 to obtain an estimate of exploitation for the 2006 fishing season. All fish were single tagged with either a standard tag

(\$5) or a higher value reward tag (\$50). The tagging reward study allowed for estimates of reporting rates (described below).

Age and Growth

Age and growth of black crappie at Lake Dora was estimated using fish collected from the recreational fishery from January through March 2005 to 2007, which is when black crappie angling effort peaks (Benton 2005; FWC 2005). Lake Dora has numerous fish camps where anglers clean harvested fish daily and these camps were the source of fish for age samples. Collecting recreationally harvested fish is an efficient way to gather age information and has been utilized for many marine species (Potts et al. 1998; Potts and Manooch 1999; Patterson et al. 2001; Fischer et al. 2004; Fischer et al. 2005), although like all sampling gears is subject to size and age selectivity.

Coolers with ice were placed at fish cleaning stations at three camps. Information signs were also posted at the fish cleaning stations explaining the purpose of the project. Some anglers may fish multiple lakes on a given day and thus, we asked anglers not to donate black crappie if they had fished more than one lake in an effort to assure all black crappie ages represented the correct population. Coolers were left for two to three days before retrieval. All black crappie collected from recreational anglers were brought back to the lab where they were measured to the nearest mm TL and sagittal otoliths were removed from ten randomly selected fish for each centimeter group. Because fish larger than 330 mm TL were rare, all black crappie greater than this size were aged.

Ages of fish collected from the recreational fishery were determined by counting annuli on whole otoliths with the aid of a dissecting microscope. The use of otoliths to determine ages of black crappie has been verified (Hammers and Miranda 1991; Ross et al. 2005). Two independent readers aged each fish. Schramm and Doerzbacher (1982) found that black crappie have relatively thin otoliths that had clearly visible bands present in patterns expected for annual marks. Older fish (fish showing four or more opaque bands) have thicker otoliths, and therefore are more likely to have bands masked in whole view (Schramm and Doerzbacher 1982). Thus,

any otoliths showing four or more opaque bands, and any otolith disagreements from whole view readings were sectioned for verification of aging accuracy. One otolith was sectioned transversally using a South Bay Technology, Inc. low speed diamond wheel saw. Two transverse sections, 0.5 mm wide, were cut from each otolith and mounted on a labeled glass slide using ThermoShandon Synthetic Mountant for reading. Two independent readers used a dissecting microscope to read the sections. A third independent reader reexamined all disagreements and the majority reading was recorded as number of annuli. Not all black crappie form new opaque bands on their otoliths at the same time during spring, although opaque bands on otoliths from all age classes should be formed by June 1st in Florida (Schramm and Doerzbacher 1982). We used an arbitrary birth date of June 1st, so that all fish collected prior to June 1st were assigned ages corresponding to the number of annuli observed plus one.

ANALYSES

Total Bycatch Assessment

We obtained estimates of total black crappie bycatch from the commercial fishery using a stratified sampling design (see Krebs 1999). Onboard observer data were stratified into three time strata (A, B, and C) for both commercial fishing seasons. The strata represented periods of high, moderate, and low fishing effort, and were grouped such that the variance of bycatch observed was homogeneous within and heterogeneous among strata. The total bycatch estimate and variance on this total were determined using the equations for a stratified design from Pollock et al. (1994):

$$\hat{X}_{ST} = N\bar{X}_{ST} \quad (4-1)$$

$$VAR(\hat{X}_{ST}) = N_h^2 \times VAR(\bar{X}_{ST}) \quad (4-2)$$

where,

$\hat{X}_{ST}$ = total bycatch estimate,

N = number of total possible fishing days in a season,

$\bar{X}_{ST}$ = stratified bycatch mean per fishing day.

h = stratum number (A, B, C)

and,

N_h = total possible fishing days in stratum

Bycatch Mortality

We measured the mortality rate for each pen replication in each year as the number of dead black crappie observed per pen divided by the total number of black crappie held in each pen. We then estimated the annual mean bycatch mortality rate as the average mortality rate across all replications for each year, with uncertainty expressed as the standard error around the yearly means. Mean and variance were also estimated for control replications.

We used the annual mean bycatch mortality rate multiplied by our estimate of total bycatch for black crappie in each year to achieve total commercial fishing mortality of black crappie by year given by the equation:

$$GD = GC \times GM \quad (4-3)$$

where,

GD = estimated total number of black crappie that died from gill net mortality,

GC = estimated total number of black crappie caught by gill nets,

and,

GM = total gill net mortality rate.

Recreational Fishing Effort and Harvest

All data were entered and analyzed in a creel survey analysis program (Larry Connor, FWC, personal communication) and were stored in a Microsoft Access[®] database on an FWC regional server (Benton 2005). Data was lost overboard from one 28-day period in 2006. We approximated the missing time period in 2006 using the percentage of effort for that period during 2005, assuming that the percentage of effort during that period in 2005 would serve as the best model to reconstruct the missing data in 2006.

Tagging Study

Tag returns were adjusted for tag-related mortality, tag loss, and non-reporting prior to estimating exploitation. We assumed 5 – 10% tagging mortality and tag loss for all black

crappie tagged. Reporting rates of higher value reward tags (\$50) in 2006 were estimated based on a linear-logistic model created by Nichols et al. (1991):

$$\lambda_H = \frac{e^{(-0.0045+0.0283(H))}}{(1 + e^{(-0.0045+0.0283(H))})} \quad (4-4)$$

where,

H = the dollar value of higher value reward tags,

and,

λ_H = the reporting rate of tags from higher reward value fish.

The reward values (H) were converted from 2006 standards to the 1988 monetary equivalents based on the Consumer Price Index. The 1988 monetary equivalents used in equation 4-4 were \$30.29 for \$50 rewards (U.S. Department of Labor 2006). Reporting rate estimates calculated from equation 4-4 were most precise at higher reward values (Nichols et al. 1991) and thus, we used equation 4-4 to estimate reporting rates of high-reward tag fish and then estimated the reporting rate of standard tags based on the assumption that all tagged fish had an equal probability of recapture regardless of reward value. Alternate methods for estimating reporting rate, such as those presented in Taylor et al. (2006) assume 100% reporting rate of higher value tags in order to estimate the reporting rate of standard tags. We felt that a \$50 tag value was not sufficient to make the assumption that all higher value reward tags were returned.

We estimated the total number of high value reward tag fish caught in 2006 using the equation:

$$\hat{C}_H = \frac{R_H}{\lambda_H} \quad (4-5)$$

where,

$\hat{C}_H$ = estimated number of higher value reward tag fish caught,

and,

R_H = total number of tags returned in 2006 from fish tagged with a higher reward value.

We assumed that standard tags and higher reward value tags had an equal probability of capture by anglers and estimated the total number of standard tag fish caught in 2006 using the ratio:

$$\frac{\hat{C}_H}{T_H} = \frac{\hat{C}_S}{T_S} \quad (4-6)$$

where,

S = the dollar value of a fish tagged with a standard tag,

$\hat{C}_S$ = estimated number of standard tag fish caught,

T_S = original number of fish tagged with standard reward tags,

and,

T_H = original number of fish tagged with higher value reward tags.

We estimated the reporting rates of standard reward tags (\$5) in 2006 using the equation

$$\lambda_S = \frac{R_S}{\hat{C}_S} \quad (4-7)$$

Reporting rate estimates for high-value reward tags were varied to evaluate how uncertainty in λ_H would influence the exploitation rate.

Estimates of exploitation for the recreation fishery (μ_{REC}) were estimated using the equation:

$$\mu_{REC} = \frac{(\hat{C}_S + \hat{C}_H)}{(T_S \times 1 - (TM + TL)) + (T_H \times 1 - (TM + TL))} \quad (4-8)$$

where TM = tagging mortality and TL = tag loss.

The instantaneous rate of fishing mortality for the recreational fishery (F_{rec}) was estimated using the equation:

$$F_{REC} = -LN(1 - \mu_{REC}) \quad (4-9)$$

Estimates of exploitation for the commercial fishery (μ_{COM}) could not be obtained directly from tagging data because a reliable reporting rate could not be calculated. There was evidence that

vulnerability with fish size to gill nets was similar to recreational angling, but commercial fishers had an incentive not to return tags. Thus, we were unable to use Nichol's equation to estimate commercial reporting rate. To estimate commercial exploitation we first estimated the vulnerable black crappie population size with the equation:

$$\hat{N} = \frac{C_{REC}}{\mu_{REC}} \quad (4-10)$$

where,

$\hat{N}$ = the number of vulnerable black crappie in the population,

and,

C_{REC} = recreational catch from creel survey data.

We estimated the exploitation rate from the commercial fishery (μ_{COM}) as:

$$\mu_{com} = \frac{GD}{\hat{N}} \quad (4-11)$$

The instantaneous fishing mortality for the commercial fishery (F_{com}) was estimated as:

$$F_{com} = -LN(1 - \mu_{COM}) \quad (4-12)$$

We simulated changes in F_{COM} by changing the gill net mortality rate (GM), which changed the number of black crappie that died from gill nets (GD). The instantaneous fishing mortality for the commercial and recreational fisheries were estimated with varying levels of reporting rates, tag loss, tagging mortality, recreational catch, and total gill net bycatch mortality to evaluate uncertainty in F values for a range of input parameters.

Age and Growth

Data collected from the recreational fishery (carcasses and creel) was used to estimate growth rates for black crappie. We created an age-length key from a subsample of black crappie aged from recreationally harvested carcasses and assigned an age to each individual from the entire sample of carcasses and the recreational creel measurements in order to obtain age and size structure of the population. Mean-length-at-age (MLA) and its associated variance (σ^2) were

found by equations for fixed-length subsamples presented by DeVries and Frie (1996). We used the Von Bertalanffy growth model (Ricker 1975) to describe growth rates. Von Bertalanffy parameter estimates (L_{∞} , K , and t_0) were obtained using Procedure NLIN (SAS 9.1).

Population-Level Impacts of Exploitation

We used Microsoft Excel® to construct a stock reduction analysis (SRA) with stochastic recruitment (see Walters et al. 2006) in order to evaluate the potential of recruitment overfishing occurring at varying exploitation rates. The SRA approach is to construct an age-structured population dynamics model that consists of leading parameters (e.g., B_0 and $recK$ in this study) that describe the underlying production and carrying capacity and subtract known removals from the population over time (Walters et al. 2006). When leading parameter estimates produce a stock size that is too low to have sustained historical catches, the model predicts that the population should have disappeared prior to today (Walters et al. 2006). When leading parameters estimates produce a stock size that is too high, it predicts too little fishing impact and a current population size that is much too large to fit recent estimates (Walters et al. 2006).

The SRA reconstructed the historic stock size of black crappie in order to match model predicted estimates of exploitation and vulnerable biomass in 2006 to empirical estimates of exploitation and vulnerable biomass in 2006, given estimates of the leading parameters B_0 and $recK$.

Typically the leading parameter B_0 is a measure of vulnerable biomass in the unfished condition. However, in this study B_0 represents an estimate of vulnerable biomass far enough back in time to achieve a stable age distribution in the simulated population prior to this study (2005). The leading parameter $recK$ is the Goodyear recruitment compensation ratio (Goodyear 1980) and is a measure of the juvenile survival at extremely low stock size relative to juvenile survival in the unfished condition. The parameter $recK$ examines relationships between maximum recruitment at low stock size and the density dependence of recruitment at high stock size or the unfished condition (Goodwin et al. 2006). The two leading parameters are correlated in the sense that a lower B_0 and higher $recK$ can produce the same stock size as a higher B_0 and lower $recK$. SRA models often have an exorbitant amount of combinations of B_0 and $recK$ that can explain the same stock size. The best combination of $recK$ and B_0 chosen must be supported statistically and biologically so that the parameter estimates are logical.

Our empirical estimate of vulnerable biomass in 2006 in the fished condition was estimated as the vulnerable biomass per acre times the surface area (acres) of Lakes Dora and Beauclair combined. Vulnerable biomass per acre was estimated as the vulnerable number of black crappie per acre ($\frac{\hat{N}}{\text{acres}}$) times the average weight of a vulnerable black crappie, where the average weight of a vulnerable black crappie was estimated using a standard weight equation for black crappie (Anderson and Neumann 1996) with an average length of vulnerable black crappie harvested in 2006 (given from carcass and creel measurements). Our empirical estimate of exploitation in 2006 was estimated for the recreational and commercial fisheries using equations 4-8 and 4-11, respectively.

We solved for my leading parameters (Bo and $recK$) by fitting the model predicted values of vulnerable biomass and exploitation in 2006 to empirical estimates in 2006 given by the log likelihood of the lognormal distribution:

$$MLE = -\ln((\ln(06predu_{total}) - \ln(06estu_{total}))^2 + (\ln(06estVB) - \ln(06predVB))^2) \quad (4-13)$$

where,

MLE = the maximum likelihood estimate,

$06predu_{total}$ = 2006 model predicted estimate of total exploitation,

$06estu_{total}$ = 2006 empirical estimate of total exploitation,

$06estVB$ = 2006 empirical estimate of vulnerable biomass (kg),

and,

$06predVB$ = 2006 model predicted estimate of vulnerable biomass (kg).

We used Excel® table function to construct a maximum likelihood profile for a range of Bo and $recK$ values that made sense biologically in order to determine combinations of parameter estimates that were supported statistically. Considering a review of maximum reproductive rates of fish at low population sizes by Myers et al. (1999), black crappie most likely have a $recK$ value between five and 20 based on fish species with similar life history characteristics. Estimates of Bo were considered from 70,000 to 100,000 kg, which were supported by our empirical estimates of adult fish density and fishing mortality rates.

When solving for leading parameter estimates, our model was very sensitive to starting values because of the correlation between leading parameters and multiple possible combinations. Thus, we were not able to solve for Bo and $recK$ simultaneously. This phenomenon is very common in SRA model fitting. Therefore, we fixed Bo and solved for $recK$, because Bo exhibited much less variability than $recK$ in the maximum likelihood profile and we had data for black crappie at Lake Dora that supported our estimate. Once reasonable parameter estimates were obtained the model was used to predict how the black crappie stock would respond in the future under different scenarios of exploitation. The output metrics of interest were vulnerable biomass (kg), total harvest (numbers) and weighted transitional spawning potential ratio (SPR).

The SRA required estimates of mean length-at-age, weight-at-age, fishing and natural mortalities, fecundity, and a vulnerability to harvest schedule in order to function. Fishing mortalities were separated into F_{REC} and F_{COM} , as described above. Estimates of total length-at-age were obtained from the Von Bertalanffy growth model and age specific weight was calculated using a standard weight equation for black crappie (Anderson and Neumann 1996). Equal vulnerability schedules were assumed for the recreational and commercial fisheries, based on the length frequencies from the recreational and commercial fisheries. Vulnerabilities at age were estimated using a cumulative normal distribution, which predicted expected catches at age in a yield-per-recruit model simulation that approximated the observed age structure of the catch. Fecundity was calculated as the weight at age minus weight at maturity (W_{mat}). Walters et al. (2007) noted that fecundity is typically proportional to body weight above the weight at maturity. Weight at maturity was assumed to be the weight predicted at age 2, given that black crappie mature at approximately age 2 in this system (FWC 2005).

Survivorship at age in the unfished condition ($Survivorship\theta_a$) was calculated as survivorship in the previous year multiplied by survivorship in the absence of fishing (S_0). The instantaneous rate of natural mortality (M) was assumed to be 0.4 for all simulations, which is similar to values found in a review of black crappies (*Pomoxis spp.*) from Allen et al. (1998). Survival from natural mortality was found by $S_0 = e^{-M}$. Survivorship at age a in the fished condition ($SurvivorshipF_a$) was calculated as:

$$SurvivorshipF_a = SurvivorshipF_{a-1} \times S_0 \times (1 - \mu_{total} \times vul_{a-1}) \quad (4-14)$$

where survivorship at age one was assumed to be 1, the first age in the model.

Expected numbers were assumed to change over a ages and t years according to the survival equation (Walters et al. 2006):

$$N_{a+1,t+1} = N_{a,t} \times S_0 \times (1 - vul_{a,t} \times u_{total,t}) \quad (4-15)$$

We used an accounting scheme with 8 ages from 1961 – 2050 ($N = 90$). Expected numbers at age in the initial year were calculated as:

$$N_{a,t=1} = R_0 \times \sum_a survivorship0 \quad (4-16)$$

where R_0 is the recruitment abundance in the unfished condition estimated as:

$$R_0 = \frac{B_0}{\Phi_{vb0}} \quad (4-17)$$

The Botsford incidence function for vulnerable biomass per recruit in the unfished condition was calculated as (Box 3.1, Walters and Martell 2004):

$$\Phi VB_0 = \sum_a wt_a, vul_a, survivorship0_a \quad (4-18)$$

Vulnerable biomass was determined annually with the equation:

$$\hat{B}_t = \sum_a N_{a,t}, vul_a, wt_a \quad (4-19)$$

The model required exploitation ($\mu_{total,t}$) and recruitment time series for all years after 1961. For each year the total exploitation rate was estimated as:

$$\mu_{total,t} = \frac{HARV_{total,t}}{\sum_a N_{a,t} vul_a} \quad (4-20)$$

Total harvest was estimated from historical creel data from 1977 to 1981 and from creel and commercial landings data in 2005 and 2006. Logical estimates of total harvest were simulated for the remaining years from 1961 to 2006. For future projections, estimates of exploitation were assumed under different fishing scenarios and total harvest estimates were calculated as:

$$HARV_{total} = \hat{N} \times \mu_{total,t} \quad (4-21)$$

This allowed the model to explore a range of assumed exploitation rates in the future and determine the expected vulnerable biomass, total harvest, and SPR given an exploitation rate.

Recruitment rates were predicted from estimates of annual egg production (E_t) as:

$$E_t = \sum_a N_{a,t} \cdot fec_a \quad (4-22)$$

using a Beverton and Holt stock-recruit relationship with recruitment variability of the form of the relationship (Walters et al. 2006):

$$N_{1,t+1} = \frac{\alpha E_t}{1 + \beta E_t} \times rand_t \quad (4-23)$$

where the alpha and beta Beverton and Holt parameters are described by the relationships:

$$\alpha = recK \times \frac{R_0}{E_0} \quad (4-24)$$

$$\beta = \frac{recK - 1}{E_0} \quad (4-25)$$

Variability around recruitment at time t ($rand_t$) was accounted for with a random number that was determined with PopTools in Microsoft Excel® by using a log normal distribution with a mean of 1.0 and recruitment coefficient of variation of 0.4. Allen (1997) observed black crappie recruitment coefficient of variation values ranging from 0.55 to 0.84 for 6 populations in Southeast and Midwest reservoirs, but there is evidence that recruitment variation in this system is considerably lower based on age-0 black crappie catch rates in bottom trawls (M. Hale, FWC, unpublished data).

Recruitment variability was added to the model simulations for future projections once estimates of the leading parameters were obtained via equation 4-13 in order to explore how abundance, catch, and spawning potential ratio varied through time with different exploitation rates. A weighted transitional SPR was used as a biological reference point to investigate the potential for recruitment overfishing at various exploitation scenarios. A weighted transitional SPR allows fishing mortality to vary by age and year and accounts for changes in the numbers at age over years. The SPR was estimated with the equation:

$$SPR_{t+1,2,3...89} = \frac{\sum_a N_{a,t+1,2,3...89} fec_a}{\sum_a N_{a,t=1} fec_a} \quad (4-26)$$

We determined the uncertainty in the terminal year SPR (2050) by using Monte Carlo analysis with 1,000 iterations to determine a terminal year mean SPR and 95% confidence limits around the mean. The same methods were applied to total harvest and vulnerable biomass estimates. We also used Monte Carlo analysis with 100 iterations to determine mean annual SPR values and 95% confidence intervals for the entire model time series to show how the SPR would be expected to vary with variation in recruitment.

Future projections were simulated from 2007 through the terminal year 2050 under three exploitation scenarios; (1) $\mu_{total} = 0.42$, (2) $\mu_{total} = 0.51$, and (3) $\mu_{total} = 0.60$. Exploitation scenario one was chosen because it was the empirical estimate of μ_{rec} in 2006, scenario two was chosen because it was the empirical estimate of μ_{total} in 2006 and scenario three was chosen as an arbitrary increase in exploitation either due to recreational fishing, bycatch mortality, or both. The model simulations examined the three different exploitation scenarios and the implications they have on black crappie abundance, total harvest, and SPR if they were sustained through the terminal year 2050.

In order to investigate the potential for growth overfishing, we constructed a yield-per-recruit model in Excel®. Yield-per-recruit (kg) was determined as:

$$YPR = \Phi VB_F \times u_{total} \quad (2-27)$$

where,

The Botsford incidence function for vulnerable biomass per recruit in the fished condition (ΦVB_F) was calculated as (Box 3.1, Walters and Martell 2004):

$$\Phi VB_F = \sum_a wt_a, vul_a, survivorship F_a \quad (4-28)$$

To investigate if growth overfishing was a concern we used Excel® table function to profile YPR values at total exploitation (μ_{total}) scenarios ranging from 0.2 to 1.0.

RESULTS

Commercial Fishing

Commercial fishing occurred from March 1 to April 22, 2005 and from January 3 to March 28, 2006. Fishing was not permitted until March 1, 2005 because pre-harvest data were being collected for the gizzard shad population. Generally, there were two permitted fishermen per fishing vessel; there was a maximum of 16 vessels and a minimum of 1 vessel per fishing day during the 2005 and 2006 commercial fishing seasons. Total commercial effort was 258 boat days in 2005 and 251 boat days in 2006 (Figure 4-1) with an average of six boats per fishing day in 2005 and five boats per fishing day in 2006.

Total Bycatch Assessment

Black crappie bycatch was higher in 2006 than 2005 (Table 4-1). For 2005, there were a total of 487 black crappie observed during gill net operations, 294 in stratum A (March 1 to March 14), 156 in stratum B (March 15 to Mar 31), and 37 in stratum C (April 1 to April 22). The average total daily bycatch per stratum ($\bar{x}_h$) was 595, 488, and 26 for strata A, B, and C, respectively.

The total bycatch estimate ($\hat{X}_{ST}$) for 2005 was 17,199 black crappie and the 95% confidence intervals were 8,777 to 25,622. For 2006, there were a total of 2,109 black crappie observed during gill net operations, 1,375 in stratum A (January 3 to January 31), 545 in stratum B (February 1 to February 28), and 189 in stratum C (March 1 to March 28). The average total daily bycatch per stratum was 979, 498, and 265 for strata A, B, and C, respectively. The total bycatch estimate ($\hat{X}_{ST}$) for 2006 was 30,258 black crappie, and the 95% confidence intervals were 19,048 to 41,469. Total daily bycatch of black crappie is reported in Figure 4-1 for days with onboard observer data in 2005 and 2006.

Bycatch Mortality

We conducted 17 pen replications from March 1 to April 8 during the 2005 commercial gill net season, and 23 pen replications from January 3 to March 15 during the 2006 season. Six control replications were made with fish caught in hoop nets, and four pen replications were made with

fish caught with electrofishing gear in 2006 from January 13 to January 29. In 2005, bycatch mortality rates ranged from 0 to 0.75 during the treatment period with a mean of 0.31 (GM_{2005}) and a standard error of 0.06. In 2006, bycatch mortality rates ranged from 0.05 to 1 during the treatment period with a mean of 0.47 (GM_{2006}) and a standard error of 0.07. In 2006, control replications of fish collected with hoop nets ($N = 6$) ranged in mortality from 0 to 0.35 during the treatment period with a mean of 0.10 and a standard error of 0.05; control replications of fish collected with electrofishing gear ($N = 4$) had zero mortality. Results are summarized in Table 4-2. Estimates of bycatch mortality were not adjusted for pen related mortality due to low mortality estimates from control replicates.

We combined the mortality estimation and total bycatch estimates to estimate the number of black crappie deaths via bycatch each year. The estimated mean number of black crappie that died from gill net mortality in 2005 (GD_{2005}) was 5,332 with a range from 2,194 to 9,480 considering the range in estimates of GM and GC . The mean number of bycatch deaths in 2006 (GD_{2006}) was estimated at 14,221 with a range of 7,619 to 22,393 given the range in estimates in GM and GC .

Recreational Fishing Effort and Harvest

Comparison of the existing creel survey data at the lake suggest that recreational fishing effort and harvest have increased at Lake Dora. The annual fishing effort for black crappie at Lake Dora historically (survey data from 1977 to 1981) ranged from 14,208 to 26,233 hours constituting 25 to 39% of total angling effort (Benton 2005), and catch ranged from 16,603 to 41,745 black crappie per year (Benton 2005). The current surveys were only during the peak fishing season from November 2004 to June 2005, November 2005 to May 2006, and November 2006 to March 2007. Directed black crappie effort ranged from approximately 27,000 to 29,000 hours and harvest ranged from about 32,000 to 39,000 from 2004/2005 through 2006/2007 (Figure 4-2). Black crappie angling effort accounted for 80 to 94% of the total fishing effort for the three survey periods. No standard error could be calculated for the estimates from the 2005/2006 survey period because of missing data for one 28-day period that was estimated by substituting the mean value of fishing effort from the same time period the previous year.

Tagging Study

Tagging was conducted from November 3, 2005 to January 13, 2006 during sixteen sampling trips at Lakes Dora and Beauclair. A total of 514 black crappie were single-tagged with standard and higher reward floy tags, 197 fish were captured with electrofishing gear (38%), 214 fish were captured with hoop nets (42%), and the remaining 105 fish were captured with an otter trawl (20%). Totals of 125, 118, 133, and 132 fish were tagged in areas 1 through 4, respectively (tagging location of six fish were not recorded). A total of 413 black crappie were tagged with \$5 standard reward tags and 101 black crappie were tagged with \$50 higher-value reward tags.

A total of 69 tags were returned, 40 \$5 tags (10% of available \$5 reward tags – 34 from recreational anglers and six from commercial fishers) and 29 \$50 tags (29% of available \$50 reward tags – 27 from recreational anglers and two from commercial fishers); recreational anglers accounted for 88% of total tag returns (61 of 69 returns) and commercial fishermen only accounted for 12% of total tag returns (8 of 69 returns). All tags were recaptured from December 7, 2005 to April 7, 2006, and recapture location was obtained from 55 of the 69 returned tags. We received six returns from area 1 (11%), nine returns from area 2 (16%), nine returns from area 3 (16%), 23 returns from area 4 (42%), and eight returns from outside our study area in adjoining canals (15%). Although 15% percent of tag returns were from outside the study area in adjoining canals, all canals had locks that prevented fish escapement from the system.

Estimates of exploitation for the recreational fishery included adjustments for tag loss, tagging mortality, and reporting rate. Tag loss and tagging mortality were simulated at values from 5 to 10%. We assumed 5% tag loss and tagging mortality for the average estimate of exploitation for model simulations; Miranda et al. (2003) estimated tag loss for black and white black crappie to be 4.6% within 24 hours of tagging using t-bar tags, and there was a significant effect of time on tag loss. Henry (2003) estimated tag loss for largemouth bass to be approximately 5% using dart tags. We felt that 5% tag loss was a reasonable estimate, based on the short amount of time between tagging and recaptures and results from other studies. Miranda et al. (2003) estimated tagging mortality for black and white black crappie to be 11% (SE = 7.2%) for fish captured with electrofishing gear and trap nets. Henry (2003) estimated tagging mortality for largemouth bass

to be 0% for fish collected with electrofishing gear and hook-and-line. Results from control replications of black crappie greater than 230 mm TL captured with hoop nets and electrofishing gear on Lake Dora (not tagged) had a mortality rate of 10% and 0%, respectively, and control replicates of black crappie greater than 180 mm TL captured with an otter trawl (pelvic fin clip) at Lake Jeffords, Florida had a mortality rate of 1% (G. Binion, UF, unpublished data). We felt that 5% tagging mortality was a reasonable estimate, based on our control replications of fish captured with hoop nets, an otter trawl, and electrofishing gear, and results from similar studies. The expected reporting rate of tags from higher value reward tag fish (λ_H) was 70% ($H = \$50$) based on equation 4-4, and the expected reporting rate of standard tags was 22% based on equation 4-7 (Table 4-3).

The recreational exploitation rate (μ_{REC}) was 42% ($TM = 0.05$, $TL = 0.05$, $\lambda_H = 0.7$) and the instantaneous rate of fishing mortality for the recreational fishery (F_{rec}) was 0.55. The commercial exploitation rate (μ_{COM}) was 16%, and the instantaneous rate of fishing mortality for the commercial fishery (F_{com}) was 0.17. We simulated a range of higher value reward tag reporting rates from 0.5 to 1.0 by intervals of 0.1 and tag loss/tagging mortality from 5 to 10% to analyze the effects of reporting rate on exploitation (Table 4-3). Lower reporting rates and higher tag loss/tagging mortality increase estimates of recreational exploitation and higher reporting rates and lower tag loss/tagging mortality decrease estimates of recreational exploitation. We simulated a range of the total number of black crappie that died from gill net mortality in 2006 (GD_{2006}) from 7,000 to 22,000, and the number of black crappie harvested in the recreational fishery in 2006 from 25,000 to 39,000 to evaluate effects on the instantaneous rate of fishing mortality for the commercial fishery (F_{com}). As expected, F_{com} values were highest at low recreational catch and high gill net deaths, and lowest at high recreational catch and low gill net deaths.

Age and Growth

A total of 882, 664, and 723 black crappie were collected and measured from the recreational fishery (whole sample – carcasses and creel) in 2005, 2006, and 2007, respectively. Sub-samples of carcasses ($N = 183$, 158, and 153 in 2005, 2006, and 2007) ranging from approximately 18 to 37 cm TL were analyzed to determine age annually. The size and age frequencies from the

recreational catch (whole sample) in 2005, 2006, and 2007 are reported in Figures 4-3 and 4-4. Ages ranged from 2 to 8 years old for all three years. Mean length-at-age and associated variance and growth for the whole sample for each year were determined. Mean length-at-age and growth were similar for black crappie in all years. Results from 2006 were used in model simulations and are reported in Figure 4-5. Ages were applied to 145 and 362 black crappie collected from the commercial gill net fishery in 2005 and 2006, respectively. The size and age frequencies from the commercial bycatch in 2005 and 2006 are shown in Figures 4-3 and 4-4.

Age-structured Population Model Simulations

Estimates of historical harvest, vulnerable biomass, and exploitation from 1961 to 2006 are presented in Figure 4-6. Values of the total number of black crappie harvested from 1977 to 1981 were from historical creel data collected by FWC, values of harvest in 2005 and 2006 were estimates of total harvest from the commercial (estimated from onboard observations) and recreational fishery (estimated from creel survey) combined, and the remaining years were logical estimates of total harvest based on limited creel survey data. The maximum likelihood profile for Bo and $recK$ is presented in Figure 4-7. We simulated a range of Bo values from 70,000 to 100,000 kg and a range of $recK$ values from 5 to 20. Given the life history and known population characteristics of black crappie in Lake Dora, the ranges of Bo and $recK$ values that were simulated include the most likely range of logical possibilities.

Based on the maximum likelihood profile a Bo estimate of 80,000 kg is supported statistically and is biologically realistic given our estimates of stock size and exploitation. Thus, we fixed Bo at 80,000 kg and used equation 4-13 to solve for a $recK$, resulting in an estimate of 15.2. The maximum likelihood estimate occurred at a Bo of 78,000 kg and a $recK$ of 20; however, we felt that the MLE was not the true best fit because it occurred at the maximum $recK$ in the likelihood profile. The model fit the $recK$ value at the highest possible value it was restricted to resulting in estimates that were not biologically reasonable. Our predicted and empirical estimates of exploitation were both 0.51 in 2006, and the model predicted vulnerable biomass in 2006 approximated our empirical estimate (Table 4-4), indicating that the model was able to predict the field estimates of exploitation and biomass.

Future simulated exploitation rates influenced the model predicted estimates of total harvest, vulnerable biomass, and SPR (Table 4-5). Mean total harvest slightly increased as exploitation increased in simulations; however, mean vulnerable biomass decreased with increases in exploitation. The mean weighted transitional SPR in the terminal year decreased from 0.32 (scenario one) to 0.19 (scenario three). The SPR target goal for most fish species is approximately 0.3 to 0.4, used as a biological reference point where values below the target goal increase the likelihood of recruitment overfishing (Goodyear 1993; Clark 2002). The terminal year mean weighted transitional SPR was operating near the target goal of 0.3 to 0.35 at the levels of exploitation found in 2006, and model simulations predicted that increased exploitation may cause concern of recruitment overfishing. At the highest exploitation rate simulated, the mean weighted transitional SPR was predicted to be well below the target goal (Table 4-5). Results for the annual weighted transitional SPR values with recruitment variability (0.4) are reported for the entire model time series from Monte Carlo analysis with 100 iterations to show how recruitment variation would influence SPR values (Figure 4-8).

Results from yield-per-recruit model simulations are presented in Figure 4-9. The YPR values exhibited an asymptotic relationship with exploitation, indicating that with the current vulnerability schedules the black crappie fishery is not likely to exhibit growth overfishing. The maximum YPR value was 0.13 occurring at a total exploitation rate of 1. Black crappie were not fully vulnerable to either recreational fishing or commercial bycatch until age four, and they become reproductively mature at age two, which allows enough reproduction to prevent growth overfishing. However, at extremely high exploitation rates a shift in the size structure toward smaller, younger fish would be anticipated.

Table 4-1. Summary of results from stratified sampling design in 2005 and 2006. Results include stratified bycatch mean per fishing day, total bycatch estimate, variances for bycatch mean per fishing day and total bycatch estimate, 95% upper and lower confidence intervals, and the number of degrees of freedom used.

Year	$\bar{X}_{ST}$	$\hat{X}_{ST}$	$Var(\bar{X}_{ST})$	$VAR(\hat{X}_{ST})$	CI low $\hat{X}_{ST}$	CI high $\hat{X}_{ST}$	DF
2005	324.52	17,199	4,011.76	11,269,026	8,777	25,622	5.50
2006	630.38	30,258	12,357	28,469,427	19,048	41,469	17.85

Table 4-2. Summary of results from secondary mortality experiment for treatment fish in 2005 and 2006 and control fish in 2006. Year, treatment type, number of replicates, and the mean mortality and associated standard error are shown.

Year	Type	Replicates	Mean mortality	Standard error
2005	treatment	17	0.31	0.06
2006	treatment	23	0.47	0.07
2006	control (hoopnets)	6	0.10	0.05
2006	control (electrofishing)	4	0	0

Table 4-3. Estimates of recreational exploitation rate (μ_{rec}) based on values of the number of higher reward value (C_H) and standard reward tag fish caught (C_S). Tagging mortality (TM) and tag loss (TL) were simulated at 5% and 10%. The total number of higher value tag fish caught (C_H), and standard tag fish caught (C_S) were calculated based on differing values of higher value reward tag reporting rate (λ_H) from 0.5 to 1.0.

λ_H	C_H	R_H	R_L	C_L	T_L	T_H	λ_L	μ_{rec} (5%TL-5%TM)	μ_{rec} (10%TL-10%TM)
0.5	54	27	34	221	413	101	0.15	0.59	0.67
0.6	45	27	34	184	413	101	0.18	0.50	0.56
0.7	39	27	34	158	413	101	0.22	0.42	0.48
0.8	34	27	34	138	413	101	0.25	0.37	0.42
0.9	30	27	34	123	413	101	0.28	0.33	0.37
1.0	27	27	34	110	413	101	0.31	0.30	0.33

Table 4-4. Empirical estimates of vulnerable biomass (kg) and total exploitation (μ_{total}) in 2006 and model predicted values of vulnerable biomass and total exploitation in 2006. Empirical estimates in 2006 were calculated with an estimated total harvest of 54,221 (recreational and commercial) and 2006 model predicted values of vulnerable biomass and total exploitation were derived with leading parameter estimates of $B_0 = 80,000$ kg and $recK = 15.22$.

Parameter	2006 empirical estimate	2006 model predicted value
vulnerable biomass (kg)	34,912	35,080
total exploitation (μ_{total})	0.51	0.51
total harvest (numbers)	54,221	.

Table 4-5. Estimates of mean vulnerable biomass (kg), mean total harvest (numbers) and mean weighted transitional SPR in the terminal year 2050 determined from Monte Carlo simulations (1,000 iterations). Three exploitation scenarios ($\mu_{total} = 0.42$, $\mu_{total} = 0.51$, $\mu_{total} = 0.60$) are shown.

Exploitation scenario	u_{total}	Mean vulnerable biomass	Mean total harvest	Mean SPR
1	0.42	32,026	41,592	0.32
2	0.51	26,359	43,491	0.25
3	0.60	21,973	44,583	0.19

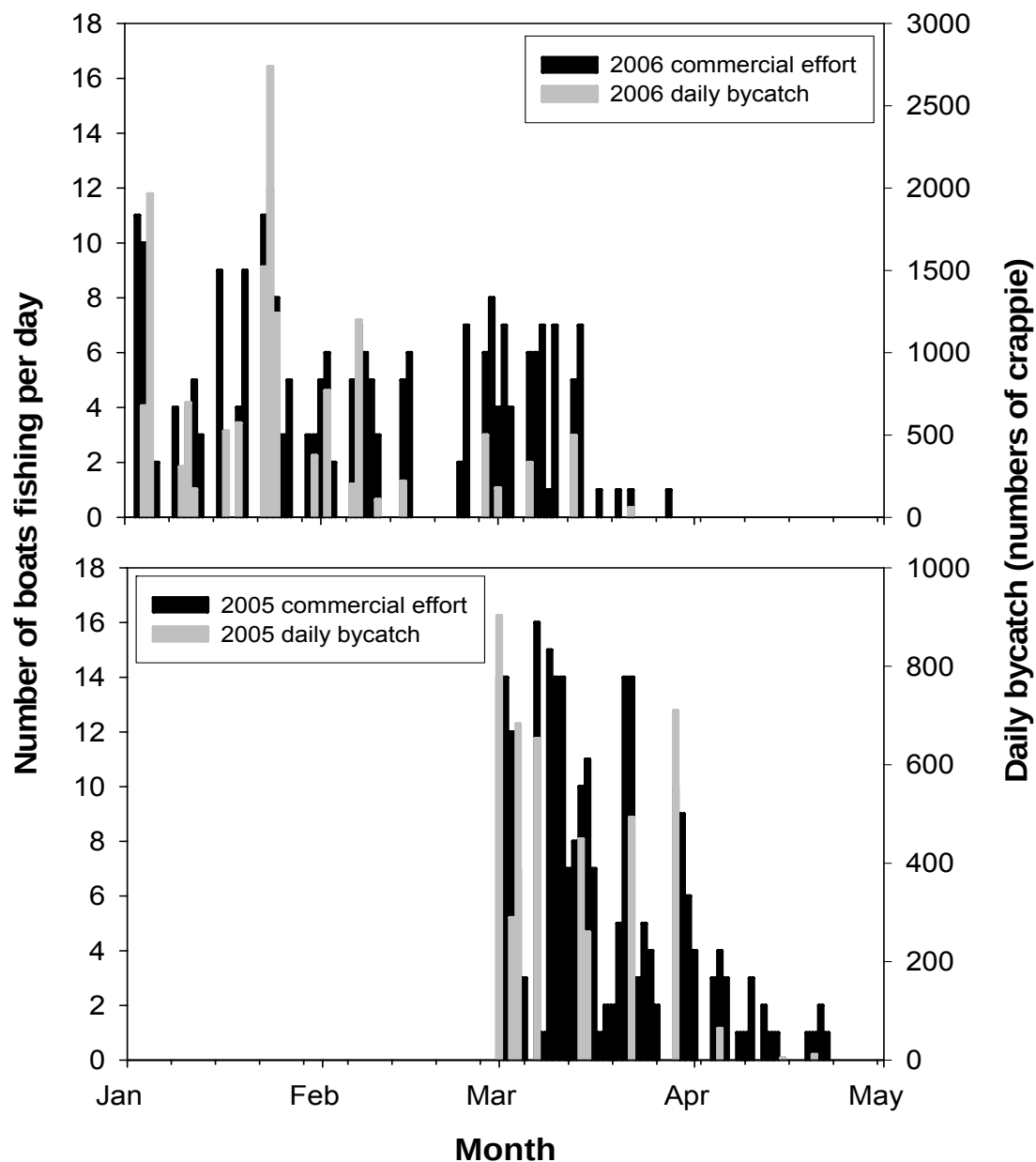


Figure 4-1. Commercial fishing effort (number of boats fishing per day) and daily black crappie bycatch (numbers) for the 2005 and 2006 commercial gill net seasons at Lake Dora. Daily bycatch estimates are shown for 2005 and 2006 for days where onboard observation data was available.

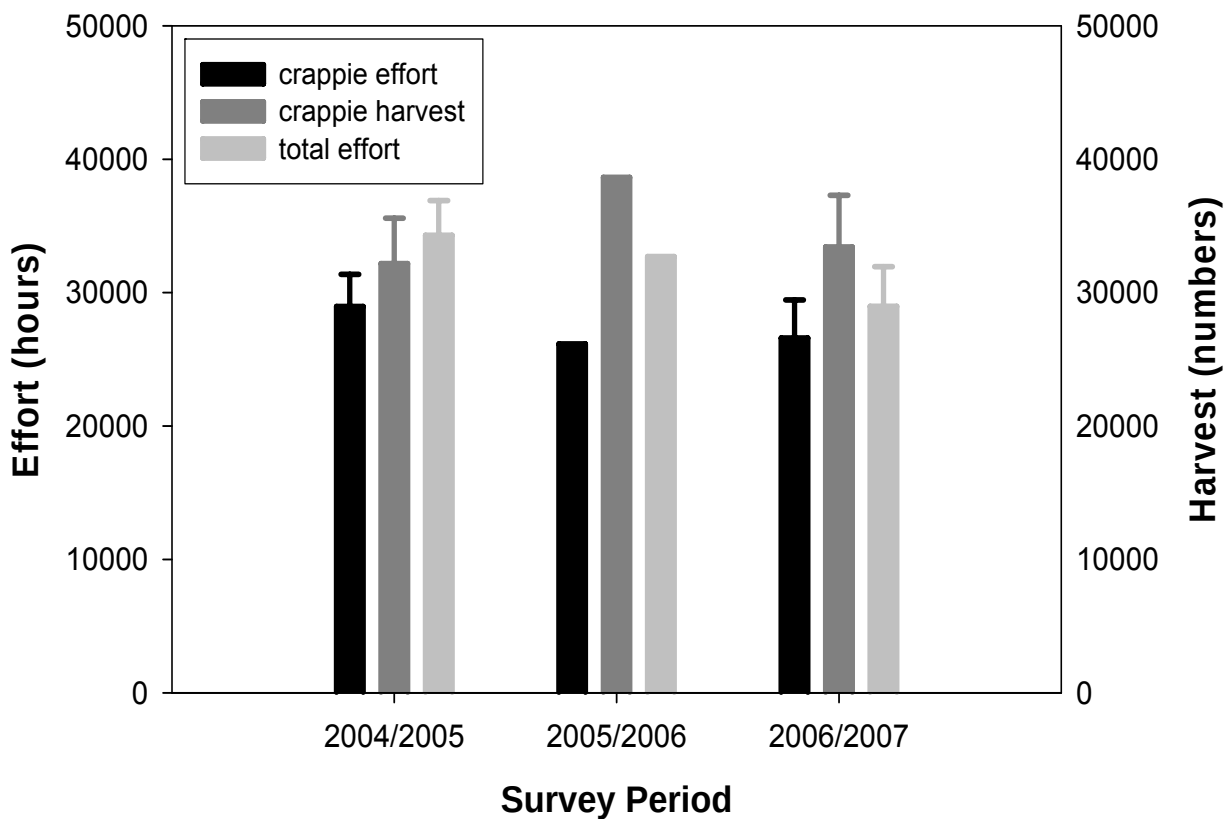


Figure 4-2. Total recreational fishing effort (hours), black crappie effort (hours), and harvest of black crappie (numbers) during the three creel survey periods at Lake Dora. The associated standard error is reported for the survey periods in 2004/2005 and 2006/2007 (no SE could be calculated in 2005/2006 due to missing data from one 28-day time period).

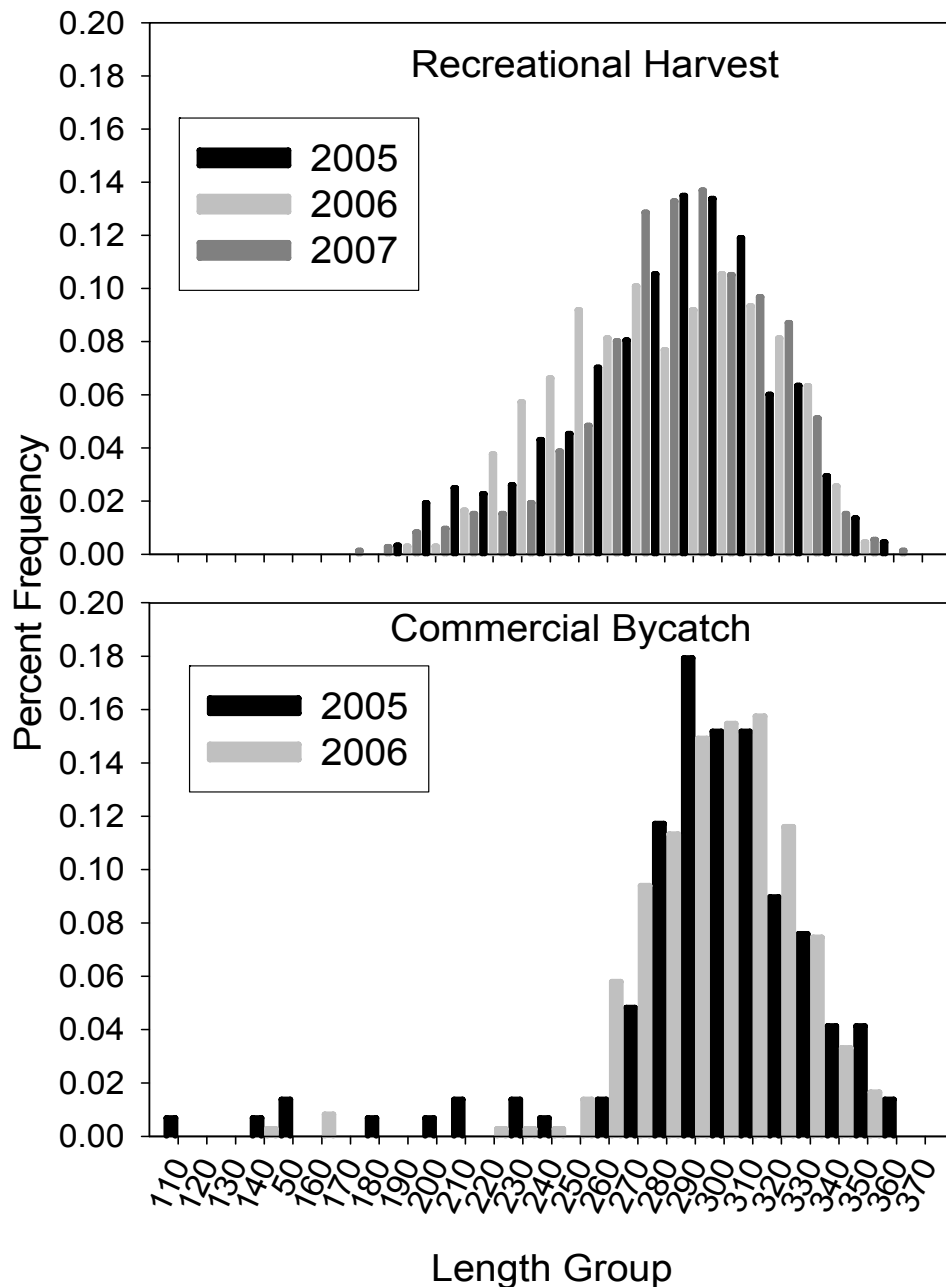


Figure 4-3. Relative length frequencies of black crappie measured from the recreational catch (carcasses and creel) and commercial gill net bycatch on Lake Dora. Measurements of black crappie were sampled from the black crappie recreational catch on Lake Dora in 2005 (N = 882), 2006 (N = 664), and 2007 (N = 723), and from commercial gill net bycatch on Lake Dora in 2005 (N = 145) and 2006 (N = 362). Length group on x-axis represents 10 mm size groups.

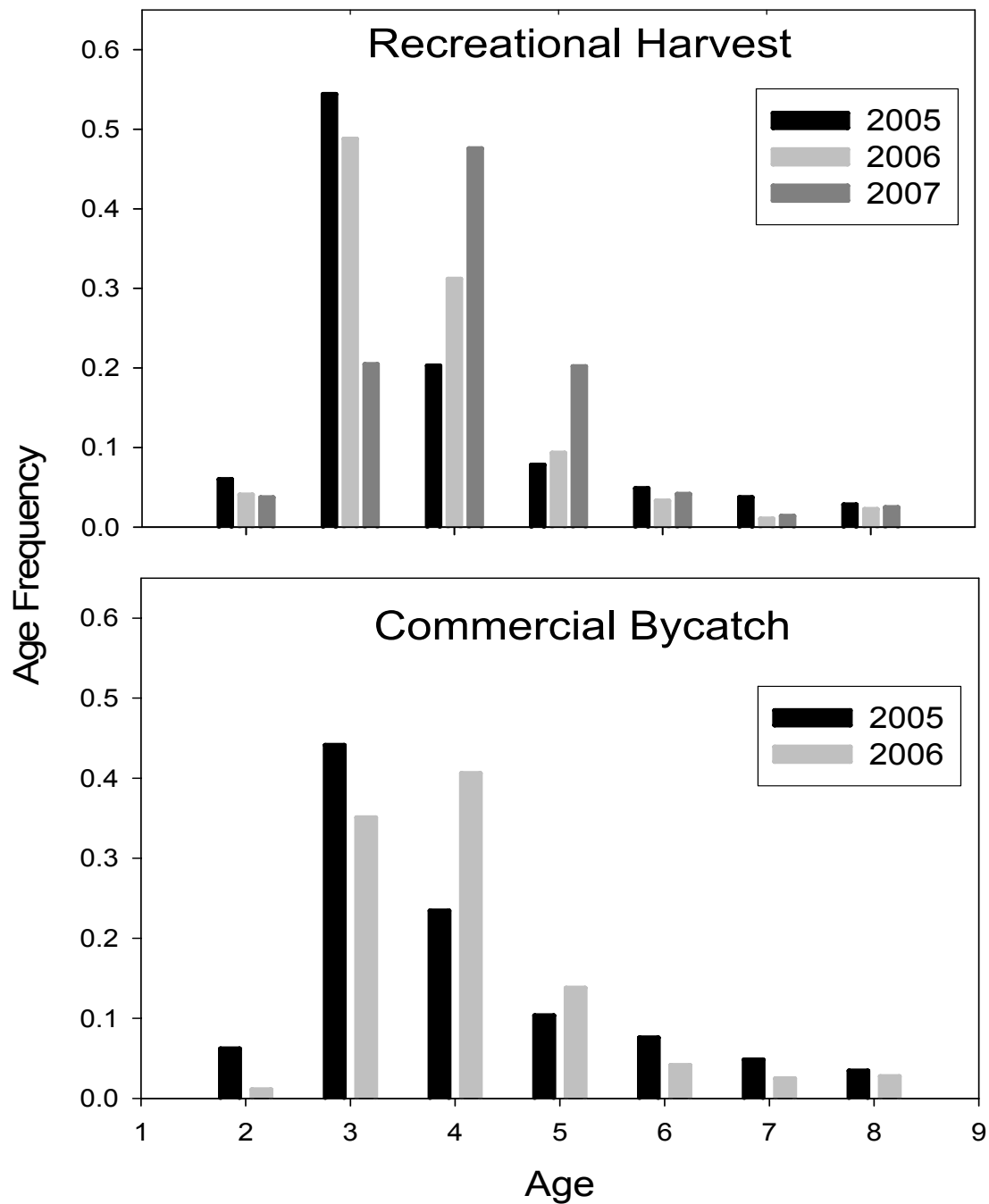


Figure 4-4. Age frequency of black crappie collected from the recreational catch (carcasses and creel) and commercial gill net bycatch on Lake Dora. Ages were determined from the recreational catch in 2005 (N = 882), 2006 (N = 664), and 2007 (N = 723), and from commercial gill net bycatch in 2005 (N = 145) and 2006 (N = 362).

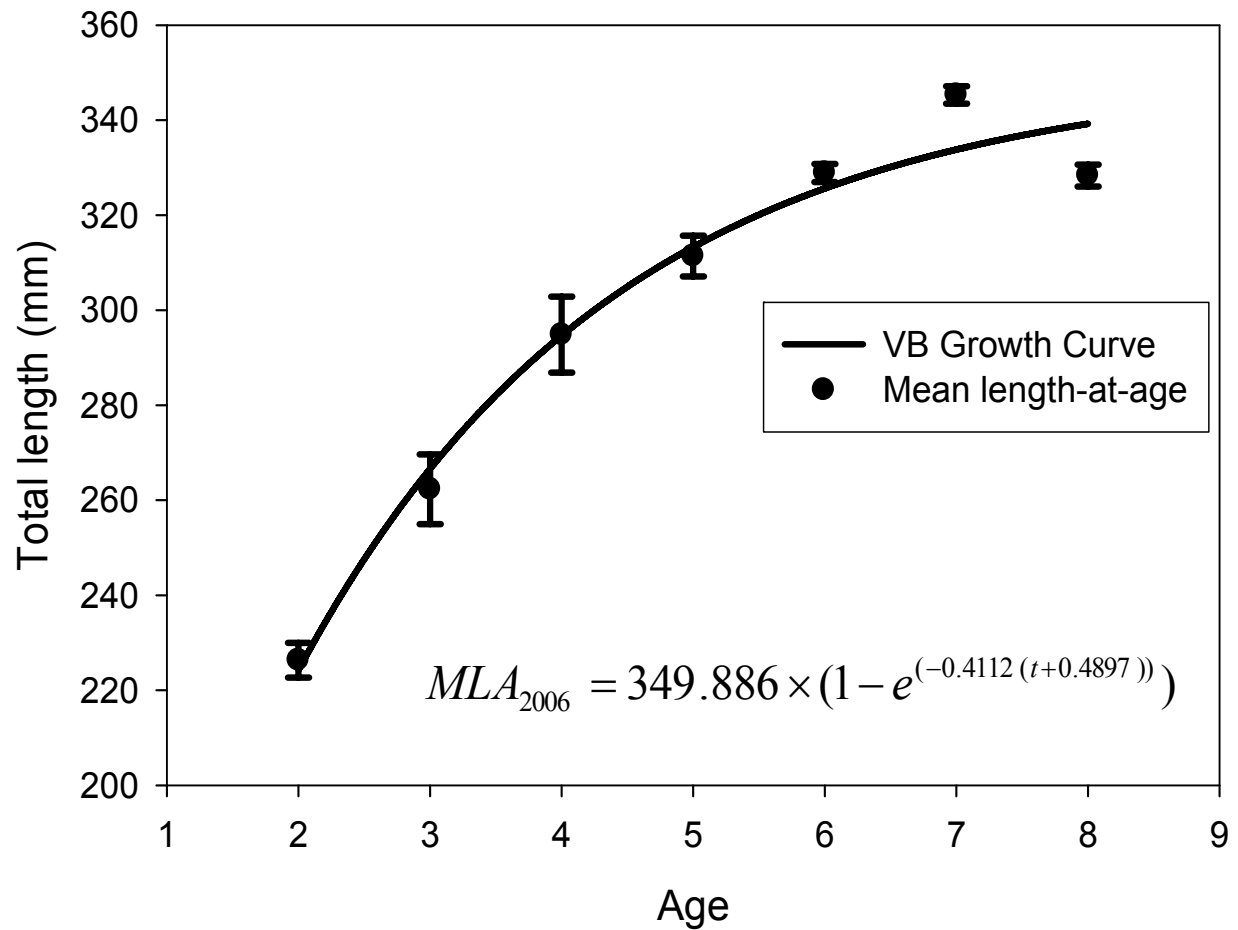


Figure 4-5. Von Bertalanffy growth curve fit to mean length-at-age values for black crappie collected from the recreational fishery (carcasses and creel) at Lake Dora in 2006. Error bars represent one standard deviation around the mean length-at-age values.

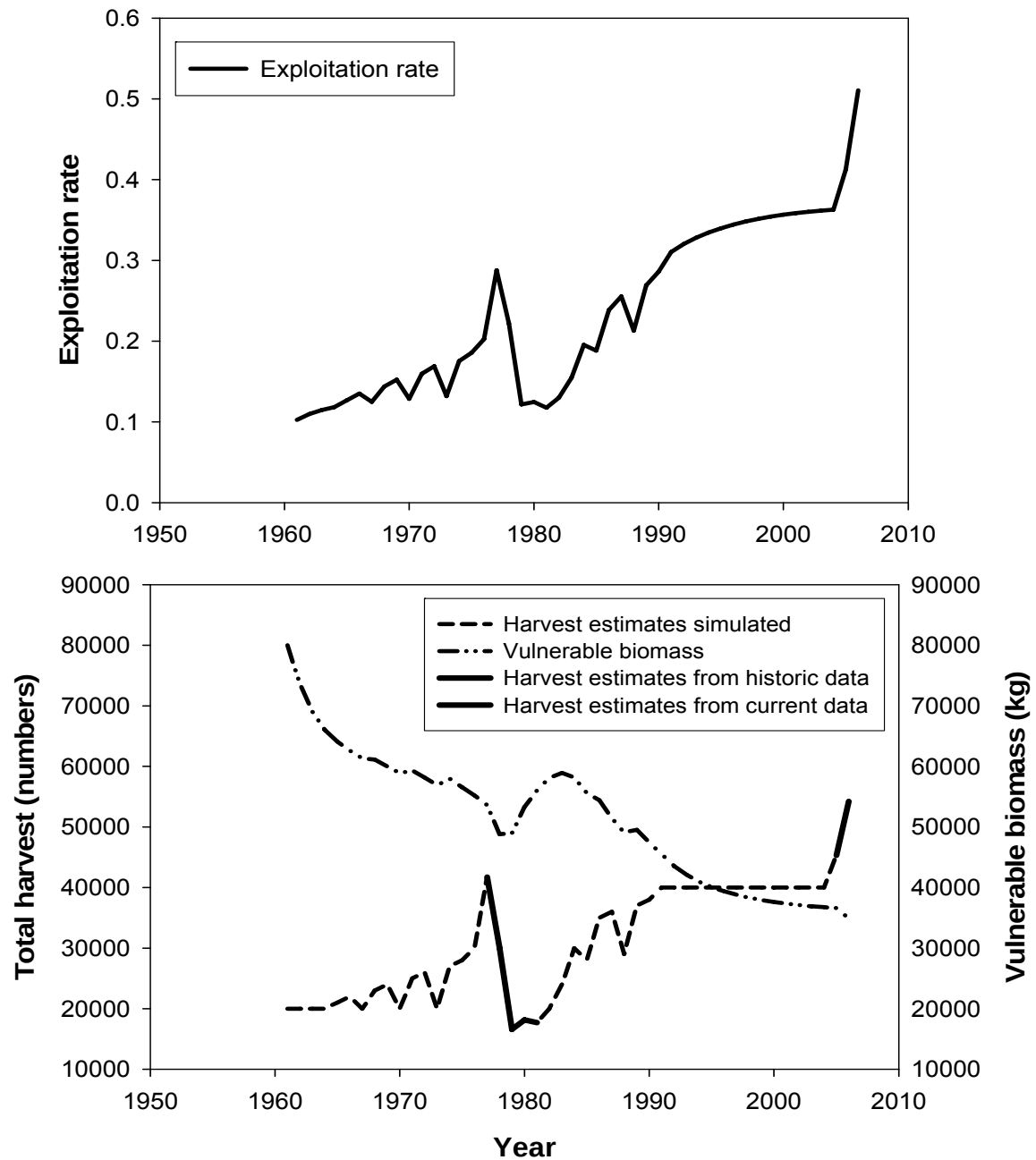


Figure 4-6. Estimates of exploitation from 1961 to 2006 and estimates of historical total harvest and vulnerable biomass from the SRA model. Values of the total number of black crappie harvested are simulated for years that harvest data is not available.

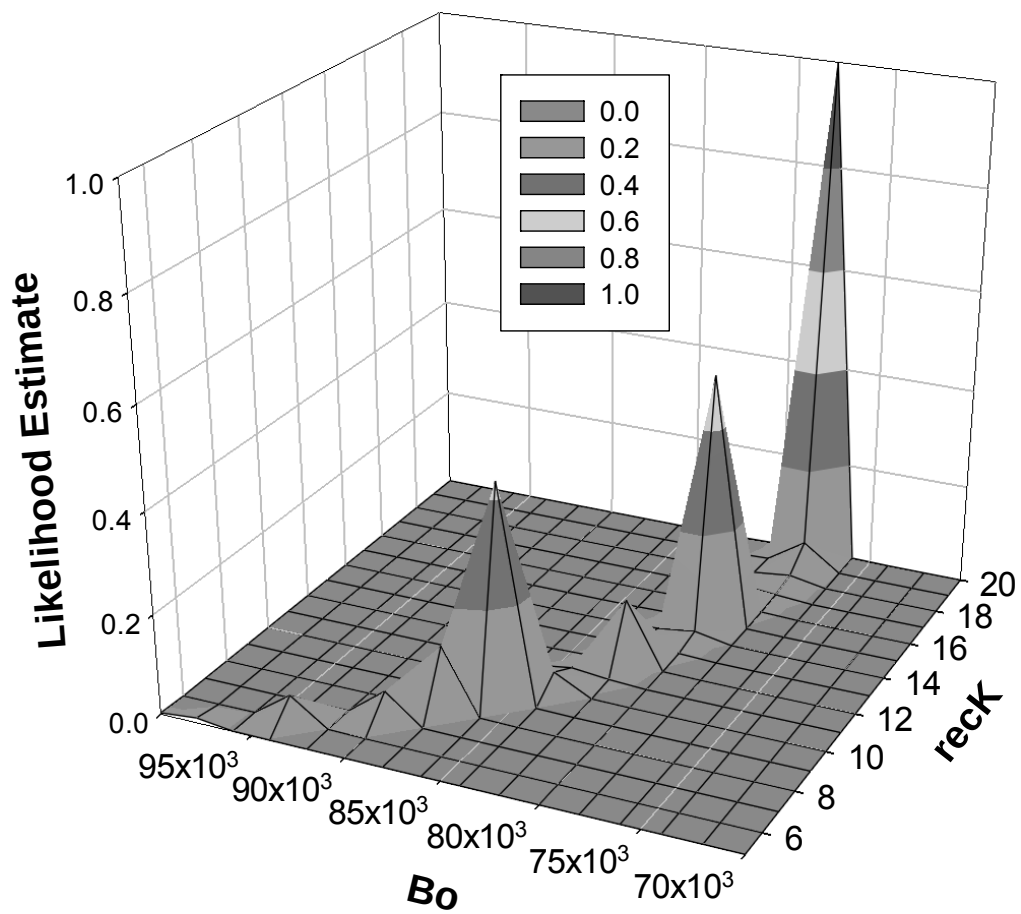


Figure 4-7. Maximum likelihood profile for recK values ranging from 5 to 20 and Bo values ranging from 70,000 to 100,000 kg.

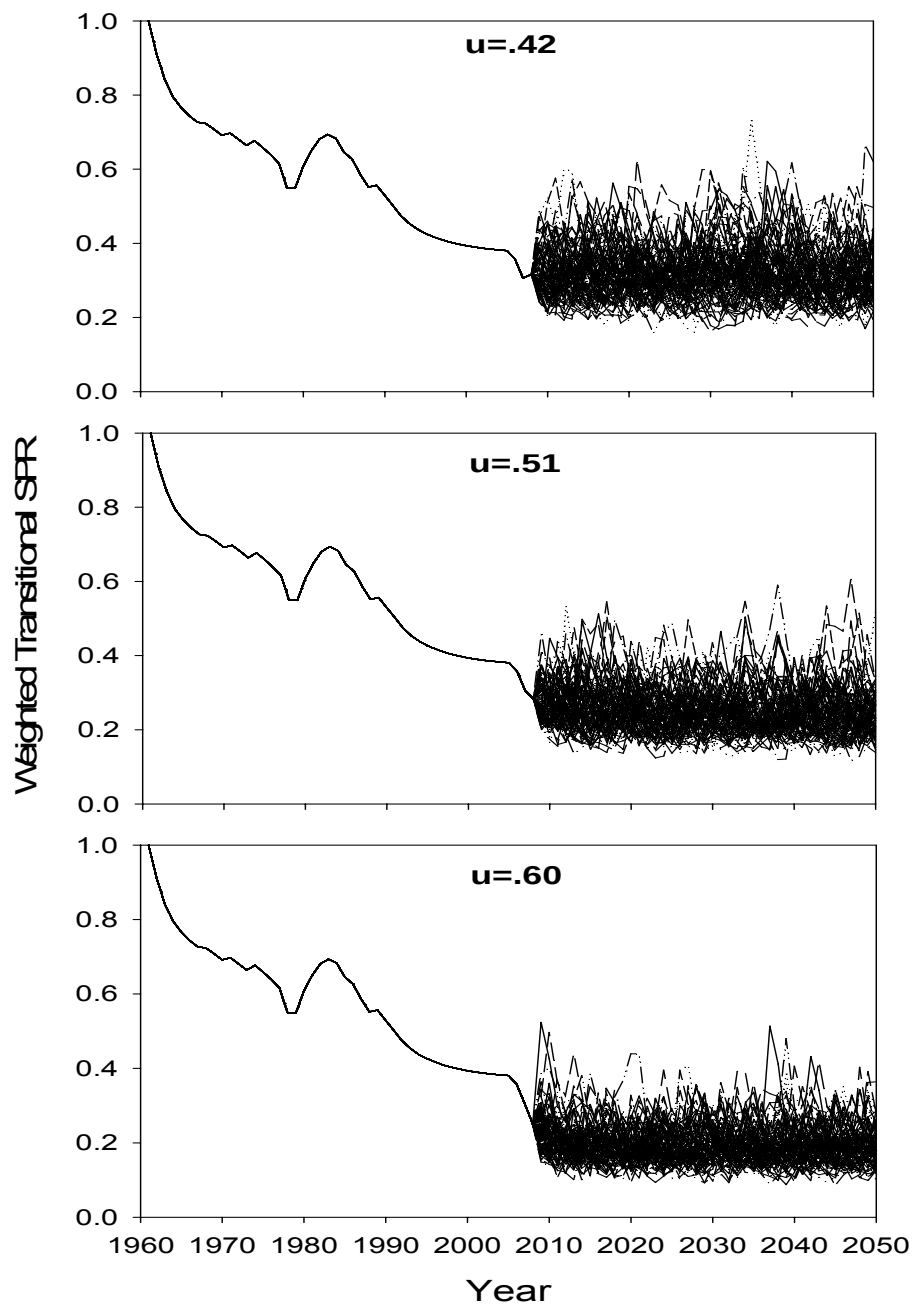


Figure 4-8. Weighted transitional SPR estimated from SRA from 1961 to 2050 with Monte Carlo simulations (100 iterations) under three exploitation scenarios. The three exploitation scenarios were $\mu_{total} = 0.42, 0.51, \text{ and } 0.6$. Recruitment variability = 0.4 from 2007 to 2050.

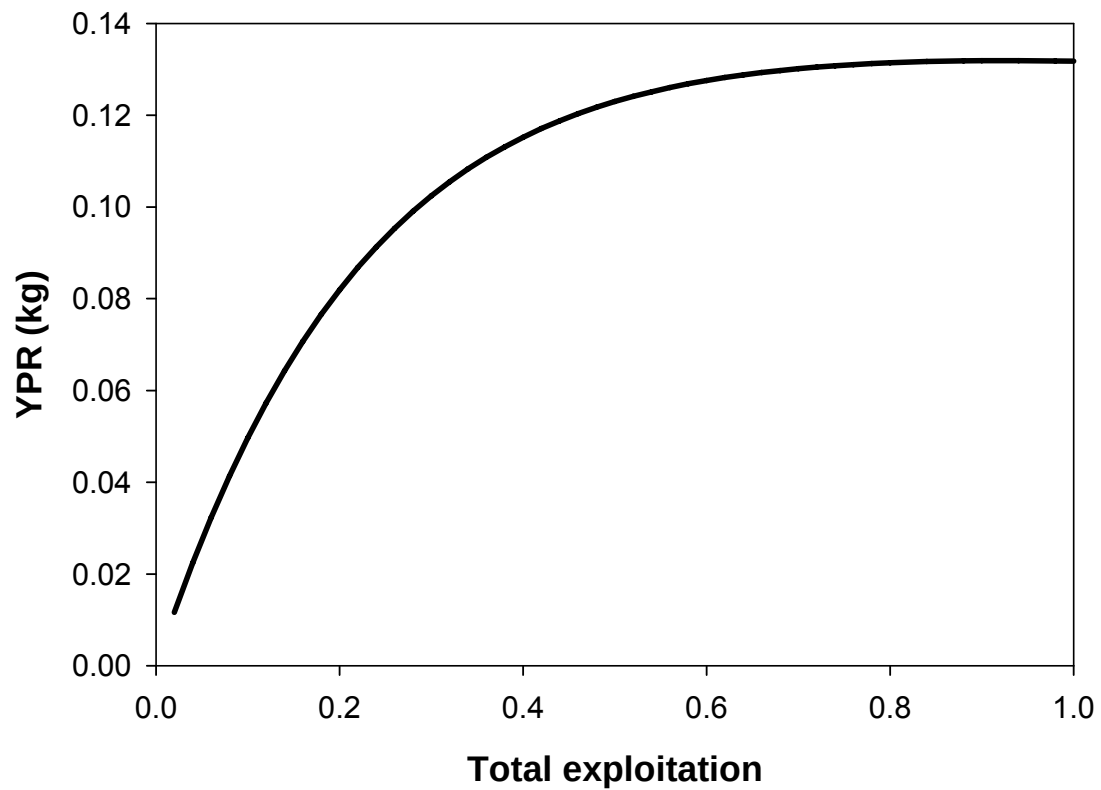


Figure 4-9. Results for YPR (kg) values at total exploitation rates from 0.1 to 1.0 from yield-per-recruit model simulations.

DISCUSSION

Black crappie is the primary sport fish targeted by recreational anglers at Lake Dora, and our results show that the population could be negatively impacted by increases in exploitation resulting from either the recreational fishery or bycatch from the commercial gill net fishery for gizzard shad. Currently, FWC has not defined a standard to measure impacts of bycatch and determine levels of commercial exploitation that are acceptable. We used a biological reference point (SPR) determined from an age-structured model to attempt to determine what levels of total exploitation could be sustainable without risking recruitment overfishing. We also used maximum yield per recruit to investigate the potential for growth overfishing to occur at varying total exploitation rates. It is important to realize that negative impacts such as reduced catch or decreased angler success may occur at fishing mortality rates below those which cause recruitment overfishing, and changes in the vulnerability to harvest schedule may influence the potential for recruitment overfishing to occur at varying total exploitation rates.

Additionally, management decisions are still required to determine how much of the total sustainable exploitation rate is allocated to the recreational fishery versus bycatch from the gill net fishery. The total sustainable exploitation rate for black crappie was approximately 0.42, which results in an SPR near the target goal of 0.3 to 0.35. The estimated recreational exploitation rate in 2006 was approximately the total sustainable exploitation rate, and increases due to recreational fishing and/or commercial bycatch greatly increase the probability of recruitment overfishing. Total exploitation in 2006 resulted in an estimated exploitation rate (0.51) that produced worrisome SPR levels and was most likely not sustainable. The exploitation via bycatch of black crappie at Lake Dora is a negative effect because it is not resulting from a directed fishery and all mortality results in waste. The gill net fishery was regulated to minimize bycatch as much as possible, but bycatch mortality occurred at rates that cause concern for recruitment overfishing. Resource managers must evaluate policy trade-offs to consider the benefit of the gizzard shad removal and the negative impacts of bycatch mortality.

Commercial fishing occurred on Lake Dora during 2005 and 2006 and total commercial fishing effort was approximately equal during the two fishing seasons. However, the temporal range of

effort differed, which may have influenced total gill net bycatch mortality among the commercial seasons. The commercial fishing season in 2005 began two months later than the commercial season in 2006, which could have resulted in differences in catchability due to differing vulnerability to capture in gill nets. This is plausible due to black crappie inshore spawning movements occurring during the later months of the fishing seasons. Total bycatch estimates in 2006 were nearly twice as high as total bycatch estimates in 2005. These results suggest that bycatch could be reduced by timing the commercial fishing season to prevent fishing during winter and early spring. Reducing total bycatch mortality is achieved by reducing the amount of total bycatch or reducing mortality resulting from bycatch. Timing of season could potentially reduce the amount of total bycatch without increasing mortality resulting from bycatch. Bycatch mortality rates would not likely increase by timing of season because we found no significant impact of water temperature or dissolved oxygen levels on bycatch mortality.

No initial mortality of bycatch was observed at Lake Dora during gill net operations, and secondary mortality was the primary mortality source for black crappie caught in commercial gill nets. This was likely due to the maximum soak time of two hours. Total mortality of black crappie captured via gill nets at Lake Apopka, Florida was estimated from 1993 to 1997 and results indicated that 87% survived the treatment (J. Crumpton, FWC, unpublished report). Similarly, secondary mortality accounted for the majority of total mortality and only a small percentage of total mortality observed was initial mortality, which generally occurred in nets fished greater than two hours.

Our results indicate that the potential for adverse population-level effects resulting from commercial bycatch is greatest when recreational exploitation is already high. A previous evaluation found negligible impacts from gill net bycatch for black crappie on Lake Apopka, Florida using a transitional SPR constructed from an SRA (M. Allen, UF, unpublished data), due to low recreational exploitation (~1 fish/acre/year). Conversely, commercial harvest of black crappie at Lake Okeechobee, Florida coupled with recreational harvest increased exploitation to 65%, but the effects were increased growth rates and the population did not show signs of overfishing (Schramm et al. 1985). However, the conclusions of this study were based on catches and angler success, and they did not investigate the potential for recruitment overfishing.

Other studies have assessed population-level impacts of bycatch with modeling techniques. Crouse et al. (1987) developed a stage-based matrix model that incorporated fecundity, survival, and growth rates, and used yearly iterations to make population projections for loggerhead sea turtles *Caretta caretta*. The model used seven life stages from eggs/hatchlings to mature breeders and tested the sensitivity of bycatch mortality on population growth rates. They found that reducing mortality in the large juvenile and adult life stages provided the best protection for population viability. Diamond et al. (1999) explored the population level effects of catch and bycatch on Atlantic croaker *Micropogonias undulatus* in the Gulf of Mexico and the Atlantic Ocean. Catch of Atlantic croaker, including bycatch, had historically been at least three times higher in the Gulf than the Atlantic; however, primarily juveniles are taken in the Gulf fisheries whereas fisheries in the Atlantic have targeted adult fish. Long-term intensive fishing in the Gulf caused severe declines in abundance of Atlantic croaker, but there was no change in size distribution and age-at-maturity, and large fish remained common. In contrast, the Atlantic fishery targeting adult fish has caused changes in age-at-maturity and size structure of that population. Diamond et al. (2000) used stage-within-age based matrix models of Atlantic croaker in the Gulf of Mexico and Atlantic to investigate population-level effects of shrimp trawl bycatch. The Gulf model showed a rapidly declining population, and the Atlantic population showed only a modest decline. Results indicated that both populations were more sensitive to survival of adults than first-year survival, and reducing late juvenile and adult mortality could reverse population declines. Results from these studies support our conclusion that population-level impacts can occur, especially when targeted-fishery exploitation is also high.

Biological reference points such as spawning potential ratio are commonly used as critical metrics to measure the potential of recruitment overfishing. Goodyear (1993) defines SPR as the ratio of fished to unfished reproductive potential of an average recruit, and is a measure of the impact of fishing on the potential productivity of a stock. Critical levels had typically been set in the range of 0.2 to 0.3, based primarily on work in the Northwest Atlantic (Goodyear 1993). SPR target values of 0.35 to 0.4 have also been suggested (Clark 2002), but the critical level for any particular species is influenced by the level of recruitment compensation for fishing mortality (Goodyear 1993). The state of Florida has adopted a target SPR of 0.35 for some heavily exploited marine species, including the spotted seatrout *Cynoscion nebulosus*, which

have shown worrisome levels of SPR values due to recreational exploitation (no commercial exploitation and very limited bycatch) (Murphy et al. 1999).

Estimates of exploitation from tagging studies are always subject to uncertainty due to tag loss, tagging mortality, and reporting rate. For our model simulations, We utilized the best estimate of recreational exploitation (0.42) from tag returns corrected for tag loss of 5%, tagging mortality of 5%, and reporting rate of higher value reward tags of 70%. Our estimate of recreational exploitation in 2006 ($\mu_{rec} = 0.42$) was comparable to estimates of exploitation for black crappie in other southeastern systems. Larson et al. (1991) estimated exploitation rates ranging from 40 to 68% in three Georgia reservoirs, Allen and Miranda (1995) estimated a mean exploitation rate of 42% for white and black crappie in 10 Southeast and Midwest lakes, and Allen et al. (1998) found that exploitation averaged 48% for 18 lakes in the Southeast and Midwest. Black crappie are one of the most heavily harvested and exploited freshwater fishes in the United States, and strong size selectivity under heavy exploitation may affect black crappie population dynamics (Miranda and Dorr 2000).

Our exploitation estimate was critical for model simulations because the model was fit to the 2006 empirical estimates of exploitation and vulnerable biomass. An unbiased estimate of exploitation was additionally important to reduce parameter uncertainty, because there is also structural uncertainty in the SRA. The SRA model reduces population size based on catches alone, and does not account for other factors that may influence recruitment such as habitat changes. This is of particular importance because if the gizzard shad removal is successful, improved water clarity could result in increased aquatic macrophyte abundance thereby changing the available habitat and factors that influence black crappie recruitment and growth.

All model simulations assumed vulnerability to harvest was equal for the recreational and commercial fisheries. This is important because the vulnerability to harvest schedule directly impacts estimates of exploitation. It is likely that vulnerability between commercial and recreational fisheries were similar based on the size and age distributions of the harvest. Although recreational anglers did tend to harvest some smaller black crappie that were not fully vulnerable to the commercial fishery, Miranda and Dorr (2000) showed that recreational anglers

tend to select for fish over 250 mm TL. Additionally, much of the recreational angling effort occurs in open water areas where gill nets are fished. The number of tag returns from the commercial fishery was significantly lower possibly indicating a difference in vulnerability to harvest, however commercial fishers had incentive to not return tags and no reliable reporting rate could be obtained for the commercial fishery.

Our future projections were conducted under the assumption that total exploitation remained constant through the terminal year. This scenario is unlikely, because changes in angler catch rates through fish reductions via recreational and/or commercial exploitation would probably influence recreational fishing effort. Cox et al. (2003) found that angling effort depends on the angler catch rate, and there is no reason to expect that the level of fishing effort that produces the maximum total yield will also provide maximum total satisfaction to anglers. Additionally, Walters and Martell (2004) state that most fisheries reach a bionomic equilibrium where they become “self-regulating” in the sense that further stock decline past some equilibrium caused by development of a fishery should trigger a reduction in fishing effort and mortality allowing the stock to begin recovery. Thus, it is likely that recreational effort would decline if total exploitation continued to increase and catch rates declined, due to decreased angler satisfaction and shifts in fishing effort to other systems. Under this scenario of bionomic equilibrium, commercial bycatch will probably not result in recruitment overfishing. However, decreased angler satisfaction and fishing effort is still a negative impact resulting from increased exploitation, which could occur due to bycatch mortality. Reduced recreational angler effort caused by commercial bycatch mortality warrants future investigation because lower effort would constitute “harm” to the recreational fishery.

Management Implications

Impact on the black crappie fishery due to bycatch mortality may be acceptable if the gizzard shad reduction is successful in improving water clarity and increasing aquatic macrophyte abundance. A management decision must be made for the future of commercial fishing with gill nets on Florida lakes that evaluates the trade-offs of the positive effects of biomanipulation and possible negative effects of bycatch on recreational fisheries. Possible management alternatives

are to 1) discontinue the gill net fishery to eradicate bycatch and optimize the black crappie recreational fisheries, or 2) increase commercial effort and gizzard shad exploitation to optimize the success of the biomanipulation. In the case of Lake Dora, it appears that continuing the program at the current level of commercial effort will not optimize either management objective.

Another alternative is to initiate an active adaptive management plan. Active management of recreational fisheries implies that a complete management procedure is in place, with clear goals or objectives for the fishery, management schemes to keep the total harvest or exploitation rates within target limits, and methods to determine whether the goals or objectives have been met (Walters 1986; Pereira and Hansen 2003). Little experience has been gained in actively managing recreational fisheries due to the extensive and diverse array of recreational fisheries, few recreational fisheries are of such singular importance that they demand the sociopolitical or economic motives, and many passive management schemes are in place in response to the need for management (Pereira and Hansen 2003). For successful active adaptive management in recreational fisheries, agencies must commit to a clear goal or objective. In the case of the Lake Dora commercial gill net fishery, possible objectives are 1) reducing the gizzard shad population enough to change the trophic structure or 2) maximize recreational harvest of black crappie and angler satisfaction. If the goal of the Lake Dora fishery is to reduce gizzard shad abundance to levels that result in trophic structure alterations, then a long-term management plan should be implemented that involves fishing the gizzard shad intensively, measuring the levels of gizzard shad reduction, measuring levels of chlorophyll reduction, and measuring the black crappie bycatch mortality and angling success. Another consideration in the evaluation of the policy trade-off is the effect that a change in the trophic structure would have on the black crappie population. A shift in the trophic structure may result in changes in water clarity, aquatic macrophyte abundance, and fish productivity that could impact black crappie population dynamics and angling success, which is not accounted for in SRA simulations.

Fisheries management inherently requires making decisions that involve trade-offs.

Management agencies often try to make decisions that optimize all alternatives, which can create a situation where none of the management alternatives are optimized. Failure to admit the severity of trade-off relationships can result in policy choices that are not beneficial for anyone

(Walters and Martell 2004). The trade-offs associated with the gizzard shad biomanipulation and black crappie bycatch must be considered and clear management objectives defined. If commercial fishing continues, methods must be set forth to measure the effectiveness of the management objectives. Our results show that the current size-selective removal of gizzard shad at Lake Dora could cause negative impacts to the black crappie population, with the potential for recruitment overfishing. Resource managers should consider these impacts and the trade-offs they represent when considering commercial fishing operations.

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APPENDIX A: GEOGRAPHIC COORDINATES FOR SAMPLE STIES ON LAKES DORA, EUSTIS AND HARRIS. THE TYPE OF SAMPLING CONDUCTED AT EACH SITE IS INDICATED BY AN X.

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