

**Evaluation of mechanical removal rates for rehabilitating over-crowded largemouth bass  
*Micropterus salmoides* populations in Alabama small impoundments**

by

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## Abstract

Largemouth bass *Micropterus salmoides* populations in small impoundments exhibit poor growth and body condition under high population densities typically found in unmanaged ponds. The effectiveness of largemouth bass harvest at reducing these conditions and restoring overcrowded populations back to desirable population size structures is unclear. We evaluated mechanical removal rates for rehabilitating over-crowded largemouth bass population in Alabama small impoundments. Via boat electrofishing, we removed 0-83% of largemouth bass populations under 356 mm over two years at eleven Auburn University Fisheries Research Unit ponds and evaluated changes in largemouth bass condition, size structure, growth and recruitment. Significant positive relationships were identified for  $\log_e$  differences in largemouth bass PSD-Q, PSD-P, mean relative weights of 254-356 mm largemouth bass, and CPUE of >356 mm largemouth bass as a function of proportion biomass removed from 2019-2021. However, the magnitude of these associations was small and driven primarily by reductions at unharvested control ponds rather than strong responses at treatment ponds. A significant negative relationship was also identified for  $\log_e$  differences in largemouth bass mean GSI. No significant relationships were identified for  $\log_e$  differences in growth or recruitment as a function of proportion biomass removed from 2019-2021. The removal effort necessary to achieve a mechanical removal rate of 0.5 (50% reduction) ranged from 4-9 complete shoreline circuits as largemouth bass catchability declined with removal effort. Despite significant relationships for some variables, two years of mechanical removals via boat electrofishing did not appear to substantially alter largemouth bass populations in these small impoundments. Rather the removal process maintained the current state of largemouth bass growth, condition, and population size structure in treated ponds compared to control ponds. Given the substantial amount of time,

effort, and funding required to conduct intensive largemouth bass removals, my results offer clarity on the practicality and value of mechanical removals via boat electrofishing as a management tool for overcrowded largemouth bass ponds.

Closed-population mark-recapture methods for estimating population size are widely used in fisheries applications. A key assumption of these methods is equal capture probability for every individual of the population; however, this assumption is often violated resulting in biased estimates of population size. Closed-population mark-recapture models often generate abundance estimates from electrofishing capture data. Varying behavioral responses induced by electrofishing likely lead to changes in capture probabilities and consequently biased abundance estimates. More complex closed population mark-recapture models are available in programs such as RMark to allow for multi-phase mark-recapture study designs to be robust to variation in capture probabilities. More clarity on the limitations of detecting differences in capture and recapture probabilities using programs like RMark are essential to understanding how to more strategically design closed population mark-recapture studies to calculate better abundance estimates. The objectives of this work were to show the limitations of detecting a recapture effect when using a mark-recapture/removal study design, investigate the effect of recapture behavior on bias in abundance estimates, and evaluate how our findings correlate with model selection of 29 mark-recapture/removal datasets. I used RMark to conduct Monte Carlo simulations of closed population capture-recapture models for ranges of variability in capture and recapture probabilities, population size, initial capture probability, and the number of removal events. Population size, initial capture probability, and variability in capture probability had the strongest influence on detecting a recapture effect and, therein, selecting for a model with recapture effect as the best fit model to the data. Ultimately, the best scenarios for high mean percent model

selection for a recapture effect contained high population size, no variability in capture probability, and high initial capture probability. Population size and variability in capture probability had the strongest influence on mean proportional error in derived abundance estimates of models with a recapture effect relative to the true population size. I found very little bias in abundance estimates of models with a recapture effect relative to the true population size for nearly all scenarios except those with low population size, a low number of removal events, and a low initial capture probability. Lastly, derived abundance estimates of models without a recapture effect overestimated true population size in all scenarios except those with both a high initial capture probability and a high number of removal events. Overall, I found that the best fit models for all 29 data sets correlated well with the results of my simulations. The results of this study provide important insight into the dangers of assuming equal capture probability and using simple closed population capture-recapture models that are not robust to potential differences in capture and recapture probabilities. My results suggest that marking fish can reduce bias in abundance estimates if differences in capture and recapture probabilities can be tested for by using a more complex model.

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## Table of Contents

Abstract .....	ii
Acknowledgments .....	v
Table of Contents .....	vi
List of Tables .....	vii
List of Figures .....	viii
<b>Chapter 1. Evaluation of mechanical removal rates for rehabilitating over-crowded largemouth bass <i>Micropterus salmoides</i> populations in Alabama small impoundments .....</b>	<b>1</b>
Abstract .....	1
Introduction .....	2
Methods .....	7
Results .....	22
Discussion .....	26
Management Implications .....	31
<b>Chapter 2. Evaluation of electrofishing and marking recapture behavior using closed population capture-recapture methods .....</b>	<b>34</b>
Abstract .....	34
Introduction .....	35
Methods .....	38
Results .....	46
Discussion .....	49
Cited Literature .....	52
Tables .....	66
Figures .....	71
Appendix .....	90

List of Tables

Table 1. Various southern agency largemouth bass harvest recommendations for private ponds.  
..... 66

Table 2. Characteristics of control and treatment ponds..... 67

Table 3. Proportion abundances removed with respect to target removal treatments ..... 68

Table 4. Population estimates of largemouth bass populations <254 mm for eight treatment  
ponds in 2019 and 2020 ..... 69

Table 5. Population estimates of largemouth bass populations 254-356 mm for eight treatment  
ponds in 2019 and 2020 ..... 70

List of Figures

Figure 1. Estimates of proportion abundance and biomass removed of largemouth bass as a function of target removal treatment..... 71

Figure 2. Log difference in largemouth bass abundance and biomass as a function of proportion biomass removed ..... 72

Figure 3. Log difference in largemouth bass PSD-Q and PSD-P as a function of proportion biomass removed ..... 73

Figure 4. Log difference in mean relative weight of largemouth bass as a function of proportion biomass removed ..... 74

Figure 5. Log difference in CPUE of stock size bluegill as a function of proportion biomass removed..... 75

Figure 6. Log difference in CPUE of largemouth bass as a function of proportion biomass removed..... 76

Figure 7. Log difference in CPUE of age-1 largemouth bass as a function of proportion biomass removed..... 77

Figure 8. Log difference in largemouth bass mean length at age-1 and mean incremental growth of age-2 as a function of proportion biomass removed..... 78

Figure 9. Log difference in mean intercept of linear incremental growth at age models of largemouth bass ages 2+ as a function of proportion biomass removed ..... 79

Figure 10. Log difference in mean GSI, HSI, and stage of visceral fat of largemouth bass as a function of proportion biomass removed..... 80

Figure 11. Log difference in largemouth bass mean length at 50% maturity as a function of proportion biomass removed..... 81

Figure 12. Log difference in frequency of occurrence of fish and mean weight of individual bluegill in largemouth bass diets as a function of proportion biomass removed..... 82

Figure 13. Estimates of mean catchability of largemouth bass in treatment ponds as a function of removal event..... 83

Figure 14. Estimates of mean cumulative proportion abundance removed from treatment ponds as a function of removal event ..... 84

Figure 15. Estimates of pounds of largemouth bass removed per acre from treatment ponds as a function of proportion abundance removed..... 85

Figure 16. Flowchart of the creation of an individual capture history used in closed-population capture-recapture model simulations ..... 86

Figure 17. Mean percent model selection of  $M_b$  and  $M_{tb}$  for a range of recapture effects as a function of initial capture probability and number of removal events across ranges of variability in capture probability and true population size..... 87

Figure 18. Mean proportional error in abundance estimates of  $M_b$  and  $M_{tb}$  for a range of recapture effects as a function of initial capture probability and number of removal events across ranges of variability in capture probability and true population size..... 88

Figure 19. Mean proportional error in abundance estimates of  $M_o$  and  $M_t$  for a range of recapture effects as a function of initial capture probability and number of removal events across ranges of variability in capture probability and true population size ..... 89

## **Chapter 1. Evaluation of mechanical removal rates for rehabilitating over-crowded largemouth bass *Micropterus salmoides* populations in Alabama small impoundments**

### **Abstract**

Largemouth bass *Micropterus salmoides* populations in small impoundments exhibit poor growth and body condition under high population densities typically found in unmanaged ponds. The effectiveness of largemouth bass harvest at reducing these conditions and restoring overcrowded populations back to desirable population size structures is unclear. We evaluated mechanical removal rates for rehabilitating over-crowded largemouth bass population in Alabama small impoundments. Via boat electrofishing, we removed 0-83% of largemouth bass populations under 356 mm over two years at eleven Auburn University Fisheries Research Unit ponds and evaluated changes in largemouth bass condition, size structure, growth and recruitment. Significant positive relationships were identified for  $\log_e$  differences in largemouth bass PSD-Q, PSD-P, mean relative weights of 254-356 mm largemouth bass, and CPUE of >356 mm largemouth bass as a function of proportion biomass removed from 2019-2021. However, the magnitude of these associations was small and driven primarily by reductions at unharvested control ponds rather than strong responses at treatment ponds. A significant negative relationship was also identified for  $\log_e$  differences in largemouth bass mean GSI. No significant relationships were identified for  $\log_e$  differences in growth or recruitment as a function of proportion biomass removed from 2019-2021. The removal effort necessary to achieve a mechanical removal rate of 0.5 (50% reduction) ranged from 4-9 complete shoreline circuits as largemouth bass catchability declined with removal effort. Despite significant relationships for some variables, two years of mechanical removals via boat electrofishing did not appear to substantially alter largemouth bass populations in these small impoundments. Rather the removal

process maintained the current state of largemouth bass growth, condition, and population size structure in treated ponds compared to control ponds. Given the substantial amount of time, effort, and funding required to conduct intensive largemouth bass removals, my results offer clarity on the practicality and value of mechanical removals via boat electrofishing as a management tool for overcrowded largemouth bass ponds.

## **Introduction**

Small impoundments or ponds are manmade bodies of water with less than 40 hectares (ha) of water surface area (Dauwalter and Jackson 2005; Willis et al. 2010). There are an estimated 9 million ponds across the continental U.S. with the highest densities in the Great Plains and the southeastern regions of the country (Renwick et al. 2005). Alabama has over 250,000 small impoundments >0.18 ha covering over 227,000 ha of state land (Chaney et al. 2012). These systems represent a significant portion of Alabama's freshwater resources and when stocked with largemouth bass *Micropterus salmoides* and bluegill *Lepomis macrochirus*, ponds can provide excellent recreational fishing opportunities (Alabama's Pond Management Biologist. 2003).

Ponds in the middle and southern latitudes of North America are most commonly stocked with largemouth bass and bluegill (Swingle and Smith 1940, Swingle 1949, Dauwalter and Jackson 2005). Both species reproduce, grow, and survive successfully in shallow littoral systems, adapt well to a wide range of pond environments, and have a highly compatible predator-prey relationship (Swingle 1949; Wright and Kraft 2012). However, as largemouth bass densities increase in pond systems, predation and high consumption rates of bluegill can result in inadequate bluegill production and high intraspecific competition (McHugh 1990).

Consequently, largemouth bass growth rates (Hill and Willis 1993), body condition (Wege and

Anderson 1978; Schindler, Hodgson, and Kitchell 1997), and size structure typically decline (Gabelhouse 1984; Hill and Willis 1993). In this state, the status of a largemouth bass population is undesirable to pond owners and anglers due to the apparent small largemouth bass population size structure. This problem is commonly referred to as “largemouth bass-overcrowding” and is typical of unmanaged largemouth bass-bluegill pond systems in southern US states.

A common pond management strategy for preventing overcrowding in largemouth bass populations is by annually removing largemouth bass from the system. The concept of this strategy is to harvest small largemouth bass to mitigate strong density dependent conditions and support higher growth rates, healthy body conditions, and improved population size structure. State and private agencies throughout the southern U.S. provide recommendations of absolute measures of largemouth bass harvest for controlling largemouth bass populations in private ponds (Table 1.). These largemouth bass harvest recommendations for small impoundments are usually based on largemouth bass biomass and pond productivity (Schramm and Willis 2012). Ponds that have moderate or high fertility are more productive and should carry a higher biomass of largemouth bass. However, no specified relationships between pond trophic state and largemouth bass biomass have been established (Schramm and Willis 2012). Consequently, the effectiveness of a harvest recommendation may vary substantially from pond to pond. Gablehouse (1987) concluded that the issue with generalized largemouth bass removal recommendations is that the number of fish removed is not as important as the number of fish left in the population. Instead, the appropriate number of largemouth bass to remove should be dictated by pond productivity and, thus, will vary among small impoundments. Novinger (1990) suggested that the appropriate numbers and sizes to harvest or release is still “more art than science”.

Boat electrofishing is a commonly used method for mechanical removal of largemouth bass to reduce their densities. A few studies across northern and middle latitudes of the continental US have conducted mechanical removals on largemouth bass populations in small impoundments. Willis et al. (2010) evaluated effects of yearly removal of less than 300 mm largemouth bass on a high density, slow growing population in Knox Pond, a 2.9 ha pond in South Dakota. The study concluded that four years of 48, 40, 40, and 21% mechanical removals of the largemouth bass population via boat electrofishing resulted in increases in largemouth size structure by year 4; however, the only prey items available to largemouth bass in Knox Pond were invertebrates, amphibians, black bullheads, and other largemouth bass. Another study evaluated the effects of mechanical removal on a 0.66 ha Kansas largemouth bass-bluegill pond and concluded that an annual removal of 20, 24, 40, 50, and 31% of largemouth bass between 200-300mm over 5 years did not significantly increase largemouth bass size structure, condition, or growth (Gablehouse 1987). Many published works on the impacts of largemouth bass removals in small impoundments, including the works of Gablehouse (1987) and Willis et. al (2010), are single pond experiments. Consequently, these studies were unable to evaluate the relationship between the intensity of largemouth bass removal (i.e., the proportion of the largemouth bass population or biomass removal) and the strength of population responses (i.e., compensation). Gablehouse (1987) suggested that an initial removal of over 60% of the largemouth bass population may achieve better results in size structure. However, little evidence is available to support the suggestion that a higher intensity of largemouth bass removal would conclude with more desirable results.

Mechanical removal of largemouth bass from overcrowded ponds may provoke compensatory responses in growth and recruitment. Density dependent processes such as

reproduction, growth, and survival are compensatory when the response to variation in population density results in a negative feedback on population growth (Rose et al. 2001). Previous research has provided strong support for the existence of compensatory density dependence in fish populations (Goodyear 1980; Myers et al. 1999; Rose et al. 2001; Catalano and Allen 2011). Density dependent growth has been detected during both juvenile and adult fish life stages (Sogard 1997; Cowan et al 2000; Post et al. 1999; Lorenzen and Enberg 2002; Pope et al. 2004; Sundstrom et al. 2013; Svedang and Hornborg 2014). Further research suggested that density dependence in adult growth alone could explain observed compensation in many exploited fish populations and that density dependence in growth may be the most important compensatory mechanism under moderate population densities (Lorenzen and Enberg 2002). However, at low population densities, studies have concluded that increased pre-recruit survival would likely be the primary mechanism for compensation (Rose et al. 2001; Lorenzen and Enberg 2002). A meta-analysis of spawner-recruit data has established that strong compensatory density dependence can be exhibited in fish populations through changes in reproduction (Myers et al. 1999; Myers 2001, 2002). Per capita recruitment rates often have an inverse relationship with fish population size (Cushing 1995; Myers et al. 1999; Rose et al. 2001; Allen et al. 2011; Shaw and Allen 2016). The nature of the compensatory relationship between spawner abundance and recruitment may have implications for largemouth bass removals in small impoundments. For example, an asymptotic Beverton-Holt (1957) relationship would be expected to maintain relatively constant recruitment in the face of density reductions. Furthermore, a dome-shaped Ricker relationship may result in increased recruitment following density reduction, which may offset improvements in growth and size structure. Reynolds and Babb (1978) fit a dome-shaped, Ricker reproduction curve to stock and recruitment densities of

largemouth bass in Missouri ponds expressing that the peak level of recruitment occurred at intermediate spawning stock abundances. Allen et al. (2011) evaluated the effect of stock size on recruitment density of largemouth bass in Florida ponds and could not identify a specific form of a stock-recruit relationship. Other research determined that the density of successful broods better explained largemouth bass recruitment densities in Florida ponds and results suggested that the number of successful broods was not related to stock abundance and that recruitment compensation plays a crucial role in year-class strength (Shaw and Allen 2016).

The potential effectiveness of mechanical removals is dependent on the capability to capture and remove largemouth bass from the overcrowded population. A better understanding of the impacts of mechanical removal effort on largemouth bass catchability (Ricker 1975; fraction of fish stock caught by a defined unit of fishing effort) would be valuable as it would provide a more relative measure of population reduction and reveal the practicality of mechanical removals via boat electrofishing. In most small impoundments, the entire shoreline can be electrofished in one sampling event, therefore, the number of removal events necessary depends on the desired level of removal and on catchability. Constant catchability among subsequent removal events would be ideal, however, a broad range of environmental and biological variables interact to cause temporal and spatial variability in catchability (Arreguin-Sanchez 1996; Pierce 1997; Speas et al. 2004). Population density, pond size and morphometry, habitat complexity, water transparency, water temperature, conductivity, time of day, and time of year are a just a few of such factors (McInerny and Cross 2000; Bayley and Austen 2002; Schoenebeck and Hansen 2005; Hangsleben et al. 2013). This suggests that catchability likely is not constant and can decrease over time even during prime sampling conditions resulting in more

removal events, lower catch rates, and difficulty in achieving the desired level of removal within a reasonable timeframe.

Understanding the effectiveness of intensive mechanical removals as a pond management tool for rehabilitating overcrowded largemouth bass populations is critical in determining the best strategy to correct overcrowded systems. Although, mechanical removals are very labor intensive, time consuming, and may be financially impractical depending on the number of removal events required. Often, the simplest and more cost-effective pond management strategy for undesirable largemouth bass populations is to drain the system, renovate, and restock. This strategy can effectively remove the overcrowded population and replace it with a desirable largemouth bass size structure within a couple years; however, draining their pond may be unfeasible or undesired by a pond owner, thus further research into potential pond management strategies to treat overcrowded largemouth bass ponds is an important necessity.

The purpose of this study was to evaluate the relationship between the intensity of largemouth bass removals and the strength of population responses in overcrowded largemouth bass populations. To test our hypotheses, my core objectives are to: (1) assess changes in largemouth bass and bluegill size structure and condition; (2) evaluate compensation in largemouth bass recruitment and growth; (3) estimate changes in largemouth bass energy allocation as a function of age and size; and lastly, (4) evaluate the relationship between largemouth bass removal effort and largemouth bass catchability. Overall, I hypothesized that there would a positive linear relationship for largemouth bass growth as a function of largemouth bass removal intensity and that increasing the intensity of largemouth bass removals would be effective in positively rehabilitating largemouth bass size structure to a more desirable status.

## **Methods**

### *Study sites*

I manipulated eleven ponds on the Auburn University Fisheries Research Unit, which is located 4 miles north of Auburn, Alabama, on Lee County Highway 147. These ponds were stocked with largemouth bass and bluegill at least seven years ago and contain mainly unharvested and unmanaged populations. As a result, these ponds were at various states of largemouth bass overcrowding. The eleven ponds selected for this study were as follows: S-2, S-5, S-7, S-15, S-16, S-22, S-24, S-28, S-30, AE-1, and FP-3. All ponds are small (mean surface area: 1.60 ha), shallow (mean max depth: 3.4 m), and eutrophic (mean Secchi depth: 1.27 m), with minimal aquatic vegetation coverage (0-8%), low total alkalinity (mean alkalinity: 23 ppm ( $CaCO_3$ )) and similar fish communities (Table 2). Other characteristics of the impoundments are summarized in Table 2.

### *Study design*

All eleven ponds were randomly selected to receive one of five possible removal treatments: 30%, 50%, 70%, 90%, and control (e.g. 0%). These percentages represented the target proportion of the largemouth bass population less than 356 mm to be removed annually. Each year, every pond underwent a population assessment first followed by a removal treatment. Each pond received two separate years of the exact same target removal treatment (i.e. Spring 2019 and 2020) and a third year of follow-up (i.e. Spring 2021). Sampling and fish collection were conducted in spring/early summer via boat electrofishing. I used a mark-recapture approach to estimate population abundance and the percentage of largemouth bass removed from each pond.

### *Population assessment and marking*

Population assessments and marking events were conducted annually in the spring. Fish were sampled during the day using 120 pulses per second (pps) DC electrofishing with electrical output between 3-8 amps, and one person netting off the bow of the boat. All ponds were sampled for at least one complete shoreline circuit. Length (mm) and weight (g) were measured and recorded for all fish species sampled. Captured largemouth bass were tallied into one of three size categories:  $\leq 254$ , 254-356, or  $\geq 356$  mm. All largemouth bass captured were batch marked with a dorsal spine clip (if  $\leq 254$  mm) and right pelvic fin clip (if  $\geq 255$  mm). Under the assumption that the largemouth bass will continue to grow, separate batch marks were necessary to distinguish the initial length group at first capture. Largemouth bass  $\geq 356$  mm received a PIT tag (i.e. Biomark HPT12 PLT tags) to acknowledge recapture in future years and track growth throughout the study. PIT tags were be preloaded in reusable needles (i.e. Biomark MK25 needles) and were inserted in muscle directly above the left operculum using an implant gun (i.e. Biomark MK25 PIT tag rapid implant gun). PIT tags were scanned with a portable PIT Tag reader (i.e. Biomark Model 601, ISO RFID Portable Reader) and ID numbers were recorded prior to release. Measurements of length and weight were be recorded for bluegill and additional captured fish species before immediate release. Additional electrofishing effort were be directed towards ponds that have less than one hundred largemouth bass batch marked following population assessments.

Post-mark and handling mortality was evaluated in each pond using cuboid net pens. Prior to release following population assessments, a subset of five largemouth bass  $\leq 254$  mm and five largemouth bass 254-356 mm were placed in a net pen for ~72 hours. Each net pen was 1.5 meters tall consisting of a 0.75 square meter frame at the end surrounded by 6 mm nylon mesh netting; floats were attached to the top frame to keep the net pen floating at the surface and brick

anchors were attached to the bottom frame to keep the net pen extended. Short-term largemouth bass mortality was recorded when net pens were removed.

### *Largemouth bass removals*

Largemouth bass removals were conducted at night using 120 pps DC electrofishing with electrical output between 3-8 amps, and one person netting off the bow of the boat. Only largemouth bass were captured during these sampling events. In Spring 2019 and 2020, all treatment ponds were sampled for one complete shoreline circuit per removal event at a rate of effort at 30 m/min. For each treatment pond, removal events were scheduled more than 2 days apart and all removals events were completed within a six-week period. Effort per pond varied relative to pond shoreline distance from 10-39 minutes per electrofishing event. Captured largemouth bass were checked for a batch mark and tallied into their associated size category. Marked largemouth bass were tallied as recaptured under  $\leq 254$  mm, 256-354mm, or  $\geq 354$  mm. Unmarked largemouth bass were tallied under three additional size categories with the same length restrictions. Marked largemouth bass  $\geq 356$  mm were scanned for a PIT tag and the ID number was recorded prior to release. Unmarked largemouth bass  $\geq 356$  mm received a PIT tag and length, weight, and ID number were recorded before immediate release. In 2019 and 2020, all captured largemouth bass  $\leq 356$  mm were collected and brought back to the lab for further analysis. In 2021, all captured largemouth bass, including largemouth bass  $\geq 356$  mm, were collected for further analysis. Tallies of marked largemouth bass collected in each pond were monitored during each removal event to determine when target removal treatments were achieved. Removals continued for each pond until the target removal percentage was reached in both  $\leq 254$  mm and 254-356mm length-groups or catchability became so low due to diminishing returns that further removal events were impractical.

### *Largemouth bass diets*

Largemouth bass diets from treatment ponds were collected from largemouth bass removed during removal treatments in Spring 2019 and 2020. Concurrent with removal events, control ponds were sampled for one complete shoreline circuit of boat electrofishing at a rate of effort at 30 m/min to collect largemouth bass diets. Stomach contents were removed using a hybrid tubing/gastric lavage technique (Seaburg 1957; Van Den Ayyle and Roussel 1980; Light et al. 1983; Soupir et al. 2000) where pressurized water was used to flush out the gut of the fish through clear acrylic tubing. Gut contents will be stored in plastic bags labeled with the fish length and weight and immediately placed on ice. Samples were placed in a freezer at the lab until analyzed. In late-summer 2019 and 2020, all treatment and control ponds were sampled for one complete shoreline circuit of boat electrofishing to collect largemouth bass diets for seasonal and post-treatment comparisons.

### *Environmental variables*

To account for possible variation between pond environments, measurements of ambient water quality parameters (i.e. water temperature and transparency) were measured monthly from February-October in every pond throughout the study. Water temperature was collected at 300 mm below the water surface using a water quality meter (i.e. YSI Professional Plus) and water transparency was collected off the shaded side of the boat as the depth, in meters, where the Secchi disk is no longer visible. Additionally, ponds were fertilized with SportMAX pond fertilizer (10N-52P-4K) at a rate of six pounds per acre (AU Extension) routinely from March-October 2019 and 2020, to increase productivity and reduce water transparencies to 0.5-0.75 meters. Fertilizer was poured directly off the side of the boat, over the center of each pond as SportMAX is 100% water soluble.

### *Laboratory work*

For each largemouth bass collected, total body length, body weight, liver weight, gonad weight, and the level of visceral fat observed in the body cavity were recorded. Gonad maturity was macroscopically staged, stomachs were removed, and sagittal otoliths were collected.

Level of visceral fat observed in the body cavity was recorded as none/low, high, or intermediate. None/low was distinguished by very little to no visible excess visceral fat surrounding the organs within the body cavity. High was distinguished by visible excess visceral fat surrounding the organs as well as occupying nearly all available space within the body cavity. Intermediate was distinguished by some visible excess visceral fat within the body cavity.

Gonad maturity was staged macroscopically for both male and female largemouth bass. Ovary maturity was assigned into three maturity stages: immature (i.e., ovaries very small, little to no eggs, and no blood vessels) pre-spawn or ripe (i.e., plump, bright orange eggs with visible oocytes and large blood vessels), and spent (i.e., flaccid, loose ovary tissue that is purple in color; James 1946; Hinton 1990). Testes maturity were assigned into three maturity stages: inactive (i.e., small, thin, or ribbon-like, often clear or pinkish in color; no spermatozoa) or developing (i.e., small, but firm, white and often triangular shaped; spermatozoa not released when testis is cut), pre-spawn or spawning (firm, white, and enlarged; spermatozoa not released when testis is cut (i.e., pre-spawn) and spermatozoa released when pressure is applied to abdomen or when testis is cut (i.e., spawning)), and spent (i.e., elongated and flaccid, often pinkish in color; no spermatozoa released; James 1946; Hinton 1990).

Removed stomachs were preserved in 70% ethanol and stored in three-inch containers with appropriate identification. Stomachs were dissected open, and the contents were evaluated

using a binocular microscope. Stomach contents collected in the field were evaluated using a binocular microscope. Contents were sorted, counted, blotted dry, and weighted for wet weights. Invertebrates were identified to the order and fish to species.

Sagittal otoliths were removed using the through-the-gills method (Schneidervin and Hubert 1986; Secor et al. 1992), rinsed in distilled water, dried and cleared of semicircular canal tissue using 1-ply tissue (i.e., Kimtech Science Kimwipes), and stored in two-inch vials with appropriate identification. Otoliths were collected from ten largemouth bass per 10 mm length-group, if present, for age and growth analysis for each pond. Otoliths were embedded in an epoxy mold and sectioned transversely along the dorsoventral plane using a low speed diamond wheel saw (i.e. South Bay Technology Model 650) with two wafering blades (i.e. Buehler Inc.) separated by a spacer. Cross-sections were cut to 0.55-0.65 mm, mounted on microslides using crystalbond mounting adhesive, and lightly covered with immersion oil. Cross sections of otoliths were read and aged by two independent readers using a dissecting scope (i.e. Nikon SMZ800) mounted with a camera (i.e. Nikon Digit Sight DS-F12), and discrepancies were resolved by consensus reading. Lastly, annuli incremental measurements (i.e. distance between two successive annuli) were measured using an imaging software (i.e. NIS Elements AR version 4.20).

#### *Population estimation and biomass*

Annual population estimates for treatment ponds were calculated for largemouth bass  $\leq 254$  mm and 254-356 mm using the Lincoln-Peterson model (Peterson 1896; Lincoln 1930). The Lincoln Peterson estimator was rearranged to represent a removal model such that the population estimate was equivalent to the number of captured fish divided by the ratio of

recaptured fish to marked fish in the population. The Chapman modification of the Lincoln-Peterson estimator (Seber 1982) was rearranged and described as:

$$\hat{N} = \frac{(C + 1)}{(R + 1)/(M + 1)} - 1$$

where, with respect to each length-group,  $\hat{N}$  was the population estimate,  $C$  was the total number of largemouth bass captured and removed during all removal events,  $R$  was the total number of marked largemouth bass captured and removed during all removal events, and  $M$  was the total number of marked largemouth bass in the population prior to the start of all removal events.

Assuming all the largemouth bass had the same capture probability and there were no differences in trap response or individual heterogeneity, the proportion of recaptures removed relative to the total number of marked largemouth bass prior to any removal events represented the percentage of the population removed. Population estimates of <356 mm largemouth bass were calculated by adding together population estimates and variances from each respective length group.

Confidence intervals were computed with a log-normal distribution, which corrects the confidence intervals to be logically consistent with  $m(t + 1)$ , which is the known number of largemouth bass marked, captured, and/or removed in/from the population at time  $t + 1$ , and  $f_0$ , which is the number of largemouth bass never captured (Lukacs 2010).  $f_0$  described as:

$$f_0 = \hat{N} - m(t + 1).$$

Therefore, the lower and upper confidence interval are described as:

$$\text{Lower CI} = \frac{f_0}{c} + m(t + 1) \text{ and } \text{Upper CI} = f_0 * c + m(t + 1),$$

where  $c$  is a bias correction factor described as:

$$c = e^{1.96 \sqrt{\log \left(1 + \frac{SE(f_0)}{f_0^2}\right)}}$$

Annual population size for control ponds was estimated for both length-groups using the Schnabel model (Schnabel 1938; Seber 1982) described,

$$\hat{N} = \frac{\sum_{i=2}^t C_i M_i}{\sum_{i=2}^t R_i + 1}$$

where, with respect to each length-group,  $\hat{N}$  was the population estimate,  $t$  was the number of sampling occasions,  $C_i$  was the number of largemouth bass caught in the  $i$ th sample,  $R_i$  was the number of marked largemouth bass caught in the  $i$ th sample, and  $M_i$  was the number of marked largemouth bass present in the population for  $i$ th sample. Population estimates of <356 mm largemouth bass were calculated by adding together population estimates and variances from each respective length group. Confidence intervals were calculated as described by Seber (1982) that if the ratio of  $R/C > 0.10$ , binomial confidence intervals were used (Wilson method; Brown et al. 2001), if the ratio of  $R/C < 0.10$  but  $R > 50$ , normal approximation confidence intervals were used, and if  $R/C < 0.10$  and  $R < 50$ , P confidence intervals were used.

Annual population biomass estimates for largemouth bass populations <254 mm and 254-356 mm were calculated for each pond using the population estimates and mean body weight estimates,

$$B = \hat{N} * W,$$

where, with respect to each length-group,  $B$  was the estimated population biomass,  $\hat{N}$  was the estimated abundance, and  $W$  was the mean individual body weight. Population biomass for largemouth bass populations <356 mm was calculated by adding together population biomass

estimates from each respective length-groups. Confidence intervals were calculated using the equation above by replacing the estimated abundance with its lower and upper confidence intervals. Annual population biomass removed from each pond was calculated by dividing total biomass removed by the estimated population biomass.

#### *Largemouth bass and bluegill size structure and condition*

Population size structure was assessed with the index of proportional size distribution, the percentage of stock length fish that are also quality length, i.e., PSD-Q, (Guy et al. 2007) which quantifies a length-frequency distribution for a population (Anderson and Neumann 1996). PSD-P, which are the percentage of stock length fish that are also preferred length (Gabelhouse 1984), was also assessed for each pond in this study. PSD-Q and PSD-P were calculated as:

$$PSD - Q = \frac{\text{number} \geq \text{minimum quality length}}{\text{number} \geq \text{minimum stock length}} * 100$$

$$PSD - P = \frac{\text{number} \geq \text{minimum preferred length}}{\text{number} \geq \text{minimum stock length}} * 100$$

When calculated for largemouth bass, a stock length of 150 mm, quality length of 300, and a preferred length of 380 were used (Anderson and Neumann 1996). Only largemouth bass captured during annual population assessments were included in the calculation of PSD indices. Largemouth bass condition was evaluated using relative weights ( $Wr$ ; Wege and Anderson 1978).  $Wr$  was calculated as:

$$Wr = 100 \times (\text{body weight} / \text{standard weight})$$

Standard weight was based on an extensive summary of length-weight data for largemouth bass (Henson 1991) and was described as

$$\text{Standard weight} = 3.273 * \log_e(\text{total length in mm}) - 5.528$$

Catch-per-unit-effort (CPUE) of stock-size bluegill (i.e., 80-150 mm) were evaluated to determine responses in larval and juvenile survival following a release from predation. CPUE of <254, 254-356, and >356 mm largemouth bass were also calculated to evaluate differences in largemouth bass catch rates following removal treatments. CPUE was calculated using the largemouth bass and bluegill electrofishing catch rates from annual population assessments and were expressed in units of fish per hour. Before-after-control-impact (BACI) analyses were used to test for the effects of largemouth bass removal intensity on the strength of responses in population size structure and condition. Differences in PSDs, mean relative weights, and CPUEs between 2019 (before removal) and each subsequent post-removal year (2020 and 2021) were modeled as a function of proportion biomass removed. These analyses were fit with a linear mixed effects model via maximum likelihood in R (R Core Team 2014) with fixed effects of proportion biomass removed, time-period (2020 and 2021), pond water surface area (ac), pond shoreline distance (m), and mean Secchi depth from March-October, and an independent random effect of pond. All possible interactions among fixed effects were also examined. The analyses were performed on the natural logarithmic scale ( $\log_e$ ) to meet assumptions of normality and homogeneity of variance.

#### *Largemouth bass recruitment and growth compensation*

Compensatory growth in largemouth bass length for age-1 recruits was evaluated by estimating mean length of age-1 largemouth bass. Mean length-at-age was obtained from otolith-aged subsamples by calculating the weighted average length of each age class, weighted by the sample size in each size class (DeVries and Frie 1996). Weighted average length of each age class for control ponds was obtained only from 2021 since largemouth bass were not removed

for aging in 2019 or 2020. Weighted average length of each age class in 2021 was used to calculate mean length-at-age for 2019 and 2020 data.  $\text{Log}_e$  differences in mean length from age 1 largemouth bass from 2019-2020 and 2019-2021 were evaluated as a function of proportion biomass removed. This BACI analysis was fit with a linear mixed effects model via maximum likelihood in R with the same fixed and random effects as listed above.

Compensatory growth in length for age-2 largemouth bass was evaluated with incremental growth analysis by using annuli incremental measurements from each sectioned otolith. Incremental measurements were back calculated assuming growth of the otolith was directly proportional to the growth of an individual largemouth bass. Back calculated length-at-age was calculated using the Dahl-Lea method (Dahl 1907; Lea 1910) as described,

$$L_i = L_c \left( \frac{S_i}{S_c} \right),$$

where  $L_i$  was the back calculated length at annulus  $i$ ,  $L_c$  was length at capture,  $S_i$  was otolith radius at annulus  $i$ , and  $S_c$  was the otolith radius at capture. A growth increment was described as the otolith length increment from the last full year of growth as a function of initial back-calculated body length at the beginning of that full year of growth. The analysis was restricted to the last growth increment to reduce bias among year-classes (Schindler et al. 2000; Michaletz 2009). Incremental growth for age-2 largemouth bass in control ponds was evaluated using otolith-aged largemouth bass in 2021 by obtaining back calculated initial body lengths and growth increments for largemouth bass that were age-2 in 2019 and 2020.  $\text{Log}_e$  differences in mean growth increment for age-2 largemouth bass from 2019-2020 and 2019-2021 were evaluated as a function of proportion biomass removed. This BACI analysis was fit with a linear

mixed effects model via maximum likelihood in R with the same fixed and random effects as listed above.

Compensatory growth in length for age-2+ largemouth bass was also evaluated with incremental growth analysis. To control for selective removal of slow or fast growing largemouth bass during treatment years, the incremental growth of each individual largemouth bass aged during the study was modeled independently with a random slope and random intercept. The  $\log_e$  incremental growth as a function of initial body length was fit separately for each pond with a linear mixed effects model via maximum likelihood in R with fixed effects of initial body length and time-period and a random effect of initial length nested in individual fish. AICc model selection, i.e. corrected Akaike's Information Criterion for small sample sizes (Akaike 1974; Hurvich and Tsai 1989), was used to verify this model as the best fit model for the data compared to simpler models. Differences in model y-intercepts from 2019-2020 and 2019-2021 were evaluated as a function of proportion biomass removed to examine changes in mean incremental growth of age-2+ largemouth bass.

Compensatory largemouth bass recruitment as a function of largemouth bass removal intensity was evaluated by estimating differences in the CPUE of age-1 recruits in annual population assessments. Number of age-1 largemouth bass captured during the annual population assessment was estimated by applying pond and year-specific age-length keys constructed from aged subsamples to unaged fish. For the control ponds, the 2021 age-length key was used to estimate ages in 2019 and 2020 because no largemouth bass were removed from these ponds for aging during spring 2019 or 2020.  $\log_e$  differences in CPUE of age-1 largemouth bass from 2019-2020 and 2019-2021 were evaluated as a function of proportion biomass removed. This BACI analysis was fit with a linear mixed effects model via maximum likelihood in R (R Core

Team 2014) with fixed effects of proportion biomass removed, time-period, pond water surface area (ac), pond shoreline distance (m), and mean Secchi depth from March-October, and an independent random effect of pond. All possible interactions among fixed effects were also examined.

#### *Largemouth bass energy allocation*

Visceral fat levels (e.g., Delahunty & de Vlaming 1980; Adams & McLean 1985), liver-somatic (*HSI*; e.g., Heidinger & Crawford 1977; Htun-Han 1978), and gonadal-somatic (*GSI*; e.g., Nikolsky 1963; Chang & Navas 1984) indices were used to indicate potential differences in energy allocation as a function of removal intensity. Condition indices, *GSI* and *HSI*, are calculated as follows:

$$GSI = 100 \times (\text{gonad weight} / \text{body weight})$$

$$HSI = 100 \times (\text{liver weight} / \text{body weight}).$$

$\text{Log}_e$  differences in *GSI*, *HSI*, and level of visceral fat from 2020-2021 were evaluated as a function of proportion biomass removed. These BACI analysis was fit with a linear mixed effects model via maximum likelihood in R with the same fixed and random effects as listed above.

Differences in largemouth bass maturity as a function of proportion biomass removed was evaluated by calculating length at 50% maturity. Length at 50% maturity was evaluated using logistic regression by fitting a generalized linear model to binomial maturity data (immature=0, mature=1).  $\text{Log}_e$  differences in length at 50% maturity from 2019-2020 and 2019-2021 were evaluated as a function of proportion biomass removed. This BACI analysis was fit

with a linear mixed effects model via maximum likelihood in R with the same fixed and random effects as listed above.

Potential changes in prey consumption as a function of proportion biomass removed was evaluated by analyzing largemouth bass diets. Wet weights of sorted stomach contents were used to calculate frequency of occurrence of fish in diets (Garvey and Chipps 2012). Frequency of fish in diets was calculated by dividing the number of diets containing fish by the total number of non-empty diets. Mean individual weight of fish in diets was also evaluated and was calculated by dividing the bulk weight of fish divided by the total count of individual fish observed. Only whole fish were included in this calculation.  $\text{Log}_e$  differences in frequency of occurrence of fish and mean individual weight of fish in largemouth bass diets from 2019-2020 and 2019-2021 were evaluated as a function of proportion biomass removed. This BACI analysis was fit with a linear mixed effects model via maximum likelihood in R with the same fixed and random effects as listed above.

#### *Largemouth bass removal effort and catchability*

Catchability was defined as the proportion abundance removed per shoreline circuit of electrofishing, expressed as:

$$q_i = (C_i/N_i)/E,$$

where, with respect to each length-group,  $q_i$  was the catchability during removal event  $i$ ,  $C_i$  was the number of largemouth bass removed during removal event  $i$ , and  $N_i$  was the largemouth bass population estimate prior to each removal event  $i$ .  $E$  was be quantified as the proportion of pond shoreline electrofished in each removal event  $i$ , which will always equal 1.0 because an entire shoreline circuit was completed for each removal event. Using the proportion of shoreline

electrofished as our unit of effort and sampling the entire shoreline resulted in catchability that was solely dependent on the number of largemouth bass removed in a removal event relative to the abundance estimate prior to that removal event. This allowed comparisons among ponds while implicitly including differences in morphometry, habitat complexity, and other variables. Mean catchability was estimated annually for largemouth bass  $\leq 254$  mm and 254-356mm for each removal event on every pond. Assuming random mixing and equal catchability of marked and unmarked largemouth bass, our estimates of catchability represented the catchability of the largemouth bass  $\leq 356$ mm in each pond during each removal event. Differences in mean catchability were evaluated as a function of the number of removal events. These BACI analyses were fit with a linear mixed effects model via maximum likelihood in R with fixed effects of removal events, year, and length-group.

## **Results**

### *Largemouth bass removals*

In 2019 and 2020, more than 100 largemouth bass were fin-clipped in every treatment pond prior to removal treatments except for S24 in 2019, which only contained 78 marked largemouth bass prior to treatment. In 2019, on average, 67.7% of marked largemouth bass were  $< 254$  mm in each pond ranging from 35.1-92.2% and, on average, 80.0% of marked largemouth bass were  $< 254$  mm in each pond in 2020 ranging from 36.5-95.6%. A total of 174 largemouth bass  $> 356$  mm were PIT tagged during my study. In 2019, 50 largemouth bass were PIT-tagged, and 124 additional largemouth bass were PIT-tagged in 2020. Thirty-three PIT-tagged largemouth bass were recaptured in subsequent years: 27 in 2020 and 11 in 2021. Five PIT-tagged largemouth bass were recaptured in all three years of my study.

Mechanical removals were more successful at achieving all target largemouth bass removal treatments in 2020 than in 2019 (Table 3; Figure 1). Estimates of proportion abundance removed were similarly achieved in both 2019 and 2020 for 30% and 50% removal treatments. In 2019, S2 was the only pond in the 70% or 90% removal treatment with an estimated proportion abundance removed greater than 50% (54.6%). Diminishing returns in largemouth bass catchability ultimately ended removal events in 2019 as catch per unit effort became too low to practically continue removal events. In 2020, 70% and 90% removal treatments were more successfully achieved with estimates of proportion abundance removed of 60.4% and 68.2% for the 70% removal treatment ponds and 76.5% and 83% for the 90% removal treatment ponds. Conversion of proportion abundance removed to proportion biomass removed resulted in no significant differences in estimates (Figure 1). Overall, no significant relationships were identified for differences in largemouth bass abundance or biomass as a function of proportion biomass removed ( $p=0.502$ ,  $p=0.615$ , respectively; Figure 2).

Following annual population assessments, 22 post-mark and handling mortality trials were conducted in 2019 and 2020 with a result of 100% survival of marked largemouth bass after ~72 hours of containment.

#### *Largemouth bass and bluegill size structure and condition*

Largemouth bass PSD-Q ( $p=0.004$ ,  $R^2=0.534$ ; Figure 3a) and PSD-P ( $p=0.025$ ,  $R^2=0.299$ ; Figure 3b) increased significantly with increasing proportion biomass removed from 2019-2021. For every 10% increase in proportion biomass removed, largemouth bass PSD-Q increased by 1.667 units from 2019-2021 relative to control ponds and largemouth bass PSD-P increased by 1.604 units relative to control ponds from 2019-2021. However, the strength of these relationships resulted mainly from declines in largemouth bass size structure in control

ponds rather than substantial improvements in treatment ponds. Mean relative weight of 254-356 mm largemouth bass increased significantly by 0.133 units for every 10% increase in proportion biomass removed relative to control ponds from 2019-2020 ( $p=0.003$ ,  $R^2=0.503$ ; Figure 4b) but not 2020-2021. Lastly, CPUE of >356 mm largemouth bass increased significantly by 2.168 fish per hour relative to control ponds for every 10% increase in proportion biomass removed from 2019-2021 ( $p=0.0248$ ,  $R^2=0.418$ ; Figure 6c). No significant relationships were identified for differences in mean relative weights of <254 mm largemouth bass ( $p=0.0989$ ; Figure 4a), mean relative weights of >356 mm largemouth bass ( $p=0.314$ ; Figure 4c), and CPUE of stock size bluegill from 2019-2021 ( $p=0.0512$ ; Figure 5). No size structure and condition variables were related to water surface acreage, pond shoreline distance, and mean Secchi depth from March-October so they were removed from the linear mixed effects models.

#### *Largemouth bass recruitment and growth compensation*

No significant relationships were identified between measures of growth or recruitment as a function of proportion biomass removed. Differences in CPUE of <254 and 254-356 mm largemouth bass did not significantly relate to proportion biomass removed ( $p=0.317$ ,  $p=0.676$ , respectively; Figure 6). Differences in CPUE and mean length-at-age of age-1 largemouth bass were unrelated to proportion biomass removed ( $p=0.624$ ,  $p=0.485$ , respectively; Figure 7, Figure 8). Lastly, no relationship was identified for mean incremental growth for age-2 and age-2+ largemouth bass as a function of proportion biomass removed ( $p=0.410$ ,  $p=0.159$ , respectively; Figure 8, Figure 9). All relationships in largemouth bass recruitment and growth were unrelated to pond water surface area, pond shoreline distance, and mean Secchi depth from March-October so they were removed from the linear mixed effects models.

#### *Largemouth bass energy allocation*

A significant negative relationship for male and females was identified for differences in largemouth bass mean GSI as a function of proportion biomass removed from 2020-2021 for both <254 and 254-356 mm length groups. Largemouth bass mean GSI decreased by 1.43% for every 10% decrease in proportion biomass removed from 2020-2021 ( $p=0.023$ ,  $R^2=0.408$ ; Figure 10a-b). Control ponds were not included in this model because no largemouth bass were removed from control ponds in 2020. No significant relationships were identified for differences in other largemouth bass energy allocation metrics as a function of proportion biomass removed from 2020-2021. Gonads, liver, and visceral fat were not evaluated in spring 2019. Differences in mean HSI and level of visceral fat did not significantly relate to proportion biomass removed ( $p=0.084$ ,  $p=0.556$ , respectively; Figure 10c-f). Length at 50% maturity for males and females were unrelated to proportion biomass removed ( $p=0.485$ ,  $p=0.0682$ , respectively; Figure 11). Lastly, frequency of occurrence and mean individual weight of fish in diets did not significantly relate to proportion biomass removed from pre-removal in spring 2020 to post-removal in summer 2020 ( $p=0.986$ ,  $p=0.194$ , respectively; Figure 12). No size structure and condition variables were related to pond water surface area, pond shoreline distance, and mean Secchi depth from March-October so they were removed from the linear mixed effects models.

#### *Largemouth bass removal effort and catchability*

On average, 6-7 removal events were conducted on each pond in 2019 to achieve the respective removal treatment with a range of 4-10 events. The average was slightly lower in 2020 as 5-6 removal events were conducted on each pond with a range of 1-9 events. Mean largemouth bass catchability for <254 and 254-356 mm length groups were statistically similar in 2019 ( $p=0.577$ ; Figure 13) with mean catchability significantly decreasing as a function of removal events from a high of 0.183 on average in the first removal event down to an average of

0.040 by tenth removal event ( $p=0.0037$ ,  $R^2=0.337$ ; Figure 13). In 2020, mean catchability for <254 mm largemouth bass followed a similar trend as mean catchability in 2019 ( $p=0.769$ ; Figure 13) with decreasing mean catchability as a function of removal events from as high as 0.218 on average in the first removal event down to an average of 0.042 by the ninth removal event ( $p=3.62e-05$ ,  $R^2=0.6651$ ; Figure 13) Mean catchability for 254-356 mm largemouth bass was more variable as a function of removal events ranging on average from 0.130-0.297, but did not significantly relate to the number of removal events ( $p=0.916$ ; Figure 13). Overall, mean cumulative proportion abundance removed across removal events revealed that largemouth bass catchability decreased following each subsequent removal event in both 2019 and 2020 (Figure 14).

## **Discussion**

Understanding population responses of largemouth bass across a range of mechanical removal intensities is critical to determining the effectiveness of the approach to rehabilitate over-crowded largemouth bass populations in small impoundments. Previous work on mechanical removals as a tool for rehabilitating over-crowded largemouth bass ponds have consisted of single pond experiments with limited to no significant improvements in largemouth bass populations (Eder 1984, Gablehouse 1987, Novinger 1990, Willis et. al 2010). These studies also achieved only modest largemouth bass population reductions (insert max percent remove here). My study was the first to use multiple replicate ponds within a controlled study design to evaluate the relationship between the strength of population responses and the intensity of largemouth bass removals. Moreover, my study was able to achieve more intense largemouth bass removal treatments than previously documented in any other study. Despite these strong reductions, I observed only modest changes in some of the largemouth bass population metrics.

### *Largemouth bass and bluegill size structure and condition*

Largemouth bass size structure in treatment ponds showed evidence of significant improvement relative to control ponds. This result was not consistent with previous largemouth bass removal experiments. For example, Willis et. al (2010) did not see significant improvements in population size structure until year 5 of their experiment. However the lack of control ponds in the Willis et al (2010) study makes interpretation of these findings difficult. Other studies did not see significant improvements in largemouth bass population size structure over the course of their experiments; however, many of these studies did not remove largemouth bass larger than 300 mm (Eder 1984, Gablehouse 1987, Novinger 1990, Martin 1995, Willis et. al 2010). In my study, I chose to remove largemouth bass 356 mm or less. Perhaps by removing largemouth bass from this larger size class, potentially more resources were available for growth due to the removal of larger competitors. An important caveat for my study is that the strength of the PSD relationships resulted mainly from declines in largemouth bass size structure in control ponds rather than substantial improvements in treatment ponds. Although PSD relationships significantly increased as a function of proportion biomass removed, the magnitude of biological changes in largemouth bass population size structure in treatment ponds were not very large (i.e., 1.6 units per 10% increase in proportion biomass removed).

Largemouth bass body condition improved in treatment ponds relative to controls from 2019-2020 only for largemouth bass in the 254-356 mm size class. However, this significant relationship did not continue into 2021 and was not present for the other two size classes. My findings were consistent with Eder (1984), that determined no changes in body condition of largemouth bass less than 305 mm but found significant increases in the condition of 305-378 mm largemouth bass (i.e., 12-14.9 inches) following imposition of slot length limit on a 100 acre

impoundment in Missouri. As to why body condition of 254-356 mm largemouth bass increased significantly from 2019-2020 but not from 2019-2021 is unclear. The response in 2019-2020 may have resulted from increased prey availability and/or a competitive release following largemouth bass removals, but no significant changes in CPUE of intermediate bluegill, <254 or 254-356 mm largemouth bass were evident in 2019-2020. Wege and Anderson (1978) found a positive correlation between body condition of 200-299 mm largemouth bass and the prey biomass in the same ponds. This could explain the strong compensatory response in body condition of 254-356 mm largemouth bass in 2020 as large proportions of that length group were removed from all the treatment ponds perhaps resulting in a release from strong density dependent conditions. However, given that CPUE of stock size bluegill did not significantly improve as a function of largemouth bass removal intensity, interpreting why body condition of 254-356 mm largemouth bass in 2021 was not significantly higher in treatments ponds compared to control ponds is unclear.

#### *Largemouth bass recruitment and growth compensation*

Despite largemouth bass removal intensities that achieved upwards of a 50% biomass reduction of target size classes, I found no evidence of compensation in growth or recruitment. Gablehouse (1987) believed a more intense removal of above 50% annually may have been necessary to achieve significantly higher growth rates in his study pond. Willis et. al (2010) concluded that, in hindsight, initial largemouth bass removal intensity should have been as high as 70% removal of the overcrowded population to achieve faster growth rates. I removed as much as 82% of an overcrowded population from one of my treatment ponds, yet I saw very limited growth compensation in any of my treatment ponds relative to the controls. It is possible that two years of annual removals is not a long enough time frame to observe the full effect of

largemouth bass removal in these systems. Willis et. al (2010) did not see significant improvements in largemouth bass growth until year 5 of annual largemouth bass removals.

I hypothesized largemouth bass growth compensation may be countered by a compensatory response in largemouth bass recruitment, but I found no significant differences between largemouth bass recruitment in treatment ponds compared to controls. Instead, recruitment was relatively constant in the face of the removals. The CPUE of <254 and 254-356 mm largemouth bass from 2019-2021 did not significantly differ in treatment ponds relative to control ponds. This shows evidence of replacement as following intensive largemouth bass removals, enough smaller largemouth bass survived to replaced largemouth bass in larger length-groups removed from the system and consistent recruitment replaced largemouth bass in smaller length-groups. This consistency in recruitment perhaps indicates an asymptotic Beverton-Holt spawner-recruitment relationship. It has been documented that in low population densities, increased pre-recruit survival would likely be the primary mechanism for compensation (Rose et al. 2001; Lorenzen and Enberg 2002). In contrast, Novinger (1990) concluded that largemouth bass recruitment may be primarily a result of the pond environment rather than the population dynamics of the system. I speculate that intensive largemouth bass removals alone may have limited success in releasing a system from strong density dependent conditions within a two-year time frame. In addition to intensive largemouth bass removals, rehabilitating an overcrowded largemouth bass population may require increasing mortality of age-0 largemouth bass. Novinger and Legler (1978) concluded that management actions to improve growth rates and size structure of high-density populations likely require reducing densities of recruited cohorts by increasing mortality of age-0 fish. Potentially a combination of intensive largemouth bass removals followed by shoreline rotenone treatments to enforce higher mortality of age-0 recruits could

effectively release the overcrowded population from strong density-dependent conditions and lead to stronger compensatory responses in growth and size structure. Coleman (2019) concluded that shoreline rotenone application reduced largemouth bass recruitment in small impoundments and improved largemouth bass growth rates and body condition. Unfortunately, no studies to my knowledge have been conducting using largemouth bass removals and shoreline rotenone application in combination.

#### *Largemouth bass energy allocation*

I hypothesized that the strength of growth responses following largemouth bass removal treatments could be hindered by allocation of energy to reproduction and condition as a function of age and size. However, I found no significant differences in HSI, stage of visceral fat, length-at-50% maturity, or in consumption of fish in treatment ponds relative to control ponds. Mean GSI significantly decreased as a function of proportion biomass removed but control ponds were not included in this model. Considering that the power of this relationship derives primarily from not including differences in mean GSI for control ponds, a more conservative interpretation of the impact of mechanical removals on mean GSI based on these results is advised. Given that I found limited compensatory responses in largemouth bass growth, it is interesting that minimal signs of allocating more energy towards reproduction and condition were evident. Strong density-dependent conditions in small impoundments have been documented to lead to earlier maturation schedules resulting in younger age and smaller length at maturity (Diana and Saltz 1990; Jennings and Phillip 1992; Danylchuk and Fox 1994; Justus and Fox 1994; Ridgway and Chapleau 1994; Jansen 1996; Claussen et al. 1998). I did not see any changes in length-at-50% maturity in treatment ponds relative to control ponds, thus any additional energy consumed because of influx prey availability following largemouth bass removals should be allocated to

reproduction or condition since there was no evidence of significant incremental growth. However, upon analysis of diets, no evidence was found that largemouth bass in treatments ponds were consuming more fish or larger fish relative to largemouth bass in controls following largemouth bass removals in 2020.

#### *Largemouth bass removal effort and catchability*

I found that largemouth bass catchability tended to decline and vary over time resulting in increased difficulty in achieving target removal treatments following each subsequent removal event. This was not surprising as studies have documented that catchability is unlikely to remain constant due to variation in environmental and biological variables (Arreguin-Sanchez 1996; Pierce 1997; Speas et al. 2004). My removal treatments were conducted at night in the spring when water temperatures ranged between 15-23 C as recommended by Pope et al. (2009) to produce the highest catch rates of largemouth bass. Yet, the higher target removal treatments required as many as 10 removal events. Particularly for the 70% and 90% target removals, treatments were halted prior to completion due diminishing returns on catch rates. This was expected as studies have shown largemouth bass catchability is inversely related to population density (Simpson 1978). Ultimately, diminishing returns on catch rates resulted in additional time, effort, and funding invested into the removal process and given the limited successes of my study, the practicality and value of mechanical removals for rehabilitating overcrowded largemouth bass ponds is called into question. It is possible that the long-term results of continued intensive mechanical removals could reflect a more rewarding outcome, but long-term studies of this magnitude would likely be impractical.

#### **Management Implications**

Two years of mechanical removals via boat electrofishing do not appear to rehabilitate overcrowded largemouth bass populations in Alabama small impoundments. In comparison with agency annual largemouth bass harvest recommendations for small impoundments, only S30 achieved more than the recommended 30 lbs per acre for fertile ponds in 2019 and only S30 achieved that mark in 2020 as well (Figure 15). Under the assumption of removing largemouth bass from infertile ponds, no ponds achieved more than the recommended 15 lbs of removal per acre in 2019 other than S30; however, AE1, S15, S2, S22, and S28 in addition to S30 achieved that mark in 2020. My results revealed that the removal process seemed to maintain the current state of largemouth bass growth, condition, and population size structure in treated ponds compared to control ponds. This supports the idea that state and private agency annual largemouth bass harvest recommendations serve to assist in maintaining a population size structure rather than rehabilitating an overcrowded population.

Pond draining and re-stocking is another approach that could be used to renovate overcrowded largemouth bass populations. Within two years of restarting a pond in Alabama and other southern states, largemouth bass and bluegill populations would be established, and largemouth bass harvest could begin again (Wright and Kraft 2012). Arguably, the first 5-7 years after stocking offer some of the most quality fishing in a pond under moderate management (Slipke and Sammons 2012). The findings from my study suggest that draining and restocking may be a more rapid approach to achieving desirable largemouth bass populations when compared with intensive harvest, at least over a short timeframe. When draining a pond is undesirable or unwarranted, potentially a combination of intensive largemouth bass removal treatments, shoreline rotenone applications, and/or supplemental stocking could produce significant improvements in the largemouth bass populations in a relatively shorter timeframe

than any one of the strategies could alone. Future research on largemouth bass removals could experiment with a combination of intensive removal treatments followed by shoreline rotenone applications. This collaboration may warrant the best-case scenario of releasing overcrowded largemouth bass populations from strong density dependent conditions.

## **Chapter 2. Evaluation of electrofishing and marking recapture behavior using closed population capture-recapture methods**

### **Abstract**

Closed-population mark-recapture methods for estimating population size are widely used in fisheries applications. A key assumption of these methods is equal capture probability for every individual of the population; however, this assumption is often violated resulting in biased estimates of population size. Closed-population mark-recapture models often generate abundance estimates from electrofishing capture data. Varying behavioral responses induced by electrofishing likely lead to changes in capture probabilities and consequently biased abundance estimates. More complex closed population mark-recapture models are available in programs such as RMark to allow for multi-phase mark-recapture study designs to be robust to variation in capture probabilities. More clarity on the limitations of detecting differences in capture and recapture probabilities using programs like RMark are essential to understanding how to more strategically design closed population mark-recapture studies to calculate better abundance estimates. The objectives of this work were to show the limitations of detecting a recapture effect when using a mark-recapture/removal study design, investigate the effect of recapture behavior on bias in abundance estimates, and evaluate how our findings correlate with model selection of 29 mark-recapture/removal datasets. I used RMark to conduct Monte Carlo simulations of closed population capture-recapture models for ranges of variability in capture and recapture probabilities, population size, initial capture probability, and the number of removal events. Population size, initial capture probability, and variability in capture probability had the strongest influence on detecting a recapture effect and, therein, selecting for a model with recapture effect as the best fit model to the data. Ultimately, the best scenarios for high mean percent model

selection for a recapture effect contained high population size, no variability in capture probability, and high initial capture probability. Population size and variability in capture probability had the strongest influence on mean proportional error in derived abundance estimates of models with a recapture effect relative to the true population size. I found very little bias in abundance estimates of models with a recapture effect relative to the true population size for nearly all scenarios except those with low population size, a low number of removal events, and a low initial capture probability. Lastly, derived abundance estimates of models without a recapture effect overestimated true population size in all scenarios except those with both a high initial capture probability and a high number of removal events. Overall, I found that the best fit models for all 29 data sets correlated well with the results of my simulations. The results of this study provide important insight into the dangers of assuming equal capture probability and using simple closed population capture-recapture models that are not robust to potential differences in capture and recapture probabilities. My results suggest that marking fish can reduce bias in abundance estimates if differences in capture and recapture probabilities can be tested for by using a more complex model.

## **Introduction**

Closed-population mark-recapture methods for estimating population size are widely used in fisheries applications (Seber 1982; Pollock et al. 1990; Williams et al. 2002; Pine et al. 2003). A key assumption of these methods is equal capture probability for every individual of the population. This implies that marked and unmarked fish are equally likely to be captured and no heterogeneity or behavior responses exist among individuals due to inherent differences or prior capture experiences. This assumption is often violated resulting in biased estimates of population size (Mahon 1980; Thurow et. al 2001). It is recognized that commonly used closed-population

models such as the Lincoln-Peterson or Schnabel are not robust to variable capture probabilities (Pine et. al 2012), yet these models continue to be among the most common population estimators, particularly in small, closed populations such as in streams or ponds (Ricker 1975; McInerny and Cross 1999; Kocovsky and Carline 2001). These models remain appealing because they are conceptually straightforward and intuitive, however, failing to account for differences in capture probability between marked and unmarked individuals may result in biased estimates of population size and ultimately lead to misinterpretation and mismanagement of fish populations (Bayley and Dowling 1993; Arreguin-Sanchez 1996).

More complex closed population mark-recapture models are available to allow for multi-phase mark-recapture study designs to be robust to variation in capture probabilities among individuals. A hierarchical suite of closed-population capture-recapture models that allow for differences in capture probabilities between marked and unmarked animals are available for use through package RMark in R Studio 3.5 (Otis et al. 1978). However, many mark-recapture studies lack enough sampling occasions (generally 2-4) to model for and detect differences in capture probabilities between marked and unmarked individuals. Additionally, fish in closed-population mark-recapture studies are routinely batch marked rather than tagged with an individual identification. Identical batch marks typically eliminate the ability to study behavior of previously marked fish during subsequent capture occasions to detect unequal capture probabilities because RMark requires matrices of capture histories of individually marked fish. Thus, few closed population mark-recapture studies have had the scope or opportunity to study recapture behavior of marked fish and model for differences in capture probabilities between marked and unmarked individuals. Electrofishing is commonly used to capture fish for marking and recapture in the context of closed-population models (Otis et al. 1978; White et al. 1982;

Thompson et al. 1998). These models often produce biased estimates of population size given the size selectivity of electrofishing, possible heterogeneity in individual vulnerabilities, and variability in environmental factors (Pine et al 2012). Additionally, varying behavioral responses induced by electrofishing and tagging may lead to changes in capture probabilities after marking and release, which leads to differences in capture probabilities between marked and unmarked fish and ultimately biased abundance estimates (van Poorten et al. 2017). Many studies have determined that mark-recapture methods using electrofishing may be biased towards underestimation of populations of largemouth bass in small impoundments, especially if the proportion of marked fish in the population was low (Robson and Regier 1964; Swingle et al. 1966; Grinstead and Wright 1973; Edwards et. al 1997) although the mechanisms for this bias are often unknown or unevaluated.

One option for closed mark-recapture models that allow for unequal capture probabilities between marked and unmarked individuals is to embed a mark recapture study within a removal experiment. In this sort of study design, fish can be marked and released during an initial capture event, then moved marked and unmarked fish can be captured and removed from the system during subsequent capture events (Rosenberger and Dunham 2005; Foley et. al 2015). Van Poorton et. al (2017) demonstrated through a series of simulations evaluating the influence of fish behavior on bias in abundance estimates that incorporating marked fish into removal methods can reduce bias but only if mark-recapture assumptions are shown to be met. These types of studies have been conducted mainly in coldwater streams, with the primary focus of estimating population abundances of various salmonid species (Mesa and Schreck 1989; Petersen 2004), but few have been conducted for largemouth bass in small impoundments. Thus understanding the potential for unequal capture probabilities in mark recapture/removal studies

in small impoundments would be useful. Moreover, determining the situation in which unequal capture probabilities can be detected and thus accounted for in estimation models would be a valuable addition to the literature.

The objectives of this study were to (1) assess factors affecting the detection of unequal capture probabilities between marked and unmarked fish when using a mark-recapture/removal study design, (2) determine potential bias in abundance estimates when unequal capture probabilities are unaccounted for, and (3) evaluate the prevalence of unequal capture probabilities from 29 largemouth bass mark-recapture/removal datasets from two size classes of fish at eight Alabama small impoundments over two years.

## **Methods**

### *Study design*

I used a combination of field-based trials and simulation studies to evaluate my objectives. The field-based trials consisted of 29 largemouth bass mechanical removals with mark-recapture/removal designs conducted in small impoundments with overcrowded largemouth bass populations. Each removal was evaluated for a potential recapture effect, i.e., unequal capture probabilities for marked and unmarked fish, to acquire the most viable abundance estimates. To evaluate the detectability of recapture effects, I conducted a series of Monte Carlo simulations of closed population capture-recapture models (Otis et al. 1978) for a range of scenarios representing all possible realistic combinations of ranges in capture and recapture probabilities, population size, initial capture probability, and the number of removal events.

### *Field-based removal trials*

I manipulated eleven ponds on the Auburn University Fisheries Research Unit, which is located 4 miles north of Auburn, Alabama, on Lee County Highway 147 (Figure 1). These ponds were stocked with Largemouth bass and Bluegill at least seven years ago and contain mainly unharvested and unmanaged populations. As a result, these ponds were at various states of largemouth bass overcrowding. The eleven ponds selected for this study were as follows: S-2, S-5, S-7, S-15, S-16, S-22, S-24, S-28, S-30, AE-1, and FP-3. All ponds were small (mean surface area: 1.60 ha), shallow (mean max depth: 3.4 m), and eutrophic (mean Secchi depth: 1.27 m), with minimal aquatic vegetation coverage (0-8%), low total alkalinity (mean alkalinity: 23 ppm ( $\text{CaCO}_3$ )) and similar fish communities (Table 2).

All eleven ponds were randomly selected to receive one of five possible removal treatments: 30%, 50%, 70%, 90%, and control (e.g. 0%). These percentages represented the target proportion of the largemouth bass population less than 356 mm to be removed relative to each pond. Each year, every pond underwent a population assessment followed by a removal treatment. Each pond received two separate years of the exact same target removal treatment (i.e. Spring 2019 and 2020) and a third year of follow-up (i.e. Spring 2021). Population assessments were conducted during the day using 120 pulses per second (pps) DC boat electrofishing and one person netting off the bow of the boat. All ponds were sampled for at least one complete shoreline circuit of electrofishing. Length (mm) and weight (g) were measured and recorded for all fish species sampled. Captured largemouth bass were tallied into one of three size categories:  $\leq 254$  mm, 254-356mm, or  $\geq 356$  mm. All Largemouth bass captured were batch marked with a dorsal fin clip (if  $\leq 254$  mm) and right pelvic fin clip (if  $\geq 254$  mm) for purpose of population estimates through mark-recapture in later sampling events. Under the assumption that the largemouth bass continued to grow, separate batch marks were necessary to distinguish the initial

length group at first capture. Additional electrofishing effort and angling was directed towards ponds that have less than one hundred Largemouth bass batch marked following population assessments.

Post-mark/handling mortality was evaluated in each pond using cuboid net pens. Prior to release following population assessments, a subset of five largemouth bass  $\leq 254$  mm and five largemouth bass 254-356mm were placed in a net pen for ~72 hours. Each net pen was 1.5 meters tall consisting of a 0.75 square meter frame at the end surrounded by 6 mm nylon mesh netting; floats were attached to the top frame to keep the net pen floating at the surface and brick anchors were attached to the bottom frame to keep the net pen extended. Largemouth bass mortality was recorded when net pens were removed.

Largemouth bass removals were conducted at night using 120 pps DC electrofishing with electrical output between 3-8 amps, and one person netting off the bow of the boat. Only largemouth bass were captured during these sampling events. In Spring 2019 and 2020, all treatment ponds were sampled for one complete shoreline circuit per removal event at a rate of effort at 30 m/min. For each treatment pond, removal events were scheduled more than 2 days apart and all removals events were completed within a six-week period. Effort per pond varied relative to pond shoreline distance from 10-39 minutes per electrofishing event. Captured largemouth bass were checked for a batch mark and tallied into their associated size category. Marked largemouth bass were tallied as recaptured under  $\leq 254$  mm, 256-354mm, or  $\geq 354$  mm. Unmarked largemouth bass were tallied under three additional size categories with the same length restrictions. Marked largemouth bass  $\geq 356$  mm were scanned for a PIT tag and the ID number was recorded prior to release. Unmarked largemouth bass  $\geq 356$  mm received a PIT tag and length, weight, and ID number were recorded before immediate release. In 2019 and 2020,

all captured largemouth bass  $\leq 356$  mm were collected and brought back to the lab for further analysis. In 2021, all captured largemouth bass, including largemouth bass  $\geq 356$  mm, were collected for further analysis. Tallies of marked largemouth bass collected in each pond were monitored during each removal event to determine when target removal treatments were achieved. Removals continued for each pond until the target removal percentage was reached in both  $\leq 254$  mm and 254-356mm length-groups or catchability became so low due to diminishing returns that further removal events were impractical.

### Lincoln-Peterson

The Lincoln Peterson estimator was rearranged to represent a removal model such that the population estimate is equivalent to the number of captured fish divided by the ratio of recaptured fish to marked fish in the population. The Chapman modification of the Lincoln-Peterson estimator (Seber 1982) was rearranged and described as:

$$\hat{N} = \frac{(C + 1)}{(R + 1)/(M + 1)} - 1$$

where, with respect to each length-group,  $\hat{N}$  was the population estimate,  $C$  was the total number of largemouth bass captured and removed during all removal events,  $R$  was the total number of marked largemouth bass captured and removed during all removal events, and  $M$  was the total number of marked largemouth bass in the population prior to the start of all removal events.

Assuming all the largemouth bass had the same capture probability and there were no differences in trap response or individual heterogeneity, the proportion of recaptures removed relative to the total number of marked largemouth bass prior to any removal events represented the percentage of the population removed. Population estimates of  $< 356$  mm largemouth bass were calculated by adding together population estimates and variances from each respective length group.

Confidence intervals were computed with a log-normal distribution, which corrects the confidence intervals to be logically consistent with  $m(t + 1)$ , which is the known number of largemouth bass marked, captured, and/or removed in/from the population at time  $t + 1$ , and  $f_0$ , which is the number of largemouth bass never captured.  $f_0$  described as:

$$f_0 = \hat{N} - m(t + 1).$$

Therefore, the lower and upper confidence interval are described as:

$$\text{Lower CI} = \frac{f_0}{C} + m(t + 1) \text{ and } \text{Upper CI} = f_0 * C + m(t + 1),$$

where  $C$  is a bias correction factor described as:

$$C = e^{1.96 \sqrt{\log \left( 1 + \frac{SE(f_0)}{f_0^2} \right)}}$$

### RMark closed population models

Collected mark-recapture/removal data was expanded into capture histories and fit in closed population capture-recapture models in RMark to calculate a derived population abundance. A set of capture histories was developed for <254 mm and 254-356 mm length groups in each treatment pond for 2019 and 2020 summing to 29 sets. Each data set was fit to a closed population capture-recapture model in RMark by distinguishing marked from unmarked largemouth bass in the first column followed distinguishing captured (1) or uncaptured (0) for each removal event in subsequent columns. Once captured or recaptured during a removal event, an individual was classified as dead to remove that largemouth bass from future removal events. Data sets were fit by a null model ( $M_0$ ) in which capture probability is constant over time and identical for marked and unmarked fish, a behavior model ( $M_b$ ) with time invariant capture

probability but unequal capture probabilities between marked and unmarked fish, a time model ( $M_t$ ) where capture probability is time-varying and identical for marked and unmarked fish, a time and behavior model ( $M_{tb}$ ) in which capture probability is time-varying and unequal for marked and unmarked fish, a continuous time model ( $M_T$ ) where capture probability is continuously decreasing or increasing over time and is identical for marked and unmarked fish, and a continuous time and behavior model ( $M_{Tb}$ ) where capture probability is continuously decreasing or increasing over time and is unequal for marked and unmarked fish. AICc model selection, i.e., corrected Akaike's Information Criterion for small sample sizes (Akaike 1973; Hurvich and Tsai 1989), was used to identify the best fit models to the data set and their associated Akaike weights. Model-averaged abundance estimates and standard errors were calculated for all 29 data sets and associated confidence intervals were computed with a log-normal distribution. Models that resulted in an error or warning revealing that all model parameters were not accounted for were discarded prior to model averaging.

### *Simulation studies*

I simulated a mark-recapture/removal study in which fish were marked and released with a batch mark on the first sampling occasion then removed and inspected for marks on subsequent removal events. Capture histories were simulated for each individual in the population through a series of Bernoulli random variables (Figure 16). Every individual during the first sampling event was simulated as marked (1) or unmarked (0) and released by a Bernoulli trial with probability of success  $p_1$ , i.e., first capture probability in the sequence, which was obtain via:

$$p_i = \frac{e^{B0_i+B1_i}}{(1 + e^{B0_i+B1_i})}$$

where capture probability  $p$  in the  $i$ th sampling occasion is informed by  $B0_i$ , which is the logit of an initial capture probability in the  $i$ th sampling occasion,  $B1_i$ , which is the log odds of capture in the  $i$ th sampling occasion. The capture and removal of unmarked fish in subsequent removal events was also simulated using this equation because it represents capture probability of unmarked fish. The capture and removal of marked fish in subsequent removal events was simulated similarly via Bernoulli trials with recapture probability obtained via:

$$r_i = \frac{e^{B0_i+B1_i+c}}{(1 + e^{B0_i+B1_i+c})}$$

where recapture probability is additionally informed by  $c$ , which is the log odds of a marked fish being recaptured. This quantity represents the differential capture probability of previously marked individuals. To simulate removal/death of captured fish in removal events, all capture histories were set to 0 after the capture of a fish in a removal event. All capture histories of individuals that were never captured in any events were discarded from the simulated data prior to modelling.

To simulate data representative of the  $M_0$  model, all  $B1_i$  were fixed to 0 to eliminate temporal variation in capture probability, and  $c$  was set to 0 so that the log odds of recapture is the same as capture. To simulate data representative of the  $M_b$  model,  $B1_i$  was fixed to 0 and  $c$  was set to a negative value less so that the log odds of recapture is less than capture demonstrating a scenario in which previously marked fish were less likely to be captured than marked fish (e.g., negative trap response). To simulate data representative of the  $M_t$  model, the value of the  $B1_i$  coefficients were allowed to vary, and  $c$  was set equal to 0. Lastly, to simulate data representative of  $M_{tb}$ , both the  $B1_i$  and the  $c$  coefficients were allowed to vary.

I conducted a series Monte Carlo simulations of closed population capture-recapture models (Otis et al. 1978) for 225 scenarios representing all possible combinations of ranges of temporal variability in capture probability ( $BI_i$ ), population size, initial capture probability ( $BO$ ), and the number of removal events. I specified five levels of initial capture probability: 0.1,0.2,0.3,0.4,0.5. The number of removal events ranged from 3 to 7 in increments of 1. I simulated three levels of temporal variation in capture probability (no variation, low, high) such that the value of the  $BI_i$  coefficients was allowed to vary stochastically within a range of 0%, 30%, or 60% of the initial capture probability. Finally, I simulated three population size levels: low (100), medium (1,000), and high (10,000 fish). I simulated unequal capture probability between marked and unmarked fish by varying the  $c$  coefficient across simulations. Because the magnitude of this effect within a population is unknown, I varied the  $c$  parameter stochastically by drawing it from a uniform distribution such that the recapture probability ( $r_i$ ) ranged from 10-50% lower for marked than for unmarked fish. I ran 500 simulations of the model for each scenario. Each simulated capture history dataset was fitted with each of the four closed population models  $M_0$ ,  $M_t$ ,  $M_b$ , and  $M_{tb}$ . The best fit model was selected using AICc corrected Akaike's Information Criterion for small sample sizes (Akaike 1973; Hurvich and Tsai 1989).

The degree to which unequal capture probability could be detected across scenarios was assessed by calculating the proportion of simulations in which either the  $M_b$  or the  $M_{tb}$  models had the lowest AICc. These two estimation models represent the assumption that marked fish had lower capture probability than unmarked fish, which was how the data were simulated. Thus, the selection of these models as the minimum AICc model indicates detection of the unequal capture probability that was simulated.

Potential bias in abundance estimates was assessed by calculating the mean percent error in the abundance estimates for each scenario. Mean percent error in abundance was estimated for the  $M_b$  and  $M_{tb}$  models to assess errors when the estimation model was correctly specified (i.e., capture probabilities were correctly allowed to vary between marked and unmarked fish). I also calculated mean percent error in abundance separately for the  $M_o$  and  $M_t$  models to assess potential biases in abundance estimates when differential capture probability between marked and unmarked fish was not properly accounted for.

## **Results**

### *Field-based removal trials*

Initial capture probabilities for all 29 data sets averaged 0.35 and ranged from 0.075-0.594 and population estimates averaged 251 individuals and ranged from 9-1017 (Tables 4 and 5). Of the 29 closed models evaluated across <254 and 254-356 mm length groups for 2019 and 2020,  $M_o$  was selected as the best fit model twice,  $M_b$  was selected four times,  $M_t$  was selected 19 times, and  $M_{tb}$  was also selected four times (Tables 4 and 5). Thus, temporal variation in capture probability appeared to be a common factor across ponds, years, and size classes. The selection of the  $M_b$  model for eight of these instances indicates that unequal capture probability between marked and unmarked fish was less important overall but detected in some cases. Model-averaged abundance estimates were generally lower for the RMark closed population models than the Lincoln-Peterson estimator when the top model allowed for unequal capture probability ( $M_b$  and  $M_{tb}$  models; Tables 4 and 5). High uncertainty in confidence intervals of derived abundance estimates were limited to ponds with 3 removal events and target removal percentages of 30%. The high uncertainty in derived abundance estimates for AE1 and S24 in 2019 and AE1 in 2020 suggests that the data were not sufficient for fitting the closed model in

these instances. Additionally, the data for the <254 mm length group for pond S24 in 2019 and both length groups in 2020 could not be fit to a closed population model in RMark because there was only two removal events conducted for all three of those length groups. Treatment ponds with target treatments of 50%, 70%, and 90% removal had at least five removal events and the resulting confidence intervals reflected lower uncertainty in these instances.

### *Simulations*

Population size, initial capture probability, and variability in capture probability had the strongest influence on detecting a recapture effect (i.e., probability of selecting  $M_b$  or  $M_{tb}$  as the best fit model; Figure 17). This suggests that identifying a recapture effect would be increasingly more difficult as population size decreases and the probability of model selection of  $M_b$  or  $M_{tb}$  is likely dependent on both the initial capture probability and the level of variability in capture probability. My simulations revealed that mean percent model selection of  $M_b$  or  $M_{tb}$  was also influenced by an interaction between the number of removal events and initial capture probability. However, the interaction was strongest when initial capture probabilities were high (above 0.3), while the number of removal events had little effect when the initial capture probability was low. Additionally, I found that variability in capture probability strongly effected model selection particularly at high population sizes. At smaller population sizes, variability in capture probability had little influence because mean percent model selection of  $M_b$  or  $M_{tb}$  was already consistently low (below 50%) in all scenarios. As population size increased, mean percent model selection of  $M_b$  or  $M_{tb}$  increased; however, at larger population sizes, higher variability in capture probability resulted in lower mean percent model selection of  $M_b$  or  $M_{tb}$ . This suggests that increased variability in capture probability likely makes it more difficult for closed population model in RMark to distinguish between constant and time-varying capture

probabilities and determine the presence of a recapture effect. As a result, scenarios with high variability in capture probability required more removal events and higher initial capture probabilities to achieve a high mean percent model selection of  $M_b$  or  $M_{tb}$ .

Population size and variability in capture probability had the strongest influence on mean proportional error in derived abundance estimates from the  $M_b$  and  $M_{tb}$  models (Figure 18).

Overall, I found very little bias in abundance estimates of  $M_b$  or  $M_{tb}$  relative to the true population size for nearly all scenarios except those with low population size, a low number of removal events, and a low initial capture probability. High variability in capture probability influenced bias in abundance estimates of  $M_b$  or  $M_{tb}$  in scenarios with a low number of removal events and a low initial capture probability but across all population sizes. Ultimately, any scenario with an initial capture probability above 0.2 with a population larger than 100 resulted in minimal bias in derived abundance estimates under these two models. In scenarios with more bias, derived abundance estimates primarily underestimated true abundance and rarely overestimated true abundance except in scenarios with a high number of removal events (above 5) and very low initial capture probability (below 0.2).

Derived abundance estimates from the  $M_o$  and  $M_t$  models overestimated the abundance in all scenarios except those with both a high initial capture probability and a high number of removal events (Figure 19). This suggests that ignoring a potential recapture effect in the data would result in overestimated abundance estimates unless both a high number of removal events were conducted and there was a high initial capture probability. I also found that the population size and variability in capture probability had little effect on mean proportional error of derived abundance estimates. However, my simulations did reveal an interaction between initial capture

probability and the number of removal events. In all scenarios, increases in both the initial capture probability and the number of removal events result in less biased abundance estimates.

## **Discussion**

My simulations revealed that given the appropriate population size, initial capture probability, and number of removal events, a recapture effect is detectable in closed population capture-recapture models using RMark. Many studies have evaluated closed capture-recapture data sets for recapture effects and have run simulations to validate their findings; however, no studies to my knowledge have used simulated closed capture-recapture data sets to evaluate the detectability of a recapture effect and, therein, expose the potential limitations of closed capture-recapture models to detect recapture effects. I found that population size had the strongest influence on detecting a recapture effect. This poses an issue considering that many closed population capture-recapture studies are conducted on small systems, such as ponds or streams, with small population sizes. In these situations, it may be difficult to detect unequal capture probabilities and AIC model selection may select for models that do not account for these effects, which could produce biased abundance estimates.

The initial capture probability is highly important for obtaining accurate and precise abundance estimates. Robson and Regier (1964) proposed that researchers must first have some understanding of the magnitude of the population size to know how many fish must be marked to calculate accurate estimates of abundance from closed population capture-recapture designs. A high proportion of marked fish in a population in collaboration with an effective sampling gear for the fish species should allow for accurate estimates of initial capture probability. In smaller systems with small populations, high initial capture probabilities are not improbable as I achieved an average initial capture probability of 0.35 in the ponds of my study and many studies

have achieved high initial capture probabilities as well (generally  $<0.65$ ; Riley and Fausch 1992; Rosenburger and Dunham 2005; Meyer et al. 2006).

The number of removal events plays an important role in decreasing the amount of potential positive bias in abundance estimates. However, the overall effect of the number of removal events is dependent on the initial capture probability. For example, given a low initial capture probability, the effect of the number of removal events on increasing the probability of detecting a recapture effect and decreasing bias in abundance estimates is minimal. But given a higher initial capture probability, the number of removal events can have a strong influence on detecting a recapture effect and lowering bias in abundance estimates. Due to funding and time constraints, the number of removal events is often limited (Kelso and Shuter 1989; Riley and Fausch 1992; Myer et. al 2006). My simulations show that limiting the number of removal events could result in positively biased abundance estimates. A few studies have attempted to evaluate closed population mark-recapture/removal data for potential recapture effects with limited success in identifying such effects (Mesa and Schreck 1989; Peterson et. al 2004; van Poorton et. al 2017). These studies were limited to 2-4 removal events which my simulations revealed is not likely to be sufficient for detecting a recapture effect and, thus, led to the uncertainty in abundance estimates in those studies.

The results of this study provide important insight into the dangers of assuming equal capture probability and using simple closed population capture-recapture models that are not robust to potential differences in capture and recapture probabilities. The analytic simplicity of Lincoln-Peterson and Schnabel methods for estimating population abundance is appealing but the rigid assumptions concerning capture probabilities often serves as a weakness for these methods. A common problem is the data requirements for using the Lincoln-Peterson and

Schnabel methods typically are not sufficient for use in more complex methods robust to variation in capture probabilities. This limits interpretation to whether the assumption of equal capture probability was violated or not rather than allowing for variation in capture probability and testing for differences in capture and recapture probabilities.

In my field-based largemouth bass removal trials, the eight cases in which unequal capture probabilities had strong AIC support likely had a low probability of detecting such effects due to their small population sizes (<1,000 fish) and low initial capture probabilities according to my simulation studies. Thus, there likely was a distinct difference between capture probabilities of marked and unmarked fish in these cases considering that they had a low probability of being detected in the first place in these small impoundments. As for the other 21 data sets that failed to detect unequal capture probabilities, many of them had a high number of removal events (7 or more) and a high initial capture probability (above 0.4). My simulations demonstrated that mean proportional error in derived abundance estimates was low in scenarios of high initial capture probability (above 0.4) and with a high number of removal events (above 6). This suggests that population estimates of those systems would be expected to have low bias. However, some of the data sets that selected for  $M_0$  or  $M_t$  had a high number of removal events but a low initial capture probability in addition to a small population estimate. Thus, these field based trials in small impoundments indicate that unequal capture probabilities are certainly possible in these types of settings but are likely not a pervasive factor in estimating abundance in small impoundments.

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## Tables

Table 1. List of various southern agency largemouth bass harvest recommendations for private ponds.

Agency	Annual Harvest Recommendations
Auburn University Extension	20-35 lbs/ac in fertilized ponds 10 lbs/ac in infertile ponds
Kentucky Department of Fish & Wildlife	25 largemouth bass/ac 30-35 lbs/ac in fertilized ponds
Louisiana State University AgCenter	15-20 lbs/ac in unfertilized ponds 20-35 lbs/ac in fertilized ponds
Mississippi Wildlife, Fisheries, & Parks	7-15 lbs/ac in unfertilized ponds
Southeastern Pond Management	30-35 lbs/ac
University of Georgia Extension	15-20 largemouth bass/ac or 35 lbs/ac

Table 2. Characteristics of eleven Auburn University Fisheries Research Unit ponds in Auburn, Alabama, used for control and treatments.

Pond	Surface area (ha)	Shoreline Distance (m)	Max depth (m)	Secchi Depth (m; April 2019)	Aquatic Vegetation (%; SA coverage)	Alkalinity (ppm, April 2019)
S-2	1.11	527.63	2.74	1.2	2	20
S-5	0.74	365.31	3.35	1.0	8	24
S-7	1.04	422.43	1.83	1.1	0	32
S-15	2.31	598.01	4.27	1.4	0	22
S-16	1.00	447.76	1.53	1.0	1	24
S-22	0.87	426.83	3.35	0.9	3	20
S-24	0.90	420.28	2.74	0.9	2	20
S-28	1.92	727.11	4.27	1.8	1	22
S-30	5.35	1180.59	3.96	1.2	5	22
AE-1	1.64	603.24	4.88	2.3	5	24
FP-3	0.67	348.89	2.74	1.2	0	24
<b>Means:</b>	<b>1.60</b>	<b>551.64</b>	<b>3.24</b>	<b>1.27</b>	<b>2.45</b>	<b>23.09</b>

Table 3. Proportion abundance removed with respect to target removal treatments in 2019 and 2020. Associated number of removal events conducted and estimated pounds of largemouth bass removed per acre are also listed.

Pond	Year	Target Removal Treatment	# of Removal Events	Proportion Abundance Removed	lbs/ac Removed
AE1	2019	30%	5	31.5% (24.2, 38.7)	8.5
S24	2019	30%	7	27.4% (19.4, 34.3)	6.52
S15	2019	50%	8	38.8% (30.6, 45.2)	7.06
S7	2019	50%	5	51.5% (44, 57.2)	14.27
S2	2019	70%	9	54.6% (47.9, 59.8)	8.11
S30	2019	70%	11	49.1% (42.2, 55.9)	30.52
S22	2019	90%	8	46.8% (37.4, 53.9)	11.86
S28	2019	90%	9	44.2% (35.8, 50.4)	11.14
AE1	2020	30%	4	30.9% (25.4, 36.5)	17.75
S24	2020	30%	2	30.2% (24.5, 35.8)	11.68
S15	2020	50%	6	39.6% (34.4, 44.6)	15.19
S7	2020	50%	4	46.5% (38.9, 53.1)	12.35
S2	2020	70%	10	68.2% (62.4, 72.8)	23.4
S30	2020	70%	10	60.4% (53.3, 66.9)	35
S22	2020	90%	9	83% (75.9, 87.4)	29.91
S28	2020	90%	10	76.5% (68.3, 82.6)	25.1

Table 4. List of population estimates for largemouth bass <254 mm for eight treatment ponds in 2019 and 2020. Population estimates for RMark closed population models are model averaged. Only models within 2 AICc units of the best fit model are listed for each pond and year. Lower and upper 95% confidence intervals are listed in parentheses following each estimate. Additionally, the number of removal events and initial capture probabilities are listed for each pond and year.

Pond	Year	Events	RMark Closed Population Models					Lincoln-Peterson
			Model	$\Delta AICc$	Weight	Initial CP	Estimate	Estimate
AE1	2019	5	MTb	0.000	0.298	0.388	202 (148, 572)	285 (224, 389)
			Mt	0.140	0.278			
			Mb	0.558	0.225			
			Mtb	1.310	0.155			
AE1	2020	4	Mb	0.000	0.347	0.312	566 (412, 1241)	794 (664,981)
			MT	0.902	0.221			
			Mt	1.340	0.178			
			MTb	1.872	0.136			
S2	2019	9	Mt	0.000	0.688	0.574	149 (120, 494)	155 (141, 178)
			Mtb	1.581	0.312			
S2	2020	10	Mt	0.000	0.641	0.407	420 (352, 704)	430 (401, 471)
			Mtb	1.160	0.359			
S7	2019	5	MTb	0.000	0.472	0.594	102 (96, 164)	127 (112, 156)
			Mtb	0.414	0.383			
S7	2020	4	Mtb	0.000	0.352	0.458	226 (194, 383)	304 (263, 368)
			Mt	0.185	0.321			
			Mb	1.132	0.120			
S15	2019	8	MT	-	1	0.32	78 (56, 127)	51 (44, 70)
S15	2020	9	Mt	-	1	0.252	844 (740, 987)	834 (737, 965)
S22	2019	8	Mt	0.000	0.697	0.528	166 (123, 797)	148 (134, 174)
			Mtb	1.666	0.303			
S22	2020	9	MT	0.000	0.609	0.35	253 (232, 318)	250 (236, 277)
			MTb	1.144	0.344			
S24	2019	7	Mt	-	0.712	0.585	117 (92, 220)	121 (102, 160)
S24	2020	2	-	-	-	-	-	426 (356, 534)
S28	2019	9	Mt	0.000	0.720	0.412	188 (152, 286)	195 (169, 241)
			Mtb	0.189	0.280			
S28	2020	10	Mt	0.000	0.716	0.203	394 (364, 467)	441 (402, 504)
			Mtb	1.856	0.283			
S30	2019	11	Mt	-	1	0.114	529 (426, 702)	525 (427, 690)
S30	2020	10	Mtb	0.000	0.583	0.157	408 (325, 738)	518 (433, 657)
			Mt	0.673	0.416			

Table 5. List of population estimates of largemouth bass 254-356 mm for eight treatment ponds in 2019 and 2020. Population estimates from RMark closed population models are model averaged. Only models within 2 AICc units of the best fit model are listed for each pond and year. Lower and upper 95% confidence intervals are listed in parentheses. Additionally, the number of removal events and initial capture probabilities are listed for each pond and year.

Pond	Year	Events	RMark Closed Population Models					Lincoln-Peterson
			Model	$\Delta AICc$	Weight	Initial CP	Estimate	Estimate
AE1	2019	3	Mb	0.000	0.299	0.333	74 (49, 206)	74 (55, 121)
			MT	0.131	0.280			
			Mo	1.357	0.152			
			Mt	1.860	0.118			
			MTb	1.963	0.112			
AE1	2020	4	MTb	-	0.816	0.289	95 (90, 250)	183 (129, 314)
S2	2019	9	MT	-	0.647	0.525	9 (8, 17)	8 (8, 12)
S2	2020	10	Mb	-	0.845	0.251	64 (60, 88)	60 (60, 103)
S7	2019	5	Mt	-	0.636	0.484	78 (59, 326)	75 (65, 99)
S7	2020	4	Mo	0.000	0.359	0.347	43 (37, 75)	36 (35, 76)
			Mb	1.282	0.189			
			Mt	1.729	0.151			
			MT	1.969	0.134			
S15	2019	8	Mt	0.000	0.470	0.574	90 (74, 181)	109 (89, 150)
			Mtb	0.456	0.374			
S15	2020	6	Mb	0.000	0.530	0.34	40 (34, 113)	53 (40, 97)
			MTb	1.710	0.226			
S22	2019	8	Mt	0.000	0.418	0.338	44 (30, 158)	57 (38, 110)
			Mtb	0.753	0.287			
			Mb	1.660	0.182			
S22	2020	9	MT	0.000	0.397	0.307	57 (52, 120)	56 (53, 72)
			Mo	0.650	0.287			
			MTb	1.855	0.157			
S24	2019	2	-	-	-	-	43 (23, 114)	
S24	2020	2	-	-	-	-	47 (35, 84)	
S28	2019	9	MT	0.000	0.506	0.342	97 (71, 320)	74 (68, 162)
			MTb	0.479	0.398			
S28	2020	10	Mo	0.000	0.412	0.203	132 (123, 169)	129 (121, 178)
			Mb	1.672	0.179			
			MT	1.901	0.159			
S30	2019	11	MT	0.000	0.713	0.075	1117 (820, 1774)	1039 (891, 1257)
			MTb	1.980	0.265			
S30	2020	10	MT	-	0.56	0.15	686 (599, 870)	728 (654, 841)

Figures

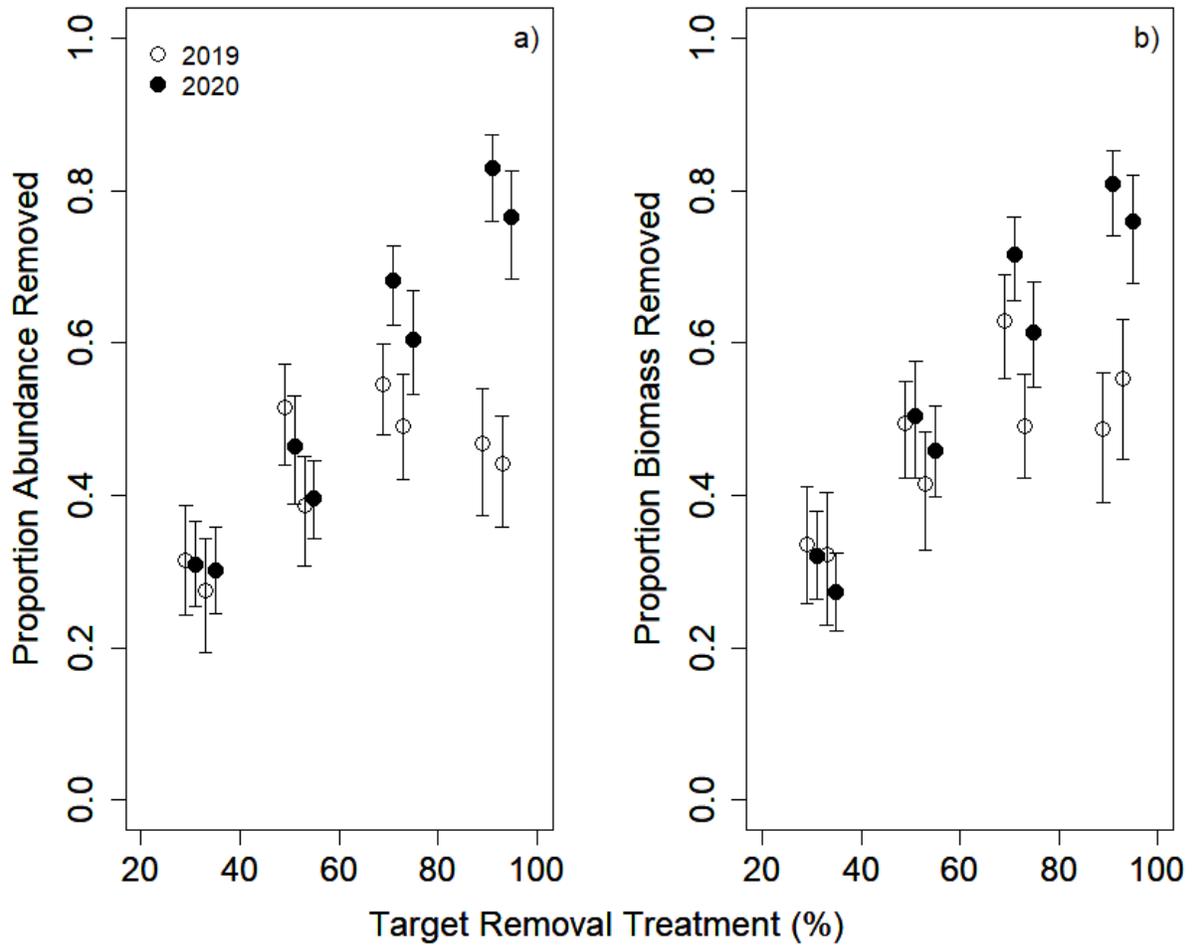


Figure 1. Estimates of proportion (a) abundance and (b) biomass removed of largemouth bass in 2019 and 2020 as a function of target removal treatment. Open circles denote year 2019 and solid circles denote year 2020. Error bars represent 95% confidence intervals.

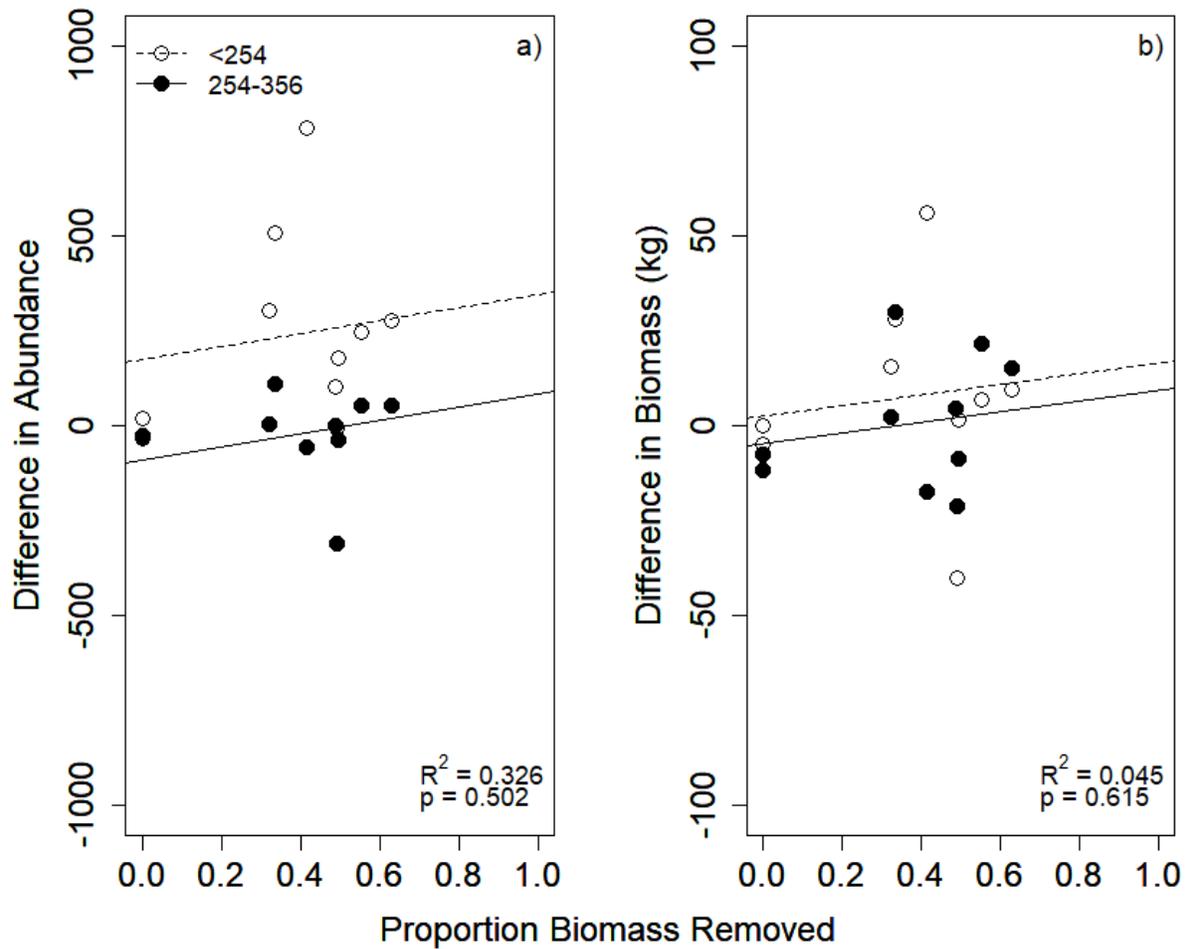


Figure 2. Log difference in largemouth bass (a) abundance and (b) biomass as a function of proportion biomass removed from 2019-2020. Open circles denote largemouth bass abundance and biomass less than 254 mm. Solid circles denote largemouth bass abundance and biomass between 254 and 356 mm. The best fit models composed of a linear model with no additional effects or interactions.

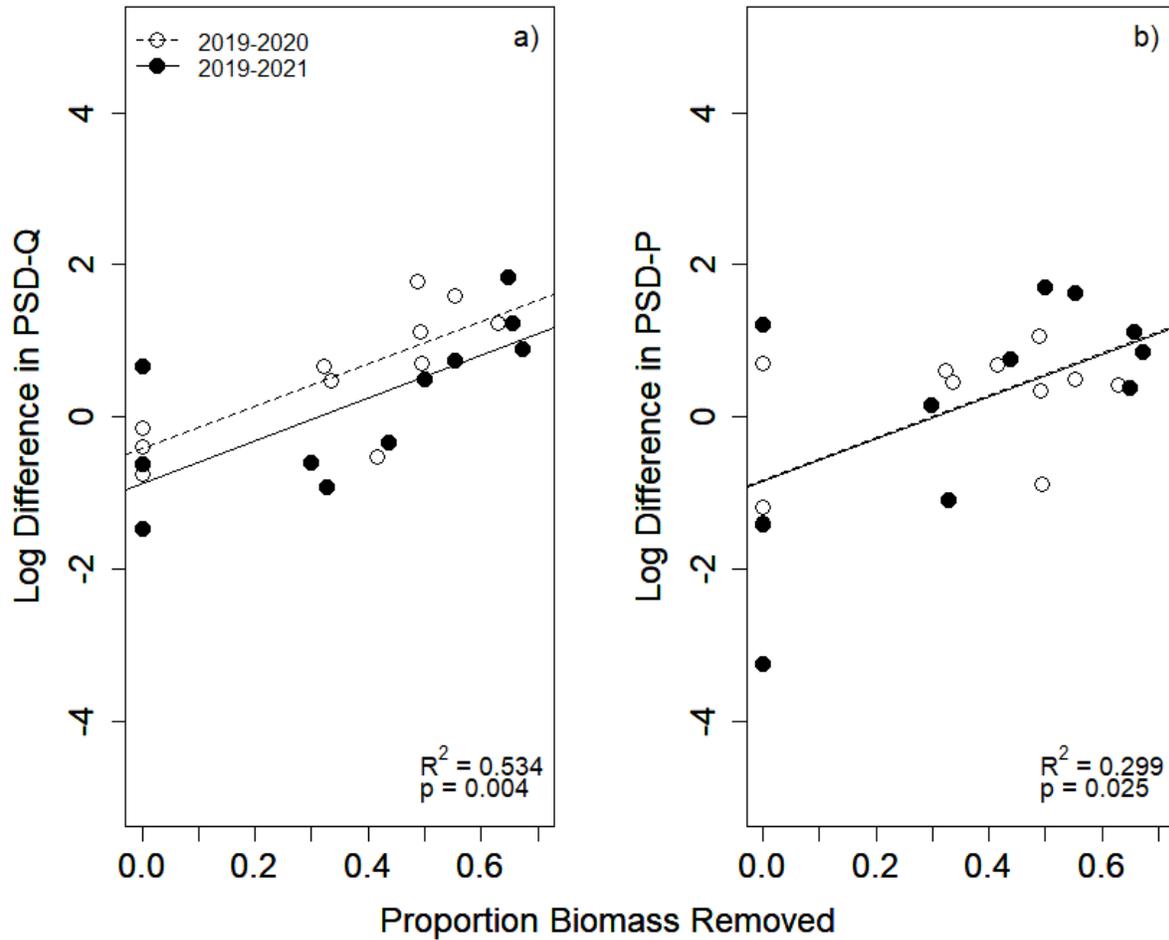


Figure 3. Log difference in largemouth bass (a) PSD-Q and (b) PSD-P as a function of proportion biomass removed from 2019-2020 and 2019-2021. Open circles denote 2019-2020. Solid circles denote 2019-2021. The best fit models composed of a linear model with no additional effects or interactions.

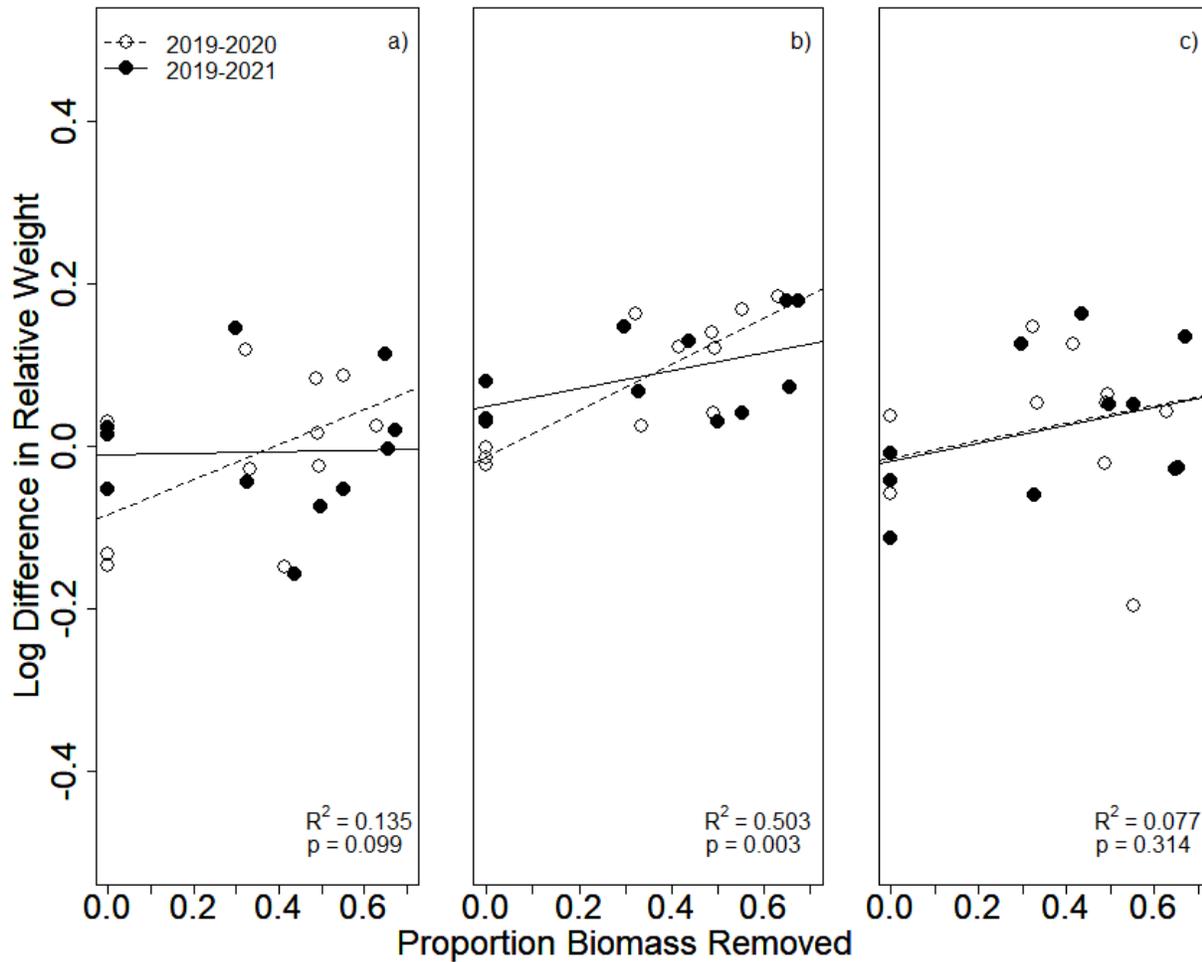


Figure 4. Log difference in mean relative weight of largemouth bass (a) <254, (b) 254-356, and (c) >356 mm as a function of proportion biomass removed from 2019-2020 and 2019-2021. Open circles denote 2019-2020. Solid circles denote 2019-2021. The best fit model for mean relative weight of largemouth bass <254 and 254-356 mm composed of a linear model with an interaction of proportion biomass removed x time-period.

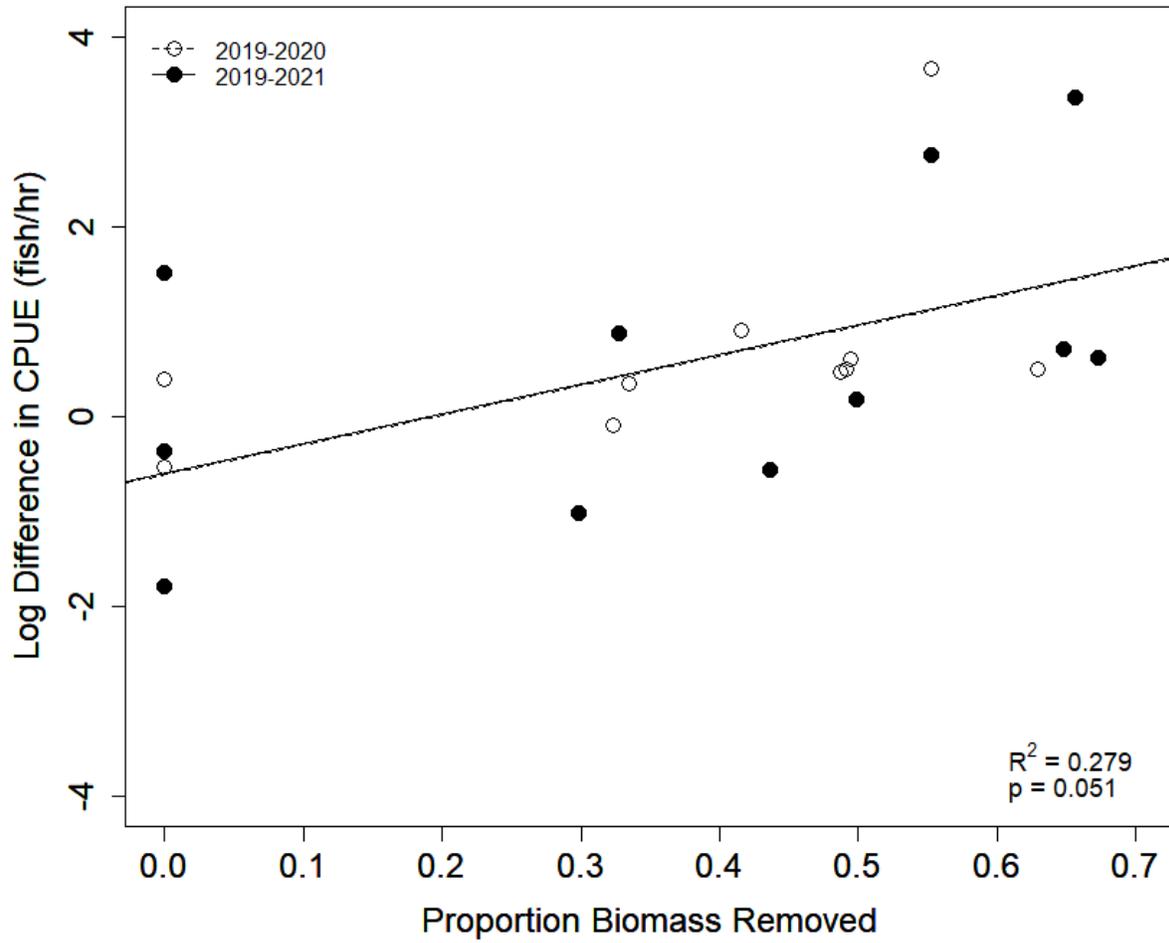


Figure 5. Log difference in CPUE of stock size bluegill (80-150 mm) as a function of proportion biomass removed from 2019-2020 and 2019-2021. Open circles denote 2019-2020. Solid circles denote 2019-2021. The best fit model composed of a linear model with no additional effects or interactions.

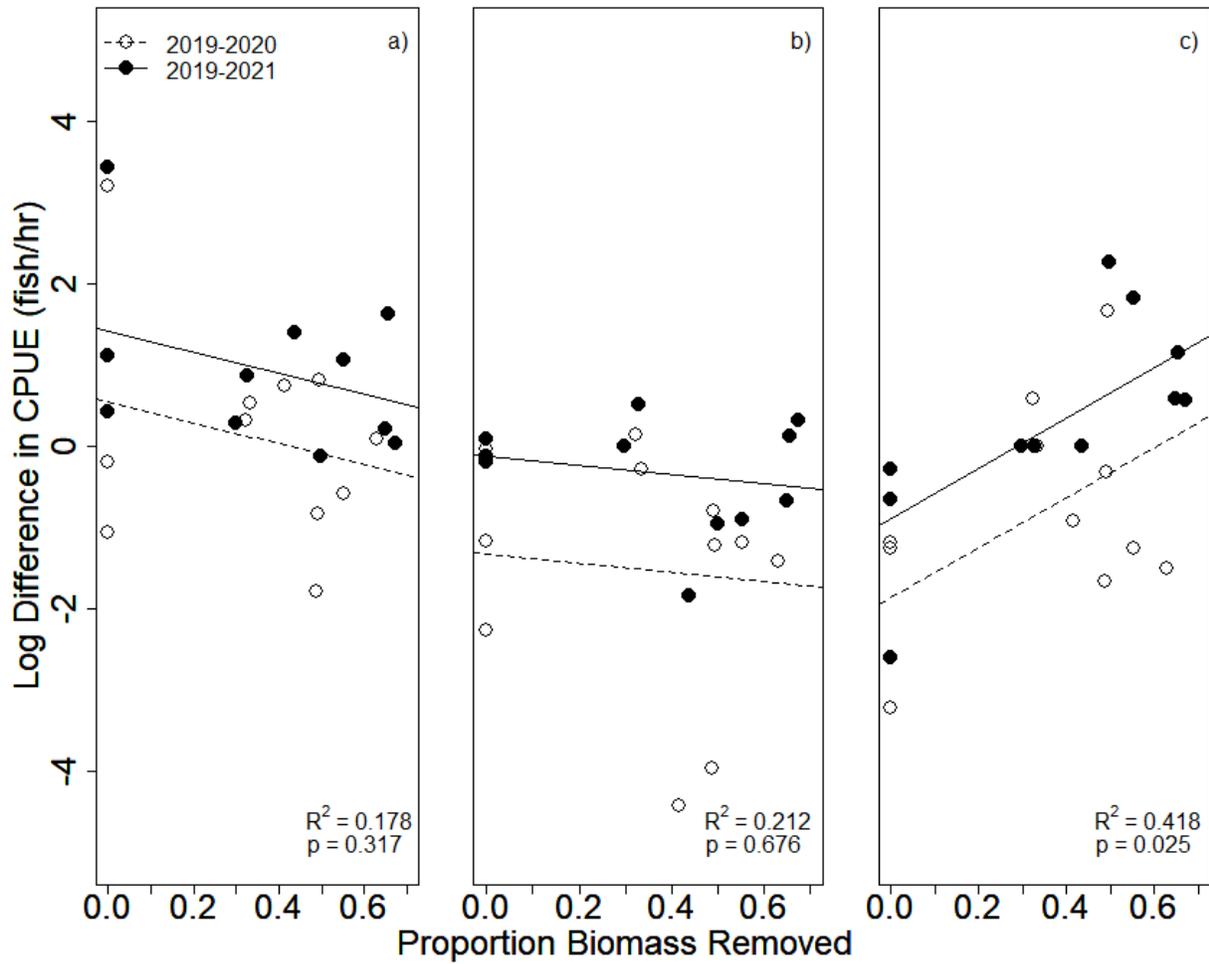


Figure 6. Log difference in CPUE of largemouth bass (a) <254, (b) 254-356, and (c) >356 mm as a function of proportion biomass removed from 2019-2020 and 2019-2021. Open circles denote 2019-2020. Solid circles denote 2019-2021. The best fit models composed of a linear model with no additional effects or interactions.

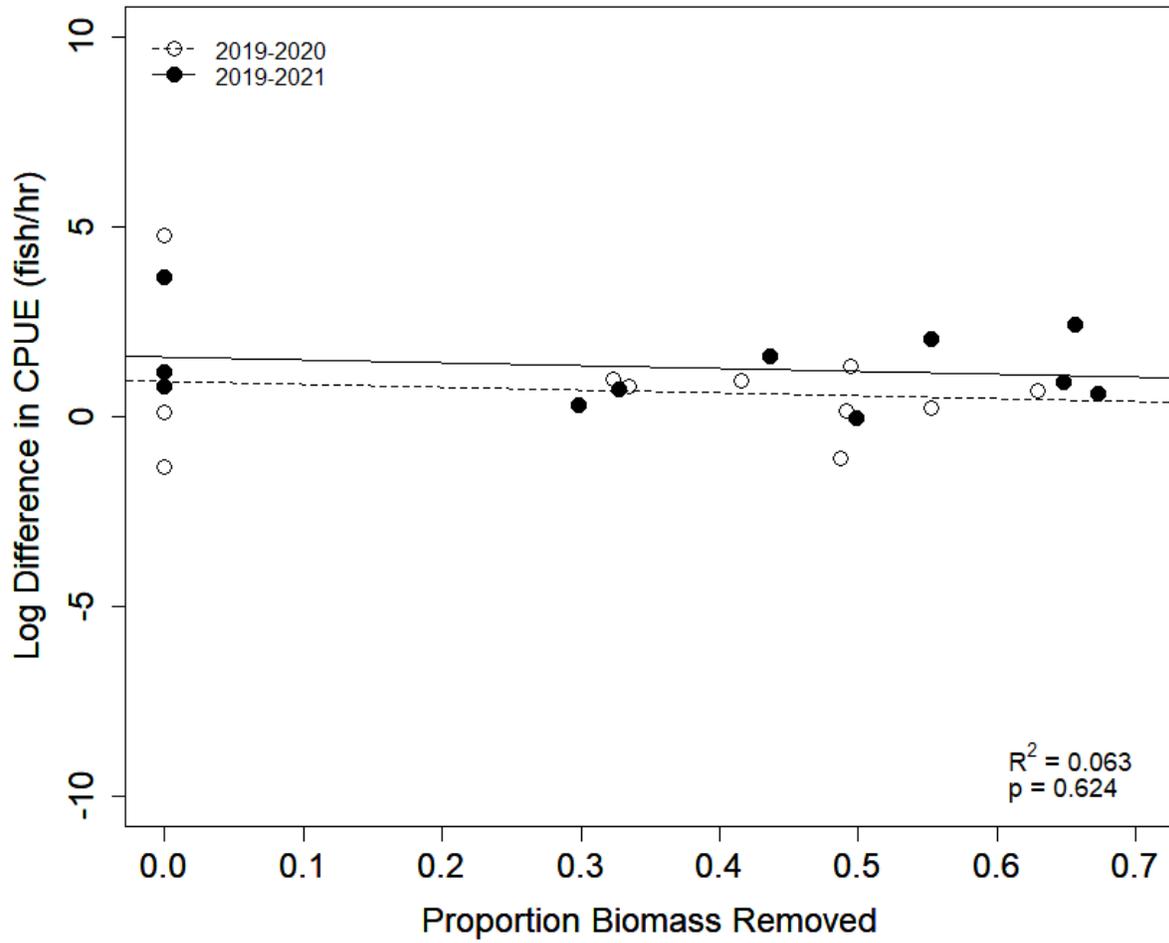


Figure 7. Log difference in CPUE of age-1 largemouth bass as a function of proportion biomass removed from 2019-2020 and 2019-2021. Open circles denote 2019-2020. Solid circles denote 2019-2021. The best fit model composed of a linear model with no additional effects or interactions.

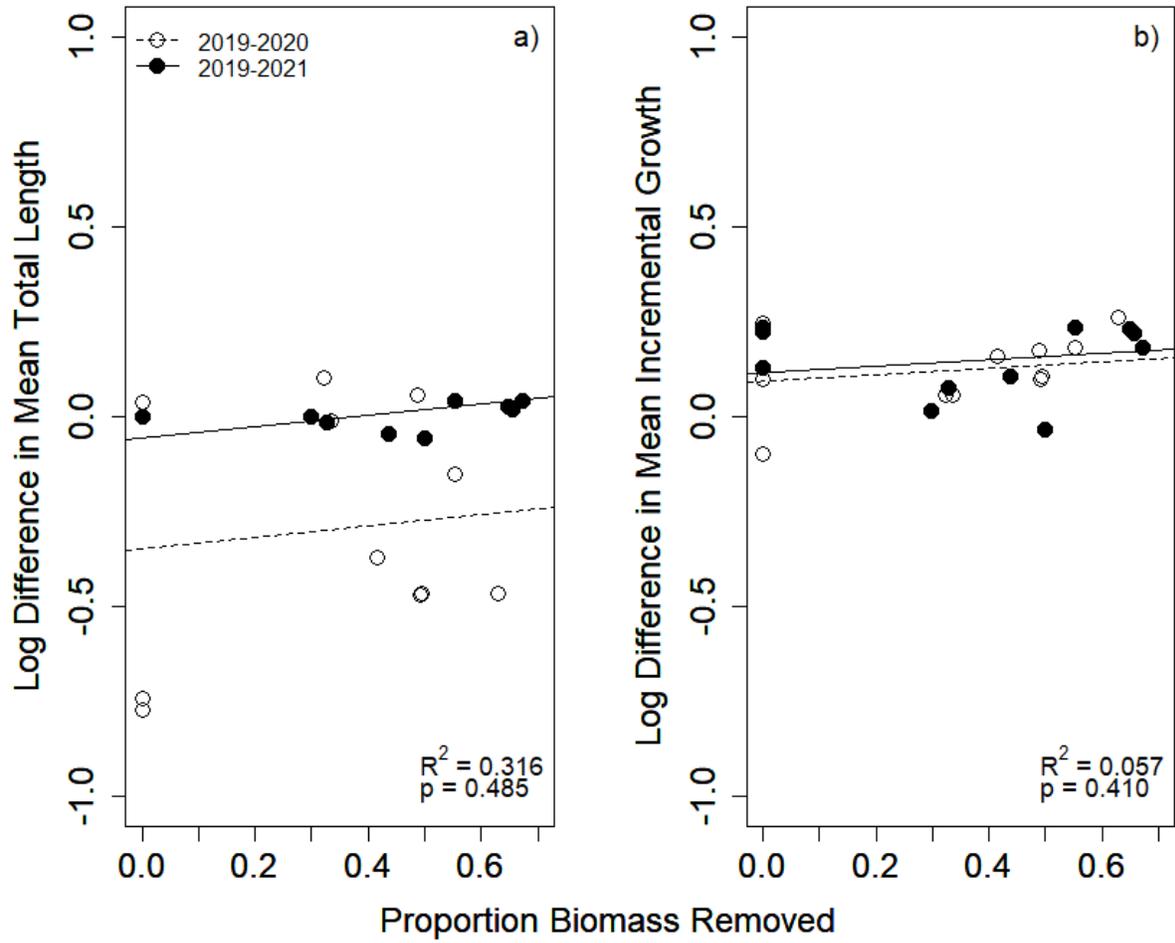


Figure 8. Log difference in largemouth bass (a) mean length at age-1 and (b) mean incremental growth of age-2 as a function of proportion biomass removed from 2019-2020 and 2019-2021. Open circles denote 2019-2020. Solid circles denote 2019-2021. The best fit models composed of a linear model with no additional effects or interactions.

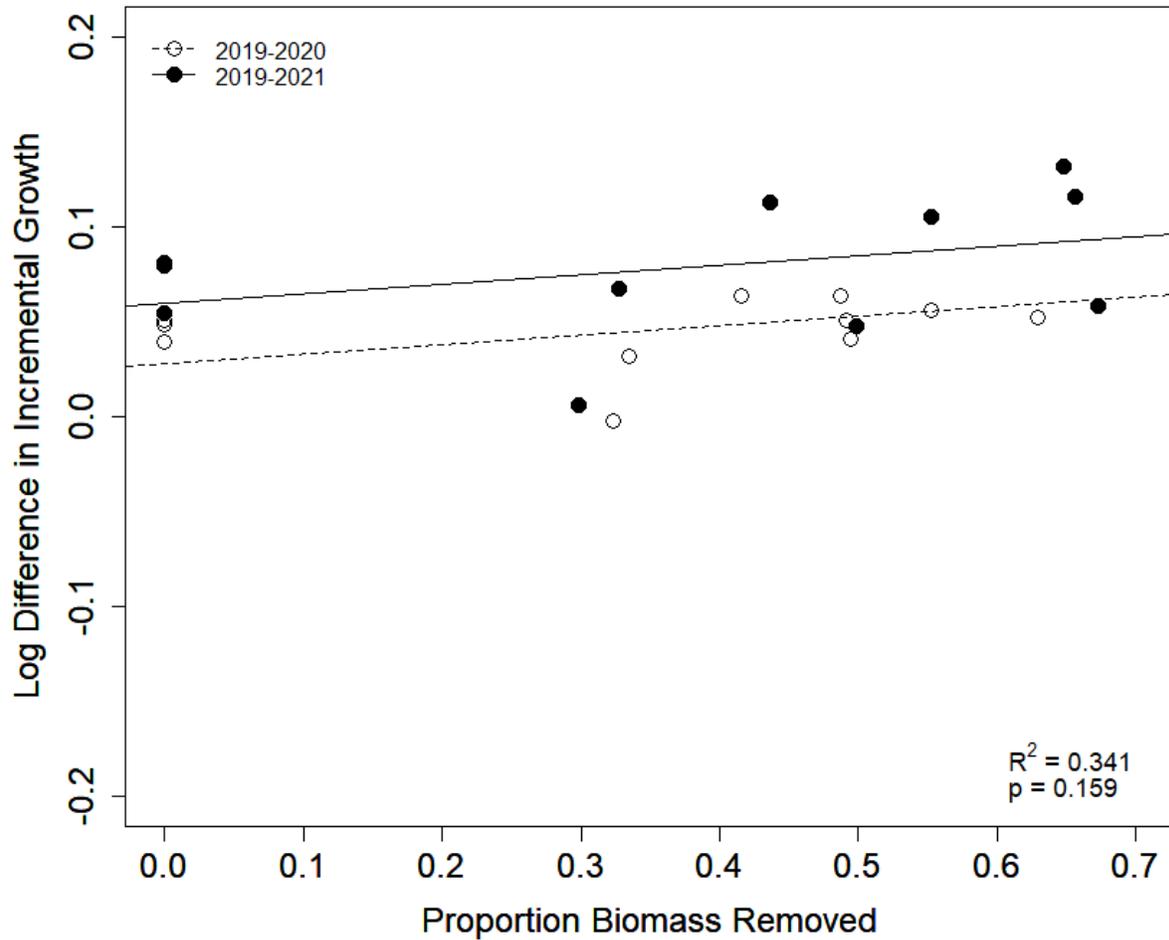


Figure 9. Log difference in mean intercept of linear incremental growth at age models of largemouth bass ages 2+ as a function of proportion biomass removed from 2019-2020 and 2019-2021. Open circles denote 2019-2020. Solid circles denote 2019-2021. The best fit model composed of a linear model with no additional effects or interactions.

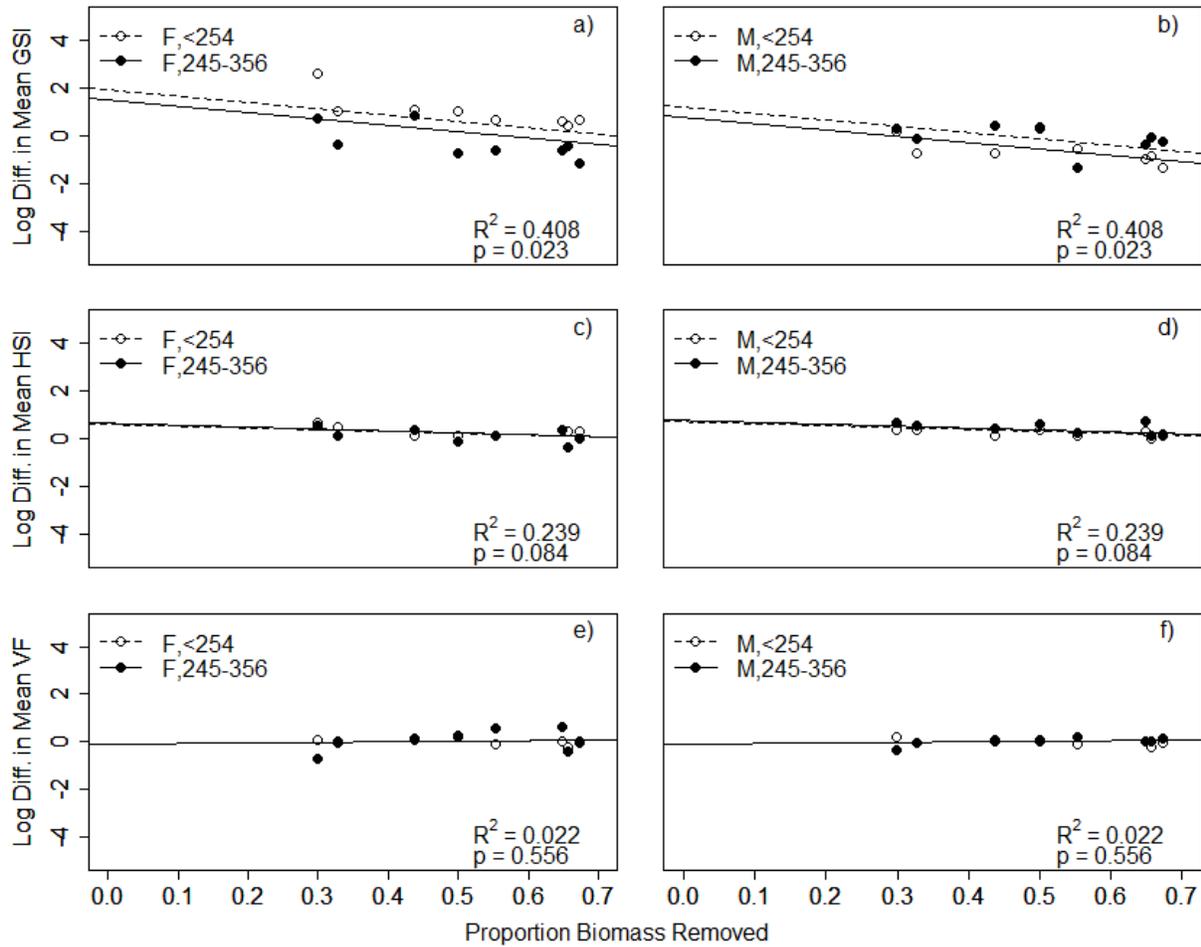


Figure 10. Log difference in (a and b) mean GSI, (c and d) HSI, and (e and f) stage of visceral fat of largemouth bass as a function of proportion biomass removed from 2020-2021. Log differences were evaluated separately for (a, c, and e) males and (b, d, and f) females. Open circles denote largemouth bass less than 254 mm. Solid circles denote largemouth bass between 254 and 356 mm. The best fit models composed of a linear model with no additional effects or interactions.

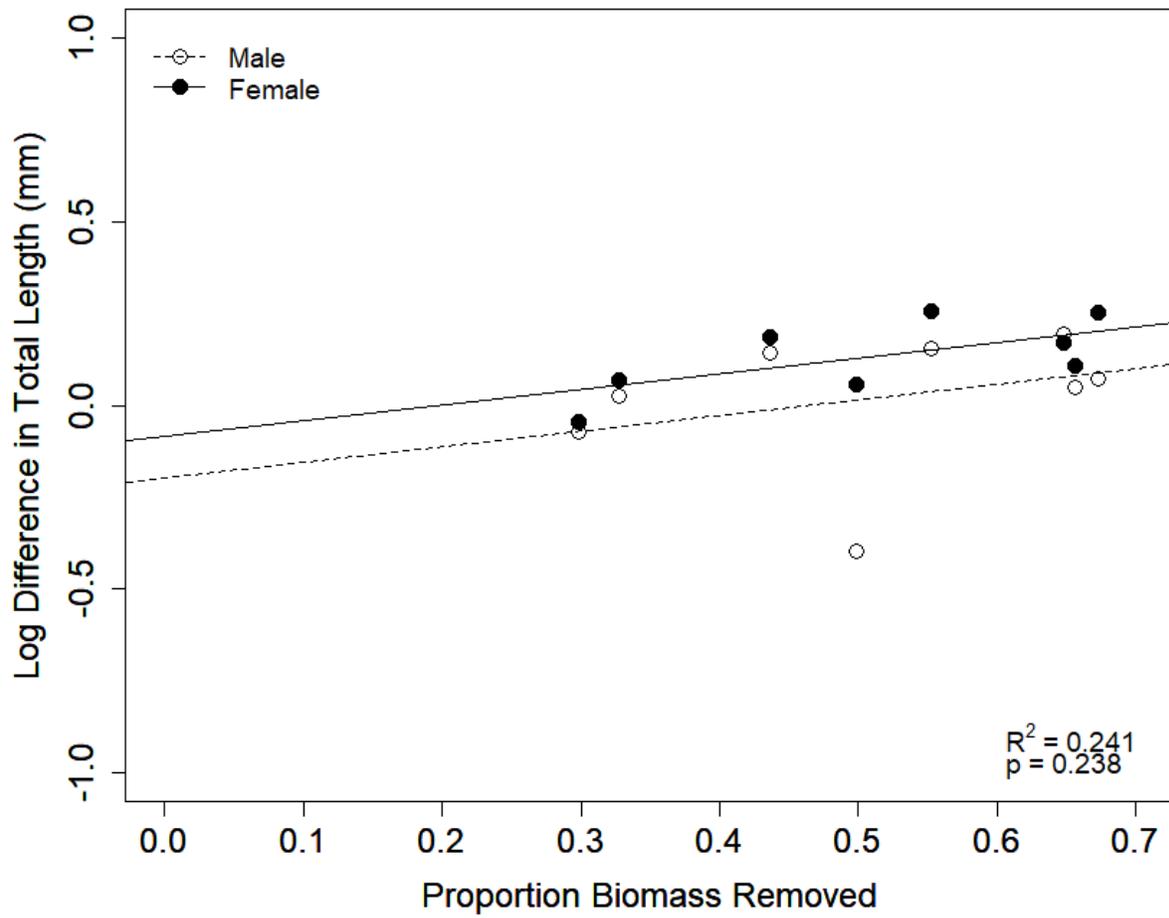


Figure 11. Log difference in largemouth bass mean length at 50% maturity as a function of proportion biomass removed from 2020-2021. Open circles denote male. Solid circles denote female. The best fit model composed of a linear model with no additional effects or interactions.

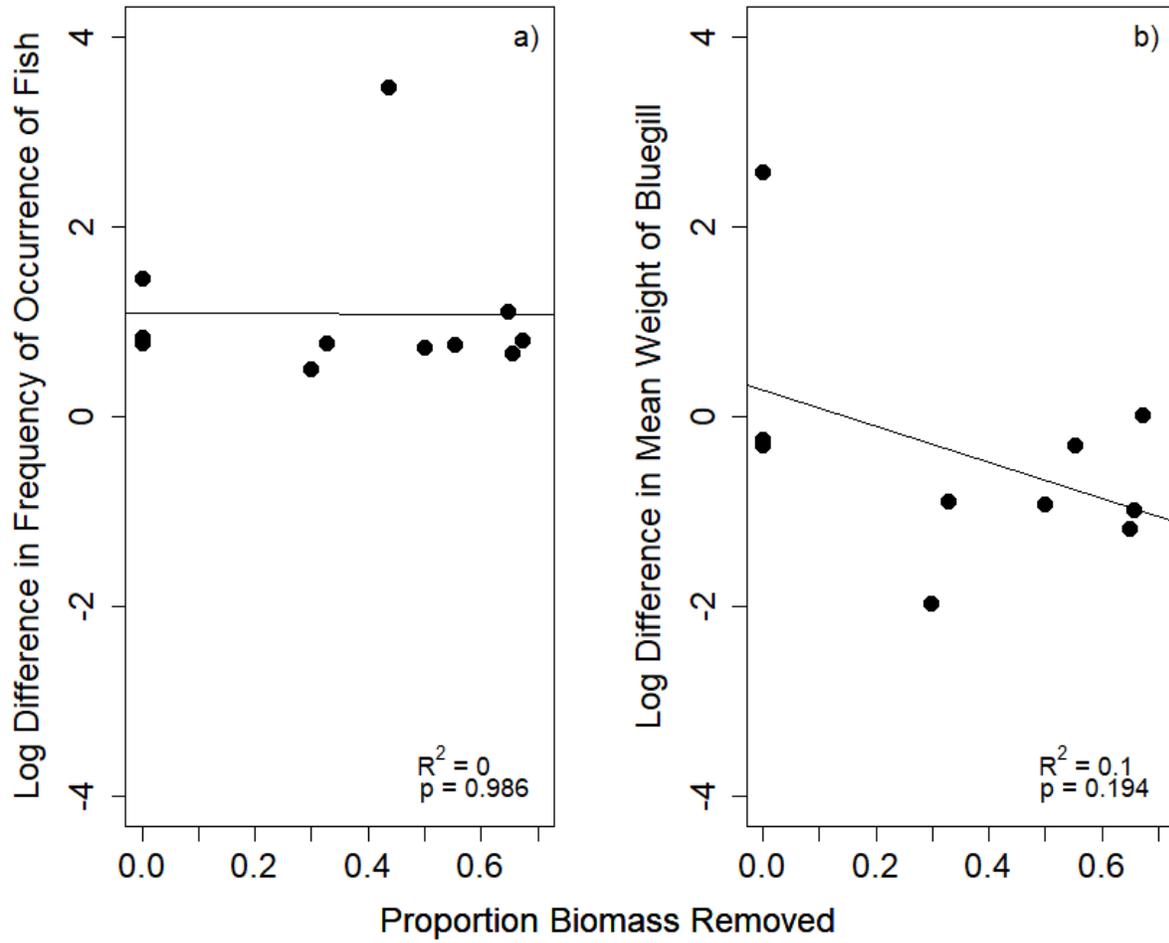


Figure 12. Log difference in (a) frequency of fish and (b) mean weight of individual bluegill in largemouth bass diets as a function of proportion biomass removed between spring 2020 and summer 2020. The best fit model composed of a linear model with no additional effects or interactions.

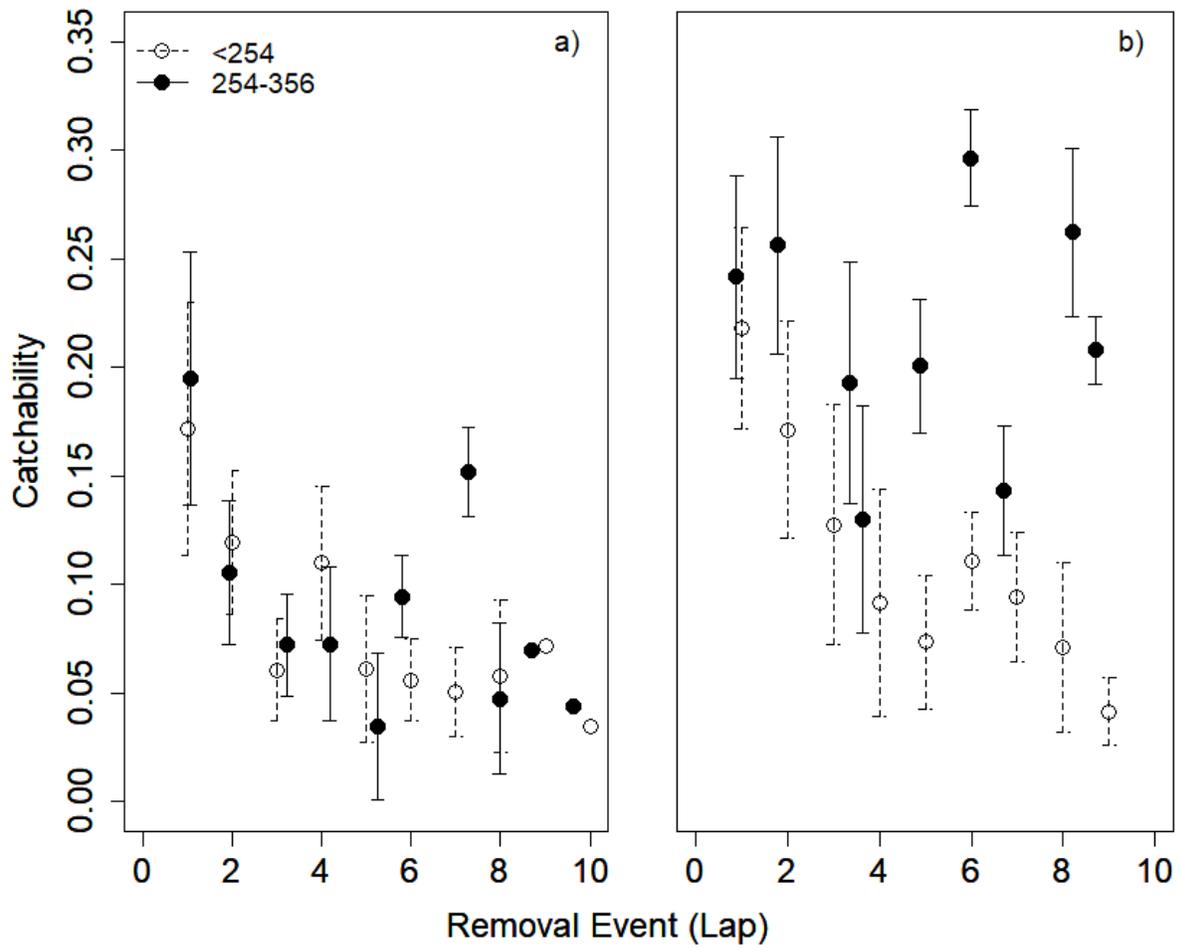


Figure 13. Estimates of mean catchability of largemouth bass in treatment ponds as a function of removal event in (a) 2019 and (b) 2020. Open circles denote largemouth bass <254 mm. Solid circles denote largemouth bass between 254-356 mm. The error bars represent the standard error of catchability estimates for a given removal event.

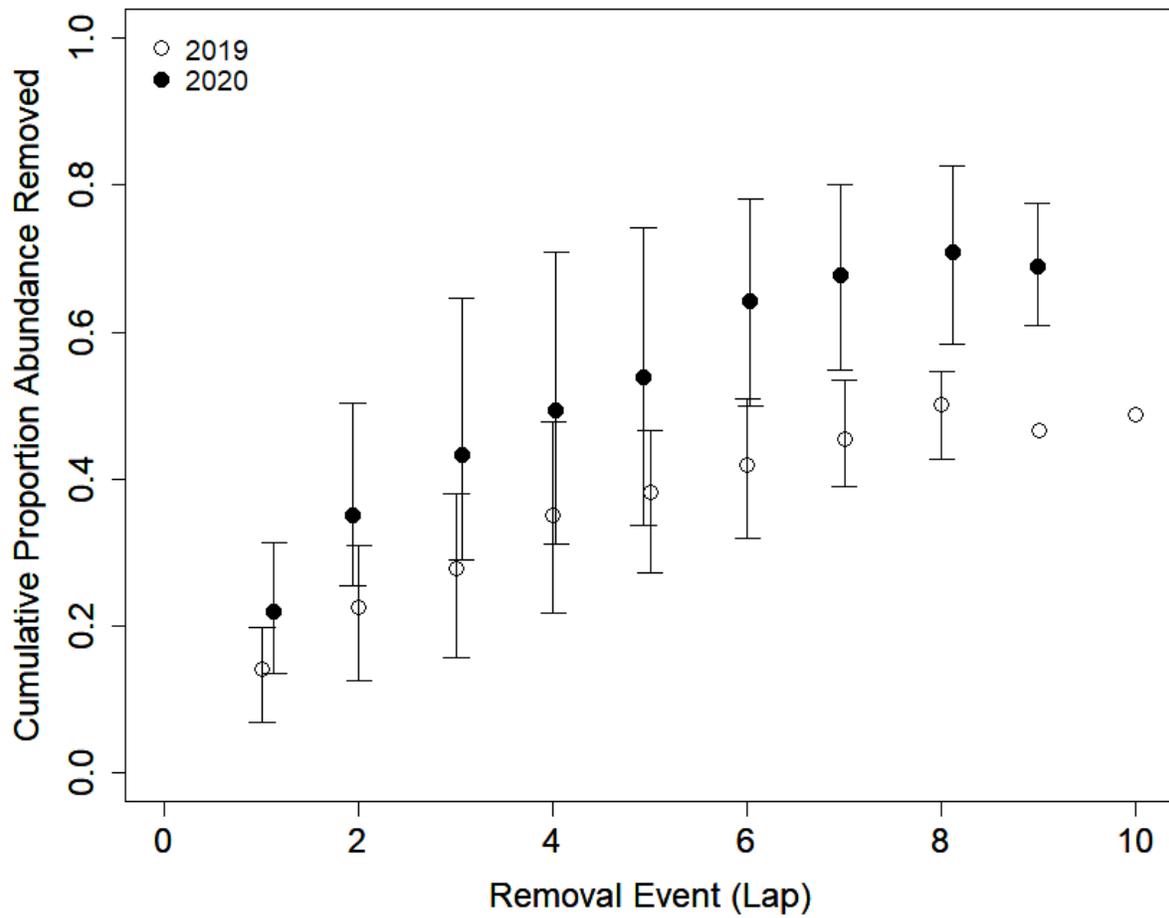


Figure 14. Estimates of mean cumulative proportion abundance removed from treatment ponds as a function of removal event in 2019 and 2020. Open circles denote 2019. Solid circles denote 2020. The error bars represent the range of cumulative proportion abundances removed for a given removal event.

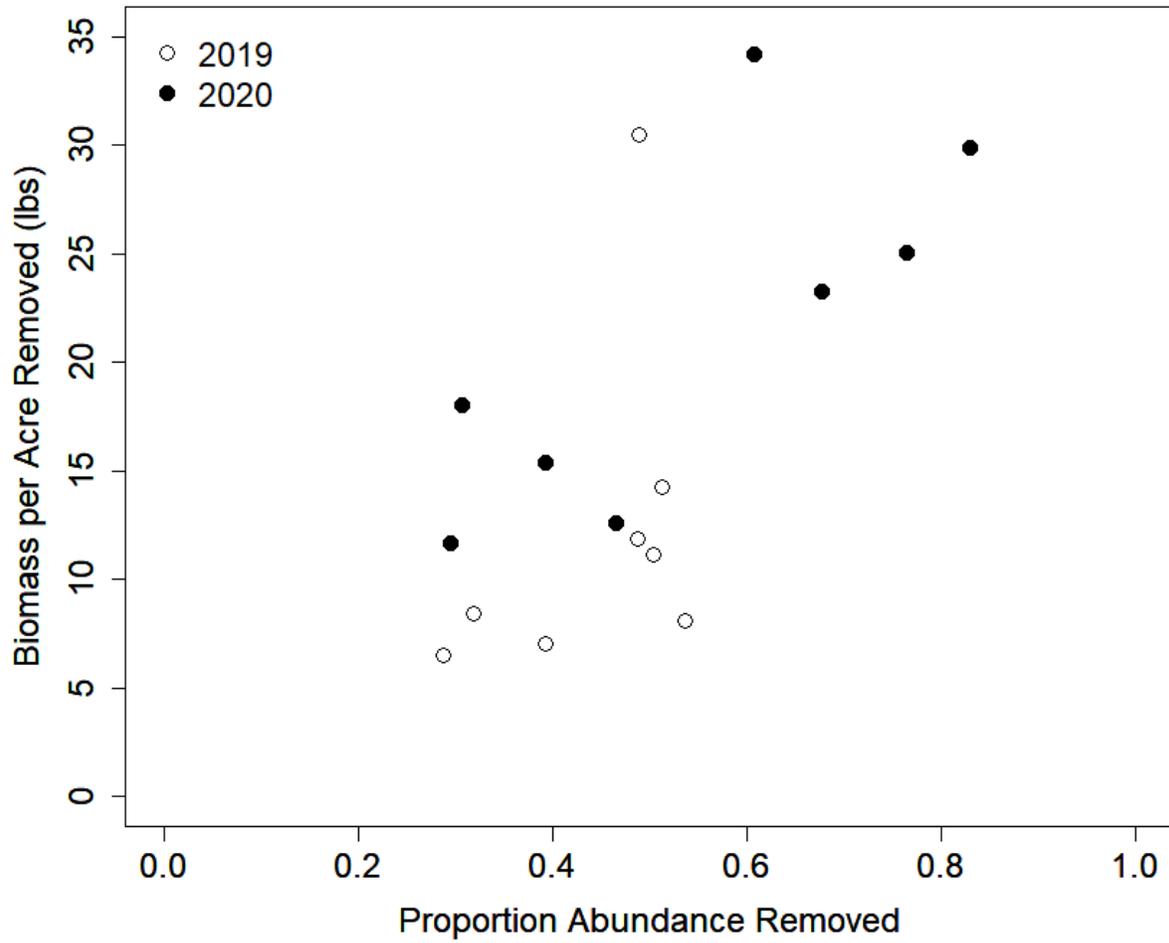


Figure 15. Estimates of pounds of largemouth bass removed per acre from treatment ponds as a function of proportion abundance removed. Open circles denote 2019. Solid circles denote 2020.

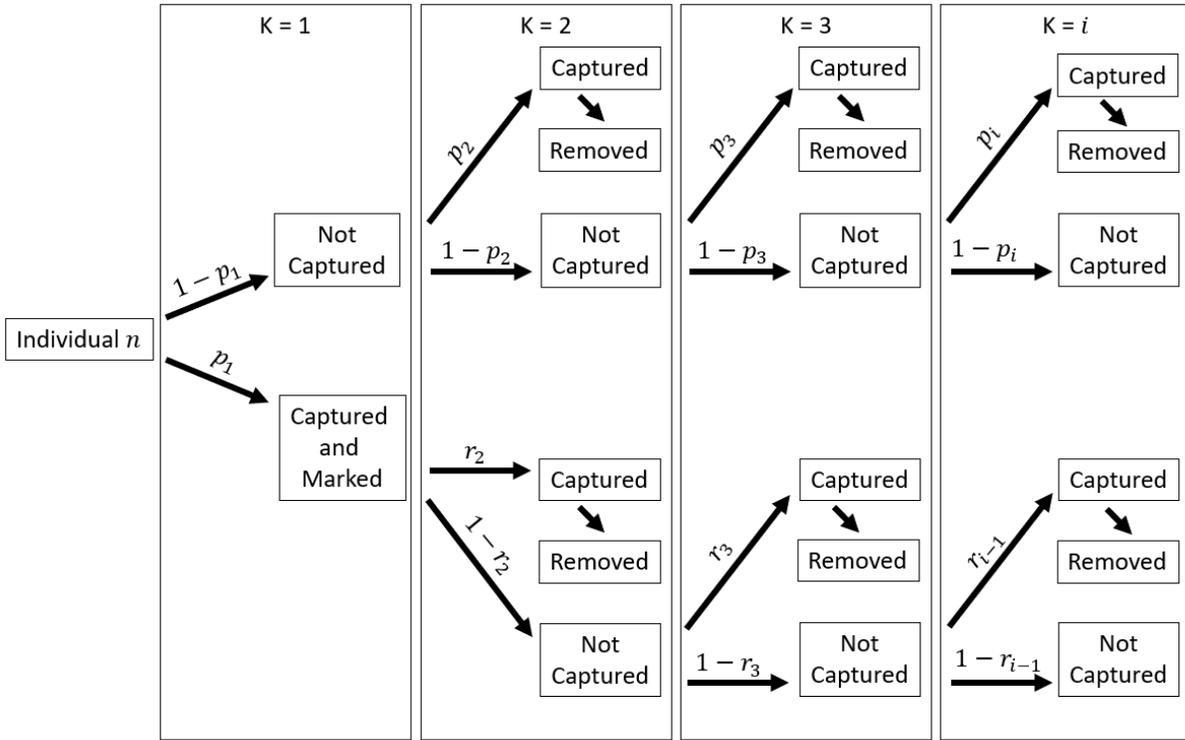


Figure 16. Flowchart of the creation of an individual capture history used in closed-population capture-recapture model simulations. Individual  $n$  has a capture probability  $p_1$  of being captured and marked in the first sampling occasion and a capture probability  $1 - p_1$  of not being captured. Unmarked individuals have a capture probability  $p_i$  or  $1 - p_i$  of being captured and removed or uncaptured in subsequent removal events. Marked individuals have a recapture probability  $r_{i-1}$  or  $1 - r_{i-1}$  of being captured and removed or uncaptured in subsequent removal events.

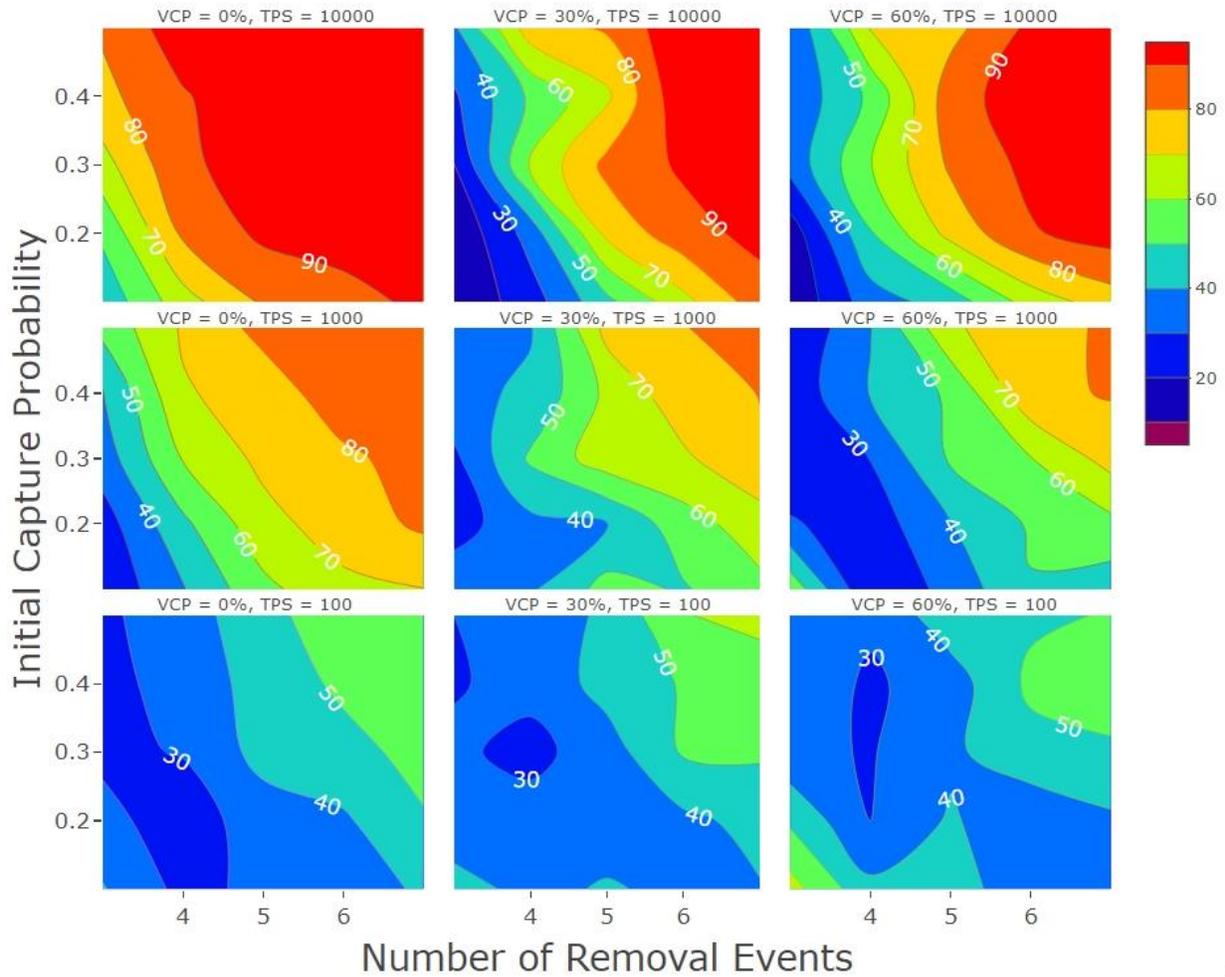


Figure 17. Mean percent model selection of  $M_b$  and  $M_{tb}$  for a range of recapture effects as a function of initial capture probability and number of removal events across ranges of variability in capture probability and true population size. Mean percent model selection was only calculated for odds of recapture 10-50% less than the odds of capture. For example, in a scenario with 0% variability in capture probability, a population size of 10,000, an initial capture probability of 0.4, and 5 removal events, the interpretation is that the mean probability of detecting unequal capture probabilities and, therefore, selecting for  $M_b$  and  $M_{tb}$  is over 90%.

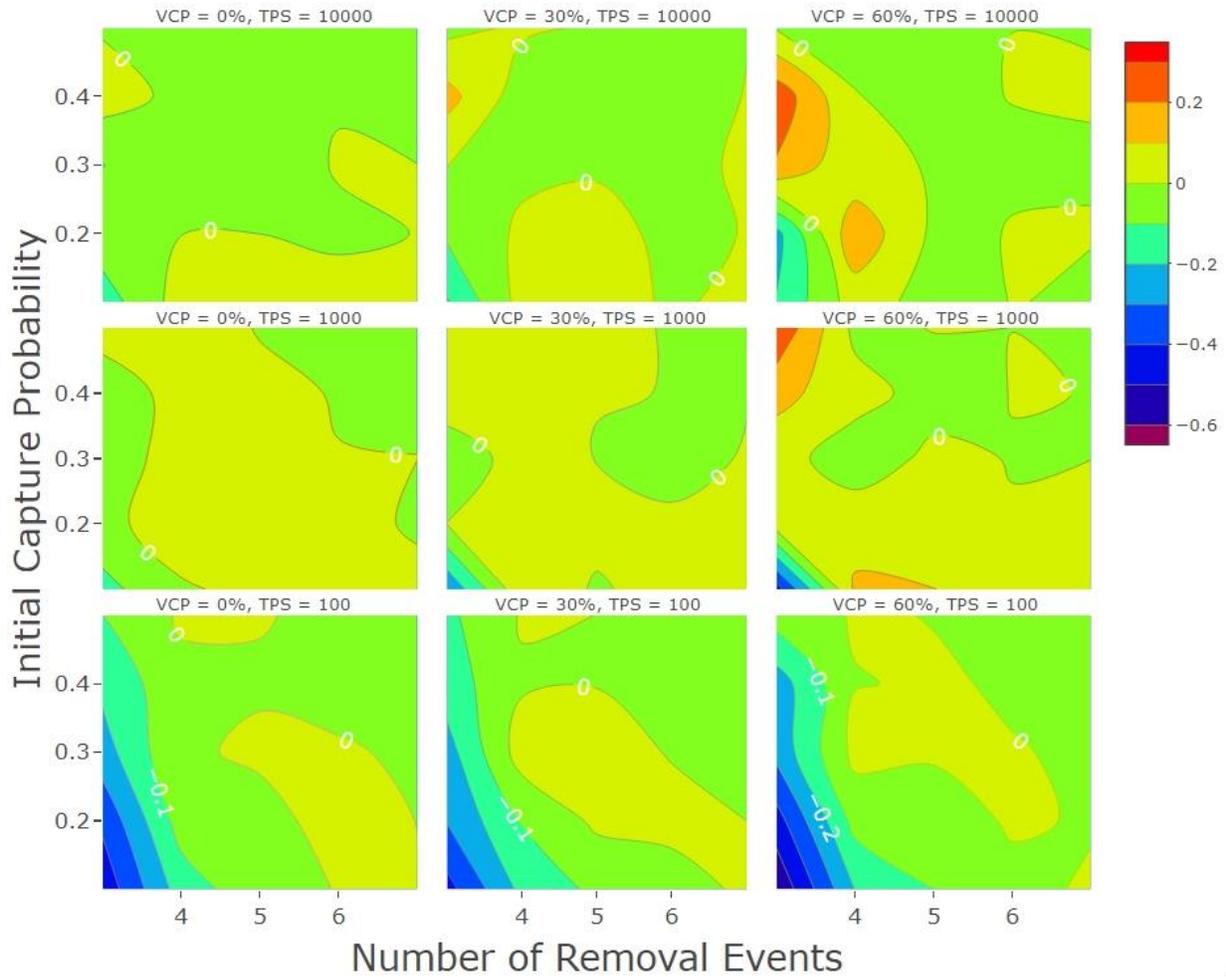


Figure 18. Mean proportional error in abundance estimates of  $M_b$  and  $M_{tb}$  for a range of recapture effects as a function of initial capture probability and number of removal events across ranges of variability in capture probability and true population size. Mean proportional error in abundance estimates was only calculated for odds of recapture 10-50% less than the odds of capture.

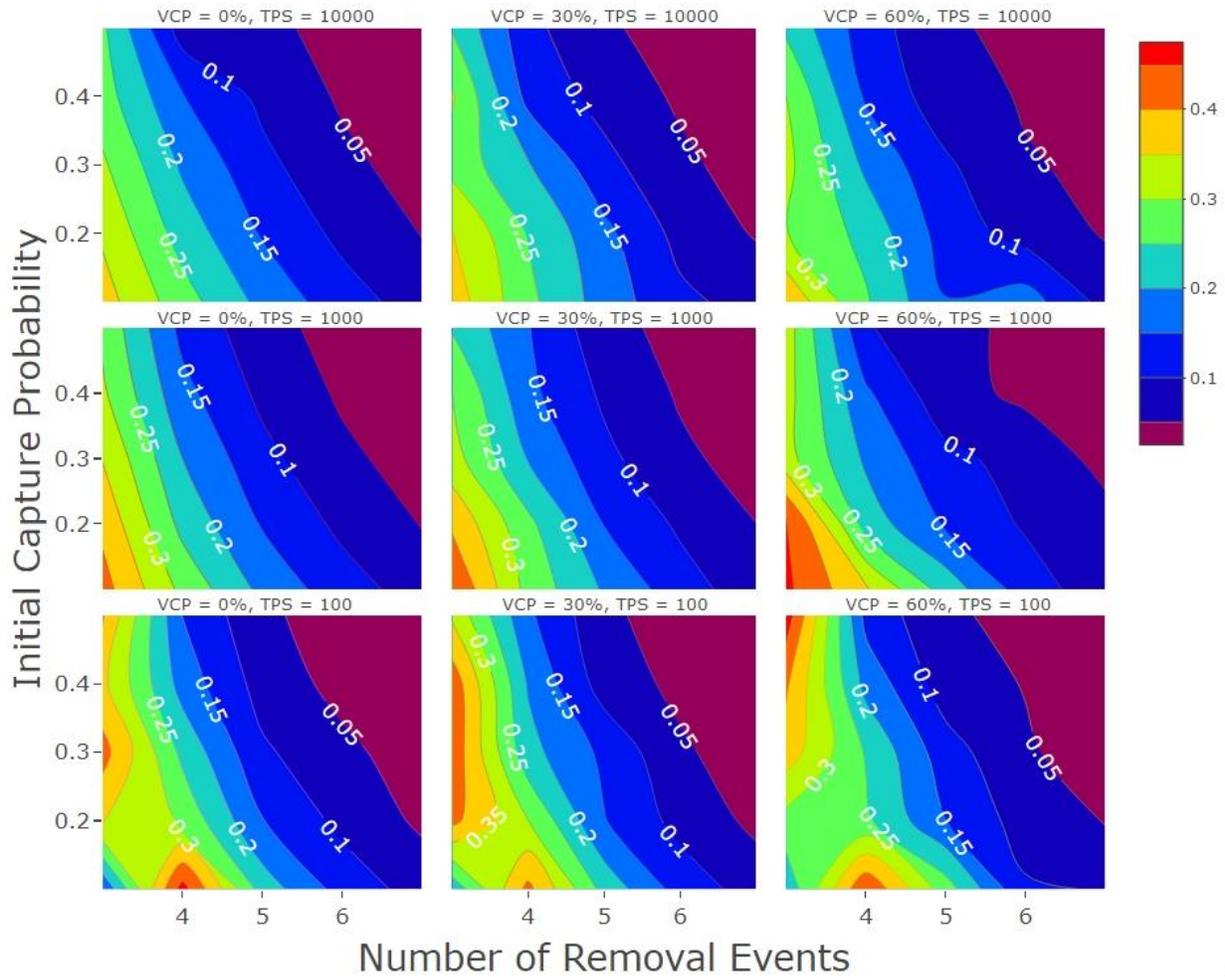


Figure 19. Mean proportional error in abundance estimates of  $M_0$  and  $M_t$  for a range of recapture effects as a function of initial capture probability and number of removal events across ranges of variability in capture probability and true population size. Mean proportional error in abundance estimates was only calculated for odds of recapture 10-50% less than the odds of capture. For example, in a scenario with 0% variability in capture probability, a population size of 10,000, an initial capture probability of 0.4, and 5 removal events, the interpretation is that the mean proportional error in abundance estimates when existing unequal capture probabilities are unaccounted for or undetected is between 0.5-0.1 higher than the true abundance.

## Appendix

```
library(RMark)

#plot matrix
layout(matrix(c(1:5), nrow=1, ncol=5, byrow=T))

#Set initial paramters for simulation
numreps=100 #number of repetitions
k=7 #number of removal events
true_abund=1000 #true abundance
chg.p=c(0.1, 0.2, 0.3, 0.4, 0.5) #initial capture probability
chg.d=c(1, 0.70, 0.40) #variation in capture probability
chg.i=c(1, 1.30, 1.60) #variation in capture probability
chg.c=c(0.9, 0.8, 0.7, 0.6, 0.5) #recapture probabilities

#Containers
estimate=matrix(NA, nrow=numreps, ncol=length(chg.c))
se=matrix(NA, nrow=numreps, ncol=length(chg.c))
lcl=matrix(NA, nrow=numreps, ncol=length(chg.c))
ucl=matrix(NA, nrow=numreps, ncol=length(chg.c))
null.modest=matrix(NA, nrow=numreps, ncol=length(chg.c))
c.modest=matrix(NA, nrow=numreps, ncol=length(chg.c))
time.modest=matrix(NA, nrow=numreps, ncol=length(chg.c))
timec.modest=matrix(NA, nrow=numreps, ncol=length(chg.c))
model.select=matrix(NA, nrow=numreps, ncol=length(chg.c))

#simulation
for (u in 1:length(chg.c)){

  N=true_abund #true abundance
  p.init=chg.p[u] #initial capture probability
  b0=qlogis(p.init) #logit of the initial capture probability
  odds.dec=runif(k, chg.d[1], chg.i[1]) #proportional change in odds each time
  step eg odds declines 1-0.9=10% per time step
  #odds.dec=runif(k, chg.d.fixed, chg.i.fixed)
  #odds.c=1 # odds of a tagged fish getting captured is 50% lower than
  nontaggers
  odds.c=chg.c[u] #odds of recapture
  #odds.c=1
  b1=log(odds.dec) #log odds of capture
  c=log(odds.c) #log odds of recapture
  r.p.seq=exp(b0+b1)/(1+exp(b0+b1)) #capture probability
  p.c=exp(b0+b1+c)/(1+exp(b0+b1+c)) #recapture probability
  r.p.seq
  p.c
  r.p.seq/(1-r.p.seq)

  p.detect=c(p.init, r.p.seq) #sequence of capture probabilities
  p.recap=p.c #recapture probability
```

```

for (z in 1:numreps){
  Y.sim=matrix(nrow=N,ncol=k)
  for(i in 1:N){
    Y.sim[i,1]=rbinom(1,1,p.detect[1])
    #create capture histories
    for(j in 2:k){
      Y.sim[i,2]=if(Y.sim[i,1]==1){Y.sim[i,2]=rbinom(1,1,p.recap[1])}else
if(Y.sim[i,1]==0){Y.sim[i,2]=rbinom(1,1,p.detect[2])}
      Y.sim[i,3]=if(Y.sim[i,2]==1){Y.sim[i,3]=0}else if(Y.sim[i,2]==0 &
Y.sim[i,1]==1){Y.sim[i,3]=rbinom(1,1,p.recap[2])}else{Y.sim[i,3]=rbinom(1,1,p
.detect[3])}
      Y.sim[i,4]=if(sum(Y.sim[i,(2:3)])>0){Y.sim[i,4]=0}else
if(sum(Y.sim[i,(2:3)])==0 &
Y.sim[i,1]==1){Y.sim[i,4]=rbinom(1,1,p.recap[3])}else{Y.sim[i,4]=rbinom(1,1,p
.detect[4])}
      Y.sim[i,5]=if(sum(Y.sim[i,(2:4)])>0){Y.sim[i,5]=0}else
if(sum(Y.sim[i,(2:4)])==0 &
Y.sim[i,1]==1){Y.sim[i,5]=rbinom(1,1,p.recap[4])}else{Y.sim[i,5]=rbinom(1,1,p
.detect[5])}
      Y.sim[i,6]=if(sum(Y.sim[i,(2:5)])>0){Y.sim[i,6]=0}else
if(sum(Y.sim[i,(2:5)])==0 &
Y.sim[i,1]==1){Y.sim[i,6]=rbinom(1,1,p.recap[5])}else{Y.sim[i,6]=rbinom(1,1,p
.detect[6])}
      Y.sim[i,7]=if(sum(Y.sim[i,(2:6)])>0){Y.sim[i,7]=0}else
if(sum(Y.sim[i,(2:6)])==0 &
Y.sim[i,1]==1){Y.sim[i,7]=rbinom(1,1,p.recap[6])}else{Y.sim[i,7]=rbinom(1,1,p
.detect[7])}
      #Y.sim[i,8]=if(sum(Y.sim[i,(2:7)])>0){Y.sim[i,8]=0}else
if(sum(Y.sim[i,(2:7)])==0 &
Y.sim[i,1]==1){Y.sim[i,8]=rbinom(1,1,p.recap[7])}else{Y.sim[i,8]=rbinom(1,1,p
.detect[8])}
      #Y.sim[i,9]=if(sum(Y.sim[i,(2:8)])>0){Y.sim[i,9]=0}else
if(sum(Y.sim[i,(2:8)])==0 &
Y.sim[i,1]==1){Y.sim[i,9]=rbinom(1,1,p.recap[8])}else{Y.sim[i,9]=rbinom(1,1,p
.detect[9])}
      #Y.sim[i,10]=if(sum(Y.sim[i,(2:9)])>0){Y.sim[i,10]=0}else
if(sum(Y.sim[i,(2:9)])==0 &
Y.sim[i,1]==1){Y.sim[i,10]=rbinom(1,1,p.recap[9])}else{Y.sim[i,10]=rbinom(1,1
,p.detect[10])}
    }
  }

  Y.captured=apply(Y.sim,1,sum)
  y.ch.all=Y.sim[which(Y.captured>0),]
  y.ch=y.ch.all[,1:k]
  y.captured.after.first=apply(y.ch[,2:k],1,sum)
  y.freq=rep(1,nrow(y.ch))
  y.freq[which(y.captured.after.first>0)]=--1 #all individuals recaptured or
captured in events >1 are removed from system
  Y.test=apply(y.ch,1,sum)
  #fit capture histories for use in RMark
  y.pdata=process.data(data.frame(ch=collapseCH(y.ch),freq=y.freq,
stringsAsFactors = FALSE),model="Closed")
  y.ddl=make.design.data(y.pdata)
  #run models
  run.bass=function(){
    p.dot=list(formula=~1,share=TRUE)

```

```

p.dot.c=list(formula=~1, share=FALSE)
p.time=list(formula=~time, share=TRUE)
p.time.c=list(formula=~time+c, share=TRUE)
bass.model.list=create.model.list("Closed")
bass.results=mark.wrapper(bass.model.list,
                           data=y.pdata,
                           ddl=y.ddl,
                           silent=TRUE)

return(bass.results)

}

bass.results=run.bass()
bass.results

model.select[z,u]=bass.results$model$model[1]

#extract population estimates and calculate proportional error

null.modest[z,u]=if(length(as.numeric(bass.results$p.dot$results$derived$'N
Population Size'[1]))>0){
  null.modest[z,u]=(as.numeric(bass.results$p.dot$results$derived$'N
Population Size'[1])-true_abund)/true_abund
}else{null.modest[z,u]=NA}

c.modest[z,u]=if(length(as.numeric(bass.results$p.dot.c$results$derived$'N
Population Size'[1]))>0){
  c.modest[z,u]=(as.numeric(bass.results$p.dot.c$results$derived$'N
Population Size'[1])-true_abund)/true_abund
}else{c.modest[z,u]=NA}

time.modest[z,u]=if(length(as.numeric(bass.results$p.time$results$derived$'N
Population Size'[1]))>0){
  time.modest[z,u]=(as.numeric(bass.results$p.time$results$derived$'N
Population Size'[1])-true_abund)/true_abund
}else{time.modest[z,u]=NA}

timec.modest[z,u]=if(length(as.numeric(bass.results$p.time.c$results$derived$
'N Population Size'[1]))>0){
  timec.modest[z,u]=(as.numeric(bass.results$p.time.c$results$derived$'N
Population Size'[1])-true_abund)/true_abund
}else{timec.modest[z,u]=NA}

#calculate model averages
num.models=nrow(bass.results$model.table)
mod.est=vector("numeric", length=num.models)
mod.se=vector("numeric", length=num.models)
weight=bass.results$model.table$weight
for(i in 1:num.models){
  model.numbers=as.numeric(row.names(bass.results$model.table))
  x=bass.results[[model.numbers[i]]]$results$derived
  mod.est[i]=x$'N Population Size'$estimate
  mod.se[i]=x$'N Population Size'$se
}

avgs=model.average(list(estimate=mod.est, weight=weight, se=mod.se), revised=TRUE)

```

```

C=exp(1.96*sqrt(log(1+(avgs$se/avgs$estimate)^2)))
avg.lcl=avgs$estimate/C
avg.ucl=avgs$estimate*C

estimate[z,u]=(avgs$estimate-true_abund)/true_abund
se[z,u]=avgs$se/true_abund
lcl[z,u]=avg.lcl
ucl[z,u]=avg.ucl
}
}

est=as.data.frame(estimate)

#Proportions of c and time+c as best model
ms1=as.data.frame(model.select)
remove=c(1,3) #add 5 and 6 if Time and Time+c are included
#remove=c("p(~1)c(~1)f0(~1)", "p(~time)c(~1)f0(~1)")
prop1=numeric()
for (i in 1:ncol(ms1)){
  prop1[i]=length(ms1[,i][!ms1[,i]%in%remove])/sum(length(ms1[,i]))*100
}

prop1

par(mar=c(3,3,4,0.25))
barplot(prop1,ylim=c(0,100),ylab=NA,xlab=NA,pch=16,cex.axis=1.5)

#model averaged estimates
par(mar=c(3,3,4,0.25))
boxplot(est,ylim=c(-0.3,0.3),ylab=NA,xlab=NA,pch=16,cex.axis=1.5)
abline(h=0,lty=2)

#time model estimates
par(mar=c(3,3,4,0.25))
boxplot(time.modest,ylim=c(-3,3),ylab=NA,xlab=NA,pch=16,cex.axis=1.5)
abline(h=0,lty=2)

#time+c model estimates
par(mar=c(3,3,4,0.25))
boxplot(timec.modest,ylim=c(-3,3),ylab=NA,xlab=NA,pch=16,cex.axis=1.5)
abline(h=0,lty=2)

#Proportions of null and time as best model
remove2=c(2,4) #add 5 and 6 if Time and Time+c are included
#remove2=c("p(~1)c(~1)f0(~1)", "p(~time + c)c(~1)f0(~1)")
prop2=numeric()
for (i in 1:ncol(ms1)){
  prop2[i]=length(ms1[,i][!ms1[,i]%in%remove2])/sum(length(ms1[,i]))*100
}

prop2

par(mar=c(3,3,4,0.25))
barplot(prop2,ylim=c(0,100),ylab=NA,xlab=NA,pch=16,cex.axis=1.5)

p1=mean(prop1)
p2=mean(prop2)
y=c(c.modest,timec.modest)

```

```
y1=na.omit(y)
y1=y1[y1<5]
m1=mean(y1)
x=c(null.modest,time.modest)
x1=na.omit(x)
x1=x1[x1<5]
m2=mean(x1)
l1=length(y1)/length(y)
l2=length(x1)/length(x)
scen1=c(p1,p2,m1,m2,l1,l2)

scen1
```

A-1. Example code of one scenario of Monte Carlo simulations of closed-population capture recapture models in RMark to evaluate the detectability of recapture effects and bias in abundance estimates.