

## ABSTRACT

LAMB, APRIL DAWN. Informing Common Carp (*Cyprinus carpio*) Removal and Submerged Aquatic Vegetation Restoration in Lake Mattamuskeet (Under the direction of Jesse Fischer).

Globally, shallow lakes and wetlands are experiencing unprecedented declines in the abundance and biodiversity of submerged aquatic vegetation (SAV). This loss is detrimental, as SAV increases ecological resilience, provides unparalleled foraging and refugia habitat for fish and waterfowl, and limits eutrophication. Declines in SAV abundance are frequently driven by changes in nutrient loading and turbidity, which disproportionately impact closed systems with high residence times and a limited capacity to self-regulate inputs. Shallow inland lakes therefore exist in one of two alternative ecological states: a clear-water state dominated by SAV, or a turbid-water state dominated by phytoplankton. These states are generally stable; however, high biomasses of invasive Common Carp (*Cyprinus carpio*, hereafter “carp”) resuspend sediment, uproot SAV, and increase nutrient availability during foraging, and can contribute to shifts from the clear to turbid-water state.

Carp removal has been shown to reverse state shifts, but this has historically been limited to smaller systems and may be short-lived as carp are resilient to eradication. Thus, when considering management in large systems where repeated system-wide removals are costly, it is important to understand baseline population characteristics that may impact success. Our first objective is to inform carp management in Lake Mattamuskeet, a 16,314-ha shallow, hypereutrophic lake in eastern North Carolina that has undergone widespread declines in water quality and a total loss of SAV. Specifically, we characterize baseline population characteristics, estimate biomass, and simulate population-level responses to harvest using age-structured models. We found that carp are young (mean age = 3.7), short lived (maximum age = 7 years), and fast growing ( $K = 0.68$ ). Annual mortality rate ( $A = 0.50$ ) was higher than expected, possibly due to the extreme environmental conditions that occur annually in this system, including sustained periods of hot water temperatures ( $> 30^{\circ}\text{C}$ ) and high pH (8 – 10), which encroach and exceed the maximum physiological tolerance of carp, respectively. Using an in-lake mark-recapture arena, we estimated a carp biomass of  $124 \text{ kg} \cdot \text{ha}^{-1}$ , which is above the reported threshold for ecological impairments due to carp presence. Finally, we ran a Beverton-Holt yield-per-recruit model to evaluate the population response to exploitation given our estimated

range of natural mortality. We found that yield does not decline with increased exploitation, indicating that a population crash is unlikely from removal alone.

The growing consensus is that an adaptive, multifaceted approach that increases ecological resilience in addition to reducing stressors is needed for successful restoration. Transplanting SAV following carp removal offers one strategy that can help reestablish native species in systems where seed banks have been depleted. Our second objective is to inform SAV restoration efforts in Lake Mattamuskeet. Specifically, we evaluate the establishment, overwinter survival, and growth potential of three native, macrophyte species [*Vallisneria americana* (submerged), *Najas guadalupensis* (submerged), *Nymphaea odorata* (floating-leaf)] when planted alone and together, and measure localized water quality parameters that may impact transplantation success. All three species successfully established, despite several water quality parameters that failed to meet median SAV habitat requirements. Submergent taxa exhibited the highest survival (*N. guadalupensis* = 92%; *V. americana* = 83%) followed by *N. odorata* (=75%). By far, *V. americana* exhibited the greatest upward and outward growth, expanding outside of the planting area in every enclosure it was detected in. We observed only one instance of vegetation (*V. americana*) growing outside of an enclosure. Total biomass of *V. americana* captured outside of the planting area averaged 126.0-g and was significantly higher in the all species treatment (*V. americana* + *N. guadalupensis* + *N. odorata*) than when planted alone or with only *N. odorata* after we corrected for differences in initial transplant numbers between treatments.

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Informing Common Carp (*Cyprinus carpio*) Removal and Submerged Aquatic Vegetation  
Restoration in Lake Mattamuskeet

by  
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## **DEDICATION**

This thesis is dually dedicated to my father, Bruce Lamb, and my childhood “hero”, the late Steve Irwin. To their curiosity, gusto, unapologetic comedy, and humility, I owe my love of learning and fascination with nature. It is safe to say that between the two, I had no option but to follow this crazy path that continues to bring me so much joy and fulfillment.

## BIOGRAPHY

I was raised in China Grove, a small crossroads town in the Piedmont region of North Carolina. I grew up hunting and lake fishing with my dad, photographing anything that moved (sorry plants, I love you now), reading, writing, drawing, playing video games, and fervently vowing that I would never work a job I did not enjoy. At 25, I am happy to report that I have somehow been both lucky and stubborn enough to make that a reality.

Research has always been an integral part of my life, but this amplified when I began my B.S. in Zoology at NC State University. As an undergraduate I worked for various research labs. I started out in the Research PackTrack program, where I learned how to interpret scientific papers, cross-section teleost brains, and perform tedious *in situ* hybridizations to evaluate gene expression in sex-changing fish. This program has no doubt been the launch point for many passionate scientists and was frankly a cool place to start my research career. I went on to continue the gene expression work in the lab of Dr. John Godwin in the Department of Biological Sciences. It was here that I discovered my love of snorkeling for “work” and gained my first research mentor, Melissa Lamm, who introduced me to the Cup A Joe “king” size. I will not say that was a particularly healthy discovery, but a tasty and necessary one for graduate school, nonetheless. Next came the USDA-ARS Genotyping lab, where I worked under Gina Brown-Guedira and graduate student Mai Xiong. Here I learned the ins and outs of DNA sequencing and genotyping. I never imagined I would enjoy working solely in a lab, much less on wheat, but this turned into one of the most enjoyable jobs I have ever had. Clearly, I still had some free time to fill (cue the sarcasm), so I began volunteering with curator, Alex Dornburg, and collections manager, Gabriela Hogue, in the Ichthyology Research and Collections Unit at the North Carolina Museum of Natural Sciences. It would take several pages to detail all the incredible projects I worked on while at the Fishes unit, which included both U.S. and international-based work with a suite of incredible scientists, so I will keep it brief by saying that I enjoyed the lab so much I stuck around for five years before getting my first paycheck. More importantly, Alex and Gabriela have been two of my most important research mentors and are largely why I went on to pursue a M.S. degree.

I remember getting the email that I had been selected to receive a National Science Foundation Graduate Research Fellowship. I was in bed and half asleep, unable to fully process what I was reading. When I finally came to my senses, I was both ecstatic and terrified.

Comically, I had accepted a lab job just a few days prior after having been denied from my top graduate school because of GRE scores. Thankfully, GRE scores are no longer considered for acceptance to many programs, a trend I am in full support of. Anyway, I received a massive fellowship but was not admitted to a graduate program which sent me into full panic mode. After *many* phone calls, the worst anxiety I have ever experienced, and an incredible amount of support from friends and loved ones, I decided that obtaining an M.S. at N.C. State was the best option forward. Around this time, I met Dr. Jesse Fischer and he explained his interest in the problematic Common Carp population in Lake Mattamuskeet. After one trip out to the lake I was hooked. I then set off on the journey detailed in this thesis.

Although I am not immediately transitioning into a PhD program, I constantly find myself researching things that interest me. Given the state of the world at this time, these exist within science as well as other fields. To stick to the science per say, I am interested in research that takes an integrative and cross-disciplinary approach to addressing applied questions that transcend traditional boundaries of ecology and evolutionary biology. Specifically, I am interested in understanding how species diversity is generated and maintained over time and how invasive species influence community composition and abundance, growth, and niche occupancy of native species to better inform management decisions regarding imperiled systems. As a first-generation college graduate, I am also passionate about fostering citizen science involvement in our communities and working to bridge the gap between researchers and the public. Finally, I am a huge proponent of art and creativity in science and feel that these are incredible, yet underutilized, tools that allow us to better conduct and convey research.

## ACKNOWLEDGMENTS

I would like to formally thank Dr. Jesse Fischer for serving as my advisor and mentor over the past three years. Jesse- it was largely your knowledge base, ambition, and dedication that made this project possible. I would also like to thank my committee members, Dr. Michael Piehler and Dr. Robert Richardson, for their unwavering support and guidance during this project, and for their critical roles in reviewing this thesis.

I would also like to acknowledge my agency-based collaborators. From the U.S. Fish and Wildlife Service, I would like to thank Pete Campbell, Wendy and John Stanton, Michelle Chappell, Debbie McGowan, and Michelle Moorman for helping me establish a study site at the Mattamuskeet NWR and navigate the benefits and challenges of working in rural North Carolina. From the N.C. Wildlife Resources Commission, I would especially like to thank Kevin Dockendorf, Katie Potoka, and Chris Smith for their repeated assistance with fieldwork and sample collection, the extent of which is beyond what I could have ever hoped for. I would also like to thank Ben Ricks, Clint Morgeson, Kirk Rundle, and Courtney Buckley from the NCWRC for assisting in the great ‘Carp Rodeo’ of 2018, and Astrid Schnetzer from N.C. State for allowing me to use her lab equipment to process my water samples. Finally, I would like to recognize Tom Kwak and Ruby Valetton at the United States Geological Services Research Co-Operative Unit for providing fieldwork vehicles, research equipment, and a home field base from which much of this project was devised.

I cannot stress enough how valuable volunteers are to the research process. To the students, scientists, and citizens who offered your time, effort, or advice at any point during my project, thank you. I would especially like to thank my technicians, Eric Torvinen, Trevor Hall, and James Daw, and repeat volunteers, Cara Kowalchyk, Connor Neagle, Sasha Periera, Carl Hintz, Jessi Pooni, Stephen Parker, Emilee Briggs, and Enie Hensel for their countless hours assisting with the project. Likewise, the success of this project would not have been possible without financial support from the National Science Foundation Graduate Research Fellowship Program, the U.S. Fish and Wildlife Service, and North Carolina State University.

Additionally, I would like to thank my research mentors Alex Dornburg, Gabriela Hogue, and the Westpunt Syndicate for encouraging me to push the boundaries of science and my own expectations.



Finally, I would like to extend my sincerest thanks to family and friends. To my parents, Bruce and Mary Lamb, thank you for supporting me in all my adventures, asking the right questions, and continuing to be the two people I know I can rely on no matter what. To my grandma, Lilly Bridges, and my aunts, Debbie and Dink Bridges, thank you for always rooting for me and for taking care of Louie during periods of fieldwork and travel. To my brother, thank you for keeping me on my toes and occasionally taking my advice. To my friends, thank you for helping me relax and escape the black hole that is occasionally graduate school. And to my partner Cole, thank you for supporting me, keeping me sane, and making me feel loved throughout this process.

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## **CHAPTER 1**

**Live fast, die young: Common Carp (*Cyprinus carpio*) exhibit fast growth, high annual mortality, and low longevity in response to extreme environmental conditions in a shallow, coastal lake**

## 1.1 Abstract

Common Carp (*Cyprinus carpio*) are one of the most widely introduced and ecologically disruptive aquatic species in the world. During foraging, Common Carp uproot submerged aquatic vegetation, alter nutrient dynamics, and re-suspend sediment into the water column, which can drastically reduce water quality and clarity and restructure entire aquatic ecosystems. Removing Common Carp from impaired waterways to improve ecosystem health has been shown to reduce or reverse these effects; but, system-wide removals have historically been limited to smaller lakes and ponds and may be short-lived as Common Carp are resilient to eradication and can exhibit a compensatory response to removal. Thus, when considering management options in large or interconnected systems where repeated system-wide removals may be especially costly, it is essential to first understand baseline population-level information that may impact removal success. The aim for this study is to inform Common Carp management efforts in Lake Mattamuskeet, a 16,314-ha shallow, hypereutrophic lake located in eastern North Carolina that has recently undergone widespread declines in water quality and a total loss of submerged aquatic vegetation. To do so, we characterize baseline population characteristics, generate a biomass estimate using mark-recapture, and simulate population-level responses to harvest using age-structured models. We find that Common Carp in Lake Mattamuskeet are young (mean age = 3.7), short lived (maximum age = 7 years), and fast growing ( $K = 0.68$ ), consistent with other shallow lake populations at southern latitudes in North America. However, annual mortality rate ( $A = 0.50$ ) for Common Carp in Lake Mattamuskeet is the highest of any carp population in North America to date. One possible explanation for this may be the extreme environmental conditions that occur annually in this system, including sustained periods where water temperatures exceed  $> 30^{\circ} \text{C}$  and pH ranges from 8 to 10, which encroach (water temperature) and exceed (pH) the maximum physiological tolerance of Common Carp. To estimate the biomass of Common Carp in Lake Mattamuskeet, we constructed a novel in-lake arena and conducted a single event mark-recapture. We estimated there to be 971,220 individuals in Lake Mattamuskeet at a biomass of  $124 \text{ kg} \cdot \text{ha}^{-1}$ , which is well above the minimum reported threshold for ecological impairments from Common Carp. Finally, we ran a Beverton-Holt yield-per-recruit model to evaluate the population response (yield, kg) to exploitation (percent harvest) given our estimated range of natural mortality ( $m = 95\% \text{ CIA}$ ; 0.41, 0.59). We found that yield does not decline with increased exploitation, indicating that a population crash is unlikely from



removal alone. Cumulatively, our results indicate that the reduction of Common Carp biomass will be difficult in Lake Mattamuskeet due to fast growth, low longevity, and high annual mortality observed within the population. Finally, this study provides the first characterization of a Common Carp population in North Carolina and highlights the challenges of attempting carp removal in large, warm system.

## 1.2 Introduction

Common Carp (*Cyprinus carpio*; hereafter “carp”) are one of the most widely introduced and ecologically disruptive aquatic species in the world (Vilizzi and Copp 2017, Weber and Brown 2009). Native to Eurasia, carp are prolific across most of their introduced range, with established populations on every continent excluding Antarctica (Koehn et al. 2004; Vilizzi et al. 2015). In North and South America, and Australia, carp are presently considered highly invasive, nuisance fish that can dominant entire systems and cause undesirable aquatic conditions, including impaired water clarity, eutrophication, and decreased sportfish and waterfowl abundance (Pinto et al. 2005; Jackson et al. 2010; Cahn 1929; Bajer et al. 2009). Removing carp from impaired waterways is a common management strategy and has repeatedly been shown to reduce or reverse these effects; but, system-wide removals are costly and have historically been limited to smaller lakes and ponds (Schrage and Downing 2004; Knopik and Newman 2018). Likewise, carp are resilient to eradication and may exhibit a partial-compensatory response to removal by maintaining or increasing recruitment and survival, making eradication difficult in large or interconnected systems where drastic reduction in population numbers is unlikely (Weber et al. 2016). Thus, when considering management options in systems where repeated system-wide removals may be especially costly, it is essential to first understand baseline population-level information that may inform management strategies and influence removal success.

Carp have been shown to engineer aquatic ecosystems through a “middle-out” framework, by altering both top-down (e.g. predator abundance) and bottom-up (e.g. nutrient availability) ecological processes (Weber and Brown 2009; Kaemingk et al 2016; Kloskowski 2011; Threinen and Wm. T. Helm 1954, Emery-Butcher et al. 2020). Specifically, carp increase nutrient availability and sediment resuspension and uproot submerged aquatic vegetation during foraging (Weber and Brown 2009; Miller and Crowl 2006; Tryon 1954; Wolfe et al. 2009). When carp

densities are high, this behavior can have cascading, ecosystem-wide effects that alter nutrient dynamics and biological communities (Huser et al. 2016; Parkos et al. 2003). Most commonly, this involves a drastic reduction in water quality and clarity, the loss of submerged vegetation beds, and eutrophication (Crivelli 1983; Qiu et al. 2019). At the consumer level, these effects have been shown to restructure food webs through decreased benthic invertebrate and zooplankton biodiversity and a shift from sight-feeding to benthivorous, tolerant fish species (Persson et al. 1991; Jeppesen et al. 2000; Jackson et al. 2010). Shallow lakes and reservoirs, which typically exist in one of two alternative stable state equilibria, are disproportionately impacted by carp (Waters et al. 2010). Specifically, the introduction of carp to shallow systems can facilitate the shift from the desired clear water (macrophyte-dominated) state a hypereutrophic (phytoplankton-dominated) state (Zambrano and Hinojosa 1999). Once this shift occurs, restoring the clear water state is difficult as many benthivorous species that increase in abundance following eutrophication perpetuate the turbid state through the resuspension of nutrients via excretion and benthic foraging (Andersson et al. 1978; Breukelaar et al. 1994). This can result in a positive feedback loop that makes it difficult or impossible for impacted fish and submerged aquatic plant communities to recover if targeted management approaches are not taken, and may cause negative, long-lasting impacts on tourism or fishing-dependent economies (Tempero 2019). Carp-dominated systems may also pose an indirect threat to human health. Sustained eutrophication in freshwater systems has been linked to the increase in frequency and severity of harmful cyanobacterial blooms (cyano-HABS), which can contain cyanotoxin-producing algae (Mohamed et al. 2018). Although research on this topic is limited, the commonly occurring cyanotoxins microcystin and cylindrospermopsin have been shown to accumulate in fish, including carp, muscle tissue following uptake across the gill epithelium, and can be hazardous to humans if consumed in high enough quantities (Drobac et al. 2016; Hardy et al. 2015). To date, the potential link between high biomass carp populations and cyanotoxin-presence has not been explored.

Reducing carp biomass through system-wide biomanipulation has been correlated with increased water clarity, reduced nutrient concentrations, and the reestablishment of submerged aquatic vegetation beds (Knopik & Newman 2018; Wanner et al. 2009; Bajer et al. 2009; Loughheed et al. 2004). Historically, removals were conducted using primarily mechanical (i.e. nets) or chemical (i.e. rotenone) methods (Cahoon et al. 1958; Marking 1992). Although

rotenone has since been largely abandoned due to environmental concerns, the mechanical removal of fish via net (seine, pound, trap, etc.) is still widely utilized in a variety of systems (Tempero et al. 2019). However, this method tends to target mainly adult individuals, leaving smaller fish still present in the system, and can be both time-consuming and costly with variable success (Ritz 1987; Weber et al. 2009). Efforts to locate, isolate, and target aggregations of carp are also common, and have shown that fish can be trained to aggregate in heavily-baited areas (Lechelt and Bajer 2016; Ghosal et al. 2018). Other management techniques include system-wide drawdowns in lakes to reduce available spawning habitat, the installation of barrier structures to prohibit migration between systems, the release of carp-specific viral agents or biotoxins, the use of attractants, and the release of native predators known to consume carp eggs (Stuart et al. 2018; Chizinski et al. 2016; Carl et al. 2016, Poole and Bajer 2019). Overall, the success of carp management varies largely by method and system, with no one approach providing a straightforward solution. The growing consensus is that to maintain reduced carp biomass, and therefore improved aquatic conditions, a long-term and adaptive management framework is necessary in most systems (Weber et al. 2009; Pellitier et al. 2020).

Broadly speaking, carp are generalists and possess life-history traits, such as rapid growth, high fecundity, high longevity, and a lack of natural predators, that allow populations to expand and spread quickly following introduction outside of their native range (Silbernagel and Sorensen 2013; Fischer et al. 2013). Carp also exhibit high environmental plasticity compared with other freshwater species, allowing individuals to survive and reproduce in a variety of waterways and under various abiotic (i.e. dissolved oxygen) and biotic (food availability) conditions (Adamek et al. 2015; Maiztegui et al. 2019). However, population-specific demographics can vary among system and geographical region. For example, Vilizzi and Copp (2017) demonstrated that carp exhibit faster early-year growth in lentic systems, such as manmade and natural lakes and ponds, and in southern latitudes. Likewise, in North America, Weber et al. (2015) found that latitude negatively correlated with growth rate, instantaneous mortality rate, and mean age of sampled individuals, but positively correlated with maximum theoretical size. This variation reinforces the need to characterize system-specific carp population demographic information and model population responses to exploitation when considering management approaches (Pearson et al. 2019). Additionally, while the global literature on carp presence, population characteristics, and ecological impacts is abundant,

certain regions remain largely understudied (Vilizzi et al. 2015). Among these is the Southeastern United States, the most rapidly urbanizing region of North America (Terando et al. 2014). Contrary to the Mississippi River Basin, which stretches from Missouri to Minnesota and has long been epicenter for common and Asian carp-related research, little to no work has been done to characterize or manage present-day carp populations in the Southeastern United States. To help address this knowledge gap, this study aims to inform carp management efforts in Lake Mattamuskeet, a large (16,314-ha) and shallow (~1-m depth) hypereutrophic lake located in eastern North Carolina, by characterizing baseline population demographics, providing a biomass estimate, and developing age-structured population models to test population response to varying levels of harvest. We hypothesize that the carp population in Lake Mattamuskeet will be characterized by young (< 5 years) individuals, fast growth rates, particularly in the first few years of growth, and a high annual mortality rate which, cumulatively, are characteristic of carp populations at southern latitudes.

### **1.3 Methods**

#### *1.3a Study Site*

Lake Mattamuskeet is a large (16,314-ha) and shallow (~1-m) lake ecosystem located on the Albemarle–Pamlico Peninsula in eastern North Carolina (Figure 1.1b). The lake constitutes roughly 80% of the federally-managed Mattamuskeet National Wildlife Refuge (MNWR), established in 1934 to protect and support migratory waterfowl that use the lake and surrounding wetlands as a necessary overwintering site (Carson 1947). Land use surrounding Lake Mattamuskeet is primarily agricultural and several farms drain into the lake through networks of canals and ditches. Additionally, four outflow canals outfitted with passive water control structures allow Lake Mattamuskeet to drain to the tidal and estuarine Pamlico Sound during high precipitation events while otherwise protecting against saltwater inundation, keeping the lake a primarily freshwater environment (Dockendorf et al. 2014). The main body of Lake Mattamuskeet is divided longitudinally into two basins via a causeway (N.C. Hwy 94), along which five culverts provide corridors for fish and other aquatic organisms to pass between the two basins.

Characteristic of shallow lakes, Lake Mattamuskeet historically supported high densities of submerged aquatic vegetation (SAV), including Wild celery (*Vallisneria americana*), Sago

Pondweed (*Stucknia pectinate*), Southern naiad (*Najas guadelupensis*), and Redhead grass (*Potamogeton perfoliatus*; Moorman et al. 2017). The abundance of aquatic vegetation, however, has fluctuated largely over the last century, accompanied by periods of drastic reductions in water quality and clarity. For over 60 years, Lake Mattamuskeet simultaneously existed in two alternative states, with the west basin dominated by phytoplankton and the east by SAV. In 1953, poor water quality was attributed to a high abundance of benthivorous fish, which prompted a baited removal of carp, Blue Catfish (*Ictalurus furcatus*), and Channel Catfish (*Ictalurus punctatus*), in the lake, with carp being the most abundant species removed. Following these removals, water clarity reportedly improved from less than six inches to over two feet of visibility and SAV expanded to cover an estimated 6,475-ha of the lakebed (Cahoon 1953). The state of each basin however, remained stable; then, from 1991 to 2017 Lake Mattamuskeet experienced another continual and severe SAV die off which caused the east basin to shift to phytoplankton-dominated and resulted in the total loss of SAV in both basins (Waters et al. 2010; North Carolina Coastal Federation 2018). Monitoring data attributed the SAV decline to poor water quality and clarity, mainly regarding observed increases in Nitrogen and Phosphorous content. In 2016, the N.C. Division of Water Resources listed Lake Mattamuskeet on the 303(d) list of impaired waters due to high pH and chlorophyll-a, which are key indicators for cyanotoxin-producing cyanobacteria harmful algal blooms (cyanoHABs; USEPA 2016). Further analysis confirmed that three cyanotoxins, cylindrospermopsin, microcystin, and saxitoxin were indeed present in the lake, with cylindrospermopsin concentrations bordering federal limits for recreational contact (Moorman et al. 2017). Cumulatively, these issues prompted Refuge officials and stakeholders to implement the Lake Mattamuskeet Watershed Restoration Plan in 2019, which outlined strategies to reduce external and internal nutrient loading. As such, carp removal was deemed a necessary step in accomplishing the latter.

### 1.3b *Sampling design*

We sampled carp from October to November in 2016, 2017, and 2018 from a combined total of 41 sites across Lake Mattamuskeet ( $n_{\text{total}} = 333$ ; Figure 1.1a). Fish were collected in 10-mm bins with a maximum of five fish per bin. All fish were sampled using daytime DC-pulsed electrofishing. Electrofishing runs lasted 15 minutes and catch-per-unit-effort (CPUE) was quantified by site as the mean number of fish captured per hour electrofishing (Supplementary Table 1.1). Sampling sites were mostly consistent across years, but some sites were added or

removed in 2017 and/or 2018 due to limited accessibility from low water levels, sedimentation, or dense stands of invasive shoreline vegetation (*Phragmites australis*).

### 1.3b Age, Weight, and Length Distributions

We recorded total length (TL, mm) and weight (g) of captured individuals and removed the proximal dorsal spine for processing. As the total maximum length of carp sampled exceeded 60 cm, length-frequency was evaluated using 5 cm bins (Anderson and Neumann 1996). Length-weight regression coefficients were generated for each capture year using the equation:  $\log_{10}W = a + b(\log_{10}L)$ , where  $W$  is the weight of the fish at capture and  $L$  is the length of the fish at capture. Ages were assigned to individuals by counting annular rings on calcified bony structures (i.e. dorsal spines) collected during sampling. Individuals who had missing data for TL, weight, or had damaged or unreadable spines were excluded from the dataset. In the laboratory, spines were mounted in epoxy and cross-sectioned on an Isomet™ Low Speed Saw. Cross-sections were examined by two readers under a dissecting scope using reflected light. To maximize clarity and reduce glare, spines were immersed in 20 mL of water and viewed against a black background. Ages were assigned independently by each reader, with a reader agreement rate of X%. Discrepancies between reader-assigned ages were resolved upon reevaluation of the spine with both readers present, and final ages were assigned after a consensus was reached between both readers. Spines were imaged at 10x magnification and the distance between annuli was measured using the Image-Pro Plus v. 10 image processing software from Media Cybernetics (Image-Pro software; Media Cybernetics, Bethesda, MD, USA). We conducted all baseline analyses of carp population characteristics in R, v. 3.4.3 (R Development Core Team 2018) using the statistical package Fish Stock Assessment (FSA) v. 0.8.20 (Ogle 2016).

### 1.3c Size Structure and Condition

Population size structure was quantified using proportional size distribution indices (PSD) and the length categories outlined in Gabelhouse (1984). Condition, a general measure of health, was evaluated among length categories by calculating relative weights:  $W_{ri} = W_i / W_{si} * 100$ , where  $W_{ri}$  is the relative weight of the individual fish,  $W_i$  is the observed weight, and  $W_{si}$  is a standardized weight for individuals of the same observed length from a given species (Wege and Anderson 1978).

### 1.3e *Growth and Mortality Rates*

We generated back-calculated lengths-at-age for all individuals using the Dahl-Lea equation:  $L_i = [S_i(S_c)^{-1}]L_c$ , where  $L$  is the length of the fish and  $S$  is the length of the structure at the annuli ( $i$ ) and capture ( $c$ ) (Dahl 1907; Lea 1910). This method assumes direct proportional growth of the structure radius and fish's total body length (Hanson et al. 2019). Mean back-calculated lengths-at-age were expressed by capture year and fit using the von Bertalanffy growth function (VBGF):  $L_t = L_\infty (1 - e^{-K(t-t_0)})$ , where  $L_t$  is the mean length-at-age at time  $t$  (Haddon 2011; Beverton and Holt 1957). Three parameters of interest,  $L_\infty$ ,  $K$  and  $t_0$ , were estimated by the VBGF, where  $L_\infty$  is the maximum mean length (mm),  $K$  is the growth coefficient, and  $t_0$  is the hypothetical age at length zero (Ogle 2016). To estimate total annual ( $A$ ) and age-specific mortality we used the Chapman-Robson (1960) method, which has been shown to outperform similar methods of analyzing catch data (Dunn et al. 2002; Smith et al. 2012). We defined catch as all fishes sampled in 2016, as this represented our most robust sampling year.

### 1.3f *Long-term environmental correlates with population dynamics*

To assess the relationship between carp growth and environmental characteristics in Lake Mattamuskeet, we summarized daily means of turbidity, water temperature, salinity, dissolved oxygen, and precipitation from 2013 to 2019 and tested for correlations with annual growth and mean back-calculated length-at-age of sampled individuals using Spearman Rank correlations. Data for aquatic parameters were obtained from two USGS continuous monitoring gauging stations, USGS 0208458892 and USGS 0208458892, located in the East (35°30'23", -76°11'02) and West (35°30'21", -76°15'14) basins of Lake Mattamuskeet, respectively (Figure 1.1a). Precipitation data was obtained from USGS 352936076125245, located on the Hwy 94 causeway that intersects Lake Mattamuskeet. Data was imported into R and analyzed using package, waterData v. 1.0.8 (Ryberg and Vecchia 2017).

### 1.3g *Biomass Estimate*

The total biomass of carp in Lake Mattamuskeet has never been quantified, likely due to difficulties associated with sampling a large (> 16,000-ha) and shallow (<1-m) water body. To circumvent these logistical challenges, we built a fully enclosed mark-recapture arena around a 53-ha bay in the southwest portion of the lake (Figure 1.1c). To construct the fence, we connected galvanized steel horse panels (4.87-m x 1.22-m) using stainless steel coils and secured the panels to "T-post style" fence posts (2.13-m) using galvanized wire clips. We then installed

fencing across the three entrances to the bay, placing gates at the two larger entrances to provide access for researchers and Refuge officials. After construction was complete, the fence was inspected for any openings large enough for carp to pass through. Once deemed fully sealed, we performed a mark-recapture study within the arena to estimate relative carp abundance and biomass. Using pulsed-DC electrofishing, 200 juvenile and adult carp were captured from outside of the arena and batch-marked by clipping a small triangle from the lower portion of the caudal fin. Fish were then stocked into holding pens located in the NW, SW, SE, and NE corners of the arena. Two additional individuals were sampled using passive trap nets and likewise marked and placed in the pens. After three days, each pen was seined. Casualties were removed and surviving fish were tallied and released into the arena.

After a 24-hour adjustment period, we conducted a three-day depletion utilizing five boats and strictly DC-pulsed electrofishing. TL (mm) and weight (g) was recorded for all individuals, and all captured individuals were released outside of the arena to prevent duplicate sampling. CPUE was quantified for each electrofishing run, with baseline electrofishing effort relatively consistent across the sampling period albeit slightly shorter sampling periods on day-2 and day-3 due to unavoidable summer storms. For analysis, we applied a Lincoln-Peterson equation (Pine et al. 2003) for estimating population size in a closed system was applied to the recapture ratio to generate relative abundance within the arena using the FSA package in R. This equation is expressed as:  $\hat{N} = [(M + 1)(n + 1) / (m + 1)] - 1$ , where  $\hat{N}$  is the total population size within the arena,  $M$  is the number of marked fish returned to the population,  $n$  is the total number of marked and unmarked fish recaptures, and  $m$  is the number of marked fish recaptured. The resulting estimate was extrapolated to account for the entire lake using:  $\hat{N}_L = [(\hat{N}_B) / (S_{bay})] (S_{lake})$ , where  $\hat{N}_L$  is estimated population size for the lake,  $\hat{N}_B$  is the calculated population size within the bay,  $S_L$  is the size of the lake in hectares, and  $S_B$  is the size of the bay in hectares. We used a Poisson distribution, which is standard for when  $m < 50$ , to calculate a 95% confidence interval for the extrapolated estimate (Seber 1982).

### 1.3h *Simulated response to exploitation*

Exploitation models are commonly used to determine how a population will respond to varying levels of harvest. To estimate the degree of exploitation needed to cause a negative population response, we ran a Beverton–Holt (1957) yield-per-recruit (YPR) model in the Fishery Analysis and Modeling Simulator (FAMS) software v. 1.64.4 (Slipke and Maceina



2014). Input model parameters included the estimated number of individuals in the population ( $N_0 = \hat{N}_L$ ), the regression coefficients ( $a = \text{slope}$ ;  $b = \text{intercept}$ ) from our length-weight equation, the observed minimum total length (TL; mm) of fish sampled, the theoretical maximum age of the population, and the growth parameters estimated by the von-Bertalanffy growth function ( $L_\infty$ ,  $K$ ,  $t_0$ ). Since carp have not been commercially or recreationally harvested from the lake within recent years, we assumed that conditional natural mortality ( $cm$ ) equals the annual mortality rate as estimated by the Chapman-Robson method. We therefore set  $cm$  to range from 0.40 to 0.60 at 0.05 increments, which encompasses the 95% CI of  $A$  as estimated by the Chapman-Robson method. Likewise, since removal has never been simulated for carp in Lake Mattamuskeet, we set conditional fishing mortality ( $cf$ ; i.e. exploitation) to range from 0.10 to 0.90 at 0.05 increments.

## 1.4 Results

### 1.4a Population Characteristics- Size Structure, Condition, Age, Mortality, Growth

Total catch of carp in Lake Mattamuskeet varied among sampling years, with the highest catch observed in 2016 ( $n = 189$ ; Figure 1.1). Anecdotal data and recorded CPUE's suggest that lower catch rates in 2017 ( $n = 75$ ) and 2018 ( $n = 69$ ) could be due to reduced availability in sampling sites rather than reduced carp abundance, as several sites visited in 2017 and 2018 yielded catch rates consistent with 2016 yields (conversation with NCWRC biologists, Table 1.1). Population characteristics, including total length and weight frequency, age and size structure, and condition were evaluated between capture years (2016, 2017, 2018) and across the entire sampling period (pooled; Table 1.2). Slight trends were observed between-years, but the significance of these variations is difficult to interpret given decreased catch each sampling year; thus, only the pooled dataset is described here. Since electrofishing was the sole sampling method utilized, most captured individuals were adults aged-2 and older. Length, weight, and age distribution of all sampled fishes were visualized using frequency distributions (Figure 1.2). Mean total length of sampled individuals was 534-mm (SE: 4.2) and total lengths ranged from 316-mm to 760-mm (Figure 1.2a). Mean weight of sampled individuals was 1898-g (SE: 53.4), which decreased slightly over the sampling period, and weights ranged from 100-g to 5367-g (Figure 1.2b). Notably, only 5 individuals exceeded the live-market preference of 4536-g (10-lb), with most fish ranging between 1361- and 1814-g (3- and 4-lb, respectively). In general, sampled

individuals were young with a mean age of 3.7 (SE: 0.1) and with 65% of individuals age-3 or age-4. Ages ranged from 1 to 7 years, although only one age-1 individual was captured (Figure 1.2c). This age range is consistent with the sampling gear utilized (i.e. DC-pulsed electrofishing), which is biased to target adult individuals. Based on age and length data alone, carp in Lake Mattamuskeet appear to exhibit rapid growth and low longevity compared to other observed populations, with 99% of individuals having reached 400-mm by age-3.

The length-weight relationship of carp in Lake Mattamuskeet showed slight positive allometric growth ( $a = -5.67$ ,  $b = 3.26$ ), indicating that individuals are increasing in weight faster than in length. For proportional size distribution, most fish fell within the quality (>384-mm) and preferred (>480-mm) length categories. PSD indices were with quality ( $n = 169$ ) and preferred ( $n = 137$ ). The mean relative weight ( $W_r$ ) of sampled fish was 83.3, with quality ( $n = 169$ ) and preferred ( $n = 137$ ) individuals scoring 81 and 85, respectively. The instantaneous mortality of fish ( $Z$ ) was 0.96 and the annual survival rate ( $S$ ) was 38.10 as estimated by the Chapman-Robson equation. We then converted instantaneous mortality to total annual mortality ( $A$ ) using the equation outlined in Hoenig et al. (1983), which yielded an estimate of 0.50 (SE: 0.05; CI: 0.41, 0.59) or a 50% mortality rate. This indicates the turnover in Lake Mattamuskeet is extremely high, with half of the total population replaced each year through mortality and recruitment. Given the lack of recreational and commercial harvest of carp in Lake Mattamuskeet, we assume that this rate reflects the rate of natural mortality in the population.

Mean back-calculated lengths-at-age were generally similar across sample years, but decreased slightly for age-2, age-3, and age-5 individuals (Figure 1.2d). Overall, carp displayed rapid early life growth, which slowed down by age-3 (Figure 1.3). The von-Bertalanffy growth function fit to back-calculated length-at-age data for all sampled individuals yielded a theoretical maximum length ( $L_\infty$ ) of 552.1 and a growth coefficient ( $K$ ) of 0.68 (Table 1.3). The estimated length at time zero ( $t_0$ ) was 0.52, although it should be noted that this value is largely arbitrary and not generally considered to be biologically significant (Ogle 2016).

#### 1.4b *Environmental correlates with population dynamics*

Environmental variables were summarized by basin from 2013 – 2017 and visualized (Figure 1.4). Parameters varied across years but were very similar between basin, so only lake-wide values were used to run Spearman Rank correlations. Additional emphasis was placed on variables prone to summer or winter extremes, namely maximum water temperature and

minimum dissolved oxygen. We assessed intercorrelations between carp growth and environmental characteristics using a series of Spearman's Rank-Order correlations and an alpha ( $\alpha$ ) level of 0.05. Overall, we found no significant correlations between environmental variables and mean back-calculated length-at-age, yearly growth, or cohort-specific growth. There was, however, a strong positive correlation between MBCL of age-4 fish and dissolved oxygen ( $\rho = 0.9$ ,  $P = 0.083$ ). Additionally, there was a strong positive correlation between yearly growth and minimum DO ( $\rho = 0.9$ ,  $P = 0.083$ ), turbidity ( $\rho = 0.6$ ,  $P = 0.42$ ), and specific conductivity ( $\rho = 0.7$ ,  $P = 0.23$ ), and a strong negative correlation with average and maximum temperature ( $\rho = -0.8$ ,  $P = 0.13$  and  $\rho = -0.8$ ,  $P = 0.13$ , respectively).

#### 1.4c Biomass Estimate

In total, 207 fish were captured during the recapture event. CPUE decreased by approximately 15% each day of the event, indicating a depletion of carp within the arena. Mean weight and mean total length of captured individuals was 2093-g (SE: 49.0) and 542-mm (SE: 3.9), respectively (Table 1.4). Of the recaptured individuals, 12 were marked. To generate a population and biomass estimate we used the Lincoln-Peterson equation for estimating population size, which is an  $\hat{N}$  an unbiased estimator of  $\hat{N}$  when  $(M + n) \geq \hat{N}$  (Chapman 1951) and nearly unbiased when  $m > 7$  (Chapman 1951; Krebs 1999; Ogle 2015). We estimated that the abundance of carp in the embayment is 3,450 (95% CI: 1975, 6677) at a density of 60 fish  $\cdot$  ha<sup>-1</sup> (CI: 35 to 118). Extrapolated to the lake, this yields a population estimate of 971,220 (CI: 566,545, 1,910,066) individuals at a biomass of 124 kg  $\cdot$  ha<sup>-1</sup> (CI: 73, 245).

#### 1.4d Simulated response to exploitation

The Beverton-Holt yield-per-recruit model indicated that yield only decreases when natural mortality ( $cm$ ) is low to moderate ( $<0.60$ ) and exploitation is high ( $>0.70$ ; Figure 1.4). When natural mortality is high ( $cm > 60\%$ ), increased exploitation has no apparent effect on yield, indicating that a population decline is not likely to occur even at high levels of exploitation. The estimated annual mortality of carp in Lake Mattamuskeet is 0.50 (CI: 0.41, 0.59), indicating that the carp population should decline with continued exploitation (i.e. harvest) of  $>70\%$  (i.e. 70% biomass removal). However, even under these conditions the decrease in overall biomass is minimal. In the most extreme case when  $cm = 0.40$  and exploitation = 0.70, yield only decreases by X%, suggesting that a rapid decrease or population crash will not occur through removal alone.

## 1.5 Discussion

Our study contributes to the global literature base detailing the deleterious effects of carp in shallow aquatic ecosystems and provides the first in-depth assessment of a destructive carp population in North Carolina. Using a constructed in-lake arena, we demonstrated a novel mark-recapture method that can be used to estimate fish biomass in large study systems where a traditional mark-recapture design may be difficult. We found that in Lake Mattamuskeet, carp occur at a biomass high enough to substantially alter basic ecological processes, supporting the hypothesis that carp played a role in the widespread ecosystem changes that occurred in the lake from 1991 to 2017 (Weber and Brown 2009; Moorman et al. 2017). To put these results into context for present-day carp management in Lake Mattamuskeet, we described baseline population demographics, developed an age-structured population model, and simulated population-level responses to removal under varying degrees of exploitation. Our results indicated that the significant reduction of carp in this system will be difficult to obtain as individuals are fast growing, short-lived, and undergo the highest rate of annual mortality of any North American carp population to date (Weber and Brown 2015). Removal simulations conducted using estimated population parameters further supported this claim as increased exploitation did not result in a substantial decreased yield of individuals, even when harvest exceeded 80%. This resiliency can likely be attributed to the high natural mortality and biomass in this system and indicates the population is able to maintain sufficient year-to-year recruitment to replenish individuals lost from mortality. Further, although we did not directly measure recruitment and fecundity, high natural mortality and biomass indicate the potential for density-dependent, or compensatory, population responses to removal (Weber et al. 2016).

Critical thresholds for carp biomass, beyond which a negative environmental response can be expected, have been identified in many shallow systems (Vilizzi et al. 2015; Parkos et al. 2003). At  $124 \text{ kg} \cdot \text{ha}^{-1}$ , our biomass estimate is above the reported global minimum threshold for increased turbidity ( $50 \text{ kg} \cdot \text{ha}^{-1}$ ) and declines in waterfowl abundance and vegetation cover ( $100 \text{ kg} \cdot \text{ha}^{-1}$ ) and approaching the threshold for which a state shift (i.e. from clear water, macrophyte-dominated to turbid, phytoplankton-dominated) is expected ( $178 \text{ kg} \cdot \text{ha}^{-1}$ ; Conallin et al. 2016). Each of these effects (turbidity, phase shift, vegetation loss, and waterfowl decline) has been observed in Lake Mattamuskeet to some degree, with changes in waterfowl abundance being the least understood (Moorman et al. 2017; Waters et al. 2010). Our results suggest that

carp biomass likely caused or contributed to these effects, but the degree to which is uncertain, especially considering the unique history of this system. Unlike most naturally-formed shallow-lakes, Lake Mattamuskeet has been anthropogenically-manipulated multiple times throughout its history, resulting in a highly altered morphology and hydrology (Waters et al. 2009). Specifically, repeated attempts to drain the lake for agricultural use reduced its original surface area significantly, the dredging of four outfall canals connected the lake to the estuarine Pamlico Sound, and the construction of Hwy 94 in 1940 split the lake into two distinct basins (Forrest 1999). Cumulatively, these events have increased nutrient availability to the main lake, contributed to historical shifts in the primary producer community, and facilitated the development of alternative stable states which persisted until the 1990's (Schippers et al. 2006; Waters et al. 2010). Due to the lack of sampling prior to 2016, we are unable to determine if carp biomass increased from 1991 to 2017 during the most recent phase shift, and whether this directly caused a reduction in water quality and loss in vegetation. However, the abundance of literature detailing how carp disproportionately impact shallow, agricultural lakes, supports this hypothesis (Roozen et al. 2007; Wahl et al. 2011). Finally, regardless of the degree to which carp contributed to the historical fluctuations in water quality and clarity in Lake Mattamuskeet, the noted increase in water clarity and macrophyte cover that occurred as a result of commercial carp removal in Cahoon (1953) provides promising initial evidence that carp removal can be utilized as a pathway to increased ecosystem health in this system.

Age and growth data for carp populations in the Southeastern United States is scarce but metabolic characteristics including growth rate, longevity, mortality, and maximum body size have been shown to significantly correlate with latitude globally (Vilizzi et al. 2017, DeLong et al. 2018). Specifically, individuals at higher latitudes exhibit slower growth, higher longevity, lower mortality, and reach higher maximum body sizes than those at southern latitudes due to increased metabolic demands associated with warmer temperatures (Weber et al. 2015). Our results are consistent with this finding. Broadly, we find that carp in Lake Mattamuskeet are young, fast growing, and short-lived. Although overall condition of fish was good by relative weight standards, quick early-life growth resulted in smaller bodied individuals that fell mostly within the -quality and -preferred PSD categories and were well below the current live market preference for carp. Additionally, parameters associated with growth and sexual maturation, including instantaneous growth rate ( $K = 0.68$ ), maximum theoretical length ( $L_{\infty} = 552.1$ ), and

mean length of age-3 fish (437.3-mm) most closely matched those of populations sampled from Oklahoma and Texas, which are similar latitudinally to North Carolina. However, mean age (3.1 years) and longevity (7 years) of sampled individuals was lower than these same populations by 2 years and up to 12 years, respectively, suggesting that the carp population in Lake Mattamuskeet is notably young and short-lived even when taking metabolic expectations into consideration (Weber et al. 2015). Additionally, we found that annual mortality ( $A = 0.50$ ) of carp in Lake Mattamuskeet is the highest of any described population in North America, followed by a shallow-lake population in Texas sampled by Weber et al. (2015); however, these systems differ in size by over 16,000-ha, making it difficult to draw meaningful comparisons. Although lake-wide fish sampling for this study was conducted over a much shorter period (three years) than most studies describing carp populations, no significant or notable differences in carp population characteristics were observed between years, suggesting that while increased sampling would bolster this exploratory dataset, it would not significantly change the major findings presented here.

Summers in Lake Mattamuskeet are characterized by sustained periods of hot water temperatures ( $> 30^{\circ}\text{C}$ ) and extremely high pH (8 to 10), which encroach (water temperature) and exceed (pH) the maximum physiological tolerance of carp,  $32^{\circ}\text{C}$  and 8.7, respectively (Edwards and Twomey 1982). Although not statistically significant, we observed a strong negative relationship between carp growth and mean daily temperature across the study period, suggesting that warm summer temperatures in Lake Mattamuskeet may be limiting yearly growth and resulting in smaller-bodied, earlier-maturing individuals. We did not observe any meaningful correlation between pH and carp growth across years, but it is reasonable to assume that extremely high pH during summer months may contribute to the high mortality observed in this system, as a pH of 10.5 was found lethal to carp (European Inland Fisheries Advisory Commission 1965). Abiotic factors generally unrelated to latitude have also been shown to influence carp size structure, recruitment, growth, mortality, and longevity in a variety of systems (Weber et al. 2010; Weber and Brown 2013). For example, in the Pampean region of Argentina which experiences dynamic flood-drought cycles that impact availability of food and spawning habitat, carp have been shown to drastically increase recruitment and cohort size during periods of high precipitation (Maiztegui et al. 2019). Lake Mattamuskeet is uniquely positioned along the eastern coast of North Carolina, a region frequently impacted by hurricanes,

floods, and other heavy rain events. These events typically occur after the spawning season but increase access to feeding and refugia habitat, raising the question of whether carp recruitment and/or growth is occurring in boom-bust cycles that can be correlated with years of heavy rain and flooding. Although not addressed in this study, this presents a potential avenue for future research and highlights the novelty of studying carp populations in coastal ecosystems frequently impacted by storm events.

Based on the findings from this study, we recommend that carp management in Lake Mattamuskeet be conducted using an adaptive, reductionist-over-holistic approach, with the goal of reducing carp biomass by 25 to 50 kg · ha<sup>-1</sup> to promote increased water clarity and quality. To achieve maximum biomass reduction and limit future recruitment, a suite of management techniques should be employed to target carp at various life stages. First, the installation of carp-specific barriers at each outfall canal can be used to disrupt adult fish movement and limit yearly access to deep-water spawning habitat. Weirs have been used before in Lake Mattamuskeet to prevent carp passage and would be relatively simple to outfit onto existing water control structures prior to the spawning period or as otherwise needed (Cahoon 1953). Canals could also serve as potential location for carp removal if permanent barriers were installed and managed. For example, ongoing research in the Murray-Darling Basin in Australia has shown that carp's natural response to a barrier (i.e. pushing and jumping) can be exploited when designing barrier structures (Connalin et al. 2016). Specifically, Stuart and Connalin (2018) developed a barrier/trap design ("the Williams' cage) that captured carp with essentially no bycatch and was successfully in drastic reducing carp biomass. In addition to limiting the movement of adult fish, identifying potential nursery areas in and around Lake Mattamuskeet, namely impoundments and agricultural irrigation canals, will be critical to limiting influx of age-0 carp as carp are capable of spawning in a variety of habitats (Adámek et al. 2015). To decrease the biomass of adult fish in the lake, we recommend conducting yearly carp removals. Taking into account how large (16,314-ha) and shallow (1-m) Lake Mattamuskeet is, removals should be conducted using strategies best suited for large systems, such as the newly described modified-unified method (MUM) developed for removing Silver Carp (*Hypophthalmichthys molitrix*) and Bighead Carp (*Hypophthalmichthys nobilis*) in Minnesota (Chapman 2020). This method has been shown effective at removing fish biomasses up to 85% and involves sectioning off areas (or "cells") using block nets and herding fish into these areas wherein they can be more easily harvested.

That said, it is important to note that further work will need to be conducted to determine whether carp exhibit a compensatory response to removal by increasing recruitment or growth, which could jeopardize the long-term benefits from carp removal (Weber et al. 2016). Finally, to improve water quality and clarity in Lake Mattamuskeet, we recommend transplanting native aquatic vegetation into caged enclosures following carp removals. Ongoing research by Piehler (unpublished) and Lamb (2020) showed that if enclosed, transplanted aquatic vegetation will successfully establish in Lake Mattamuskeet even given the current, impaired conditions. Areas of protected vegetation will also provide refugia for larval Bluegill (*Lepomis macrochirus*), which have been shown to consume carp eggs and significantly reduce carp recruitment (Poole and Bajer 2019). Together, these actions will work to 1) limit spawning potential and recruitment of carp, 2) reduce overall carp biomass, and 3) reestablish the macrophyte community in Lake Mattamuskeet.

Mitigating the impacts of invasive species to improve habitat quality and preserve ecosystem services constitutes one of the most important and daunting undertakings of this century (Gallardo et al. 2016; Charles and Dukes 2017). For carp and other generalist species adapted to thrive in human-altered environments, creative and multifaceted approaches will be required for the long-term success of habitat improvement projects. At this time, the eradication of carp from most waterways, including Lake Mattamuskeet, should be disregarded as a feasible restoration solution (Weber and Brown 2009). Instead, efforts should be focused on reducing carp biomass to a manageable level and improving the habitat through other mechanisms, such as the reduction of external nutrient inputs and the restoration of submerged aquatic vegetation. Cumulatively, our study establishes critical baseline data for the carp population in Lake Mattamuskeet, highlights the importance of characterizing population-level dynamics prior to attempting carp removal, and details the novelty and challenges of managing carp in warm, coastal-lake ecosystems.



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## 1.7 Tables

**Table 1.1:** Sample size ( $n$ ) and population characteristics of Common Carp sampled from 2016 to 2018 by capture year. Population characteristics include total length (TL; mm), weight (g), age, relative weight (Wr), and proportional size distribution (PSD). PSD categories shown here include that for quality- (PSD; TL >384-mm), preferred- (PSD-P; TL >480-mm), and memorable- (PSD-M; TL >660-mm) sized individuals (Gabelhouse 1984). The number of individuals in each PSD category is shown in parentheses. Summary statistics include mean, standard error (SE), minimum (min), and maximum (max) for TL, weight, and age and standard error (SE) for relative weight. The bottom, bolded row represents pooled data from all sampled fishes.

Capture year	$n$	Total Length (mm)				Weight (g)				Age				Relative Weight		Proportional Size Distribution		
		mean	SE	min	max	mean	SE	min	max	mean	SE	min	max	mean	SE	PSD ( $n$ )	PSD-P ( $n$ )	PSD-M ( $n$ )
2016	189	543	5.9	316	760	1983	78.6	181	5367	3.9	0.1	1	7	81.6	1.6	99 (85)	56 (85)	10 (17)
2017	75	517	8.9	355	710	1821	107.1	636	5226	3.4	0.1	2	6	88.6	1.3	99 (46)	54 (22)	9 (3)
2018	69	528	6.9	440	666	1748	78.8	100	3575	3.3	0.1	2	7	82.2	2.1	95 (38)	33 (30)	4 (1)
<b>Pooled</b>	<b>333</b>	<b>534</b>	<b>4.2</b>	<b>316</b>	<b>760</b>	<b>1898</b>	<b>53.4</b>	<b>100</b>	<b>5367</b>	<b>3.7</b>	<b>0.1</b>	<b>1</b>	<b>7</b>	<b>84.6</b>	<b>1.3</b>	<b>100 (81)</b>	<b>45 (97)</b>	<b>1 (15)</b>

**Table 1.2:** Summarized catch data [total length (TL) and weight (g)], catch-per-unit-effort (CPUE), and number of recaptured Common Carp sampled during 2018 mark-recapture event. Catch data is summarized using mean, standard error (SE), minimum (min), and maximum (max).

Day	Effort (hr)	N	Total Length (mm)				Weight (g)				CPUE (fish/hr)	Recaptures
			mean	SE	min	max	mean	SE	min	max		
1	11.08	78	538	5.6	451	676	2068	80.0	1191	4365	7.04	8
2	11.25	67	545	7.6	441	688	2086	105.0	1071	3998	5.96	1
3	12.22	62	545	7.4	454	711	2133	82.8	1030	4908	5.07	3
<b>Pooled</b>	<b>34.55</b>	<b>207</b>	<b>542</b>	<b>3.9</b>	<b>441</b>	<b>711</b>	<b>2903</b>	<b>49.0</b>	<b>1030</b>	<b>4908</b>	<b>5.99</b>	<b>12</b>

**Table 1.3:** Population parameter estimates employed in Beverton-Holt (1957) yield-per-recruit (YPR) model in the Fishery Analysis and Modeling Simulator (FAMS) version 1.64. Parameters were estimated using catch data from Common Carp sampled from 2016 to 2018 using boat electrofishing. The number of individuals in the population ( $N_0$ ) was estimated from a single mark-recapture event in 2018 conducted within a constructed in-lake arena. Growth coefficients, including  $K$ ,  $t_0$ , and  $L_\infty$ , were estimated using a von-Bertalanffy growth function fit to mean back-calculated length-at-age data from sampled fish. Annual mortality, or conditional natural mortality ( $cm$ ) was estimated using the Chapman-Robson method for analyzing catch-curve data and is expressed here as a range of values that encompasses the estimated confidence interval. Finally, additional mortality imposed by harvesting individuals from the population, or conditional fishing mortality ( $cf$ ), is expressed as a range that encompasses all possible levels of exploitation.

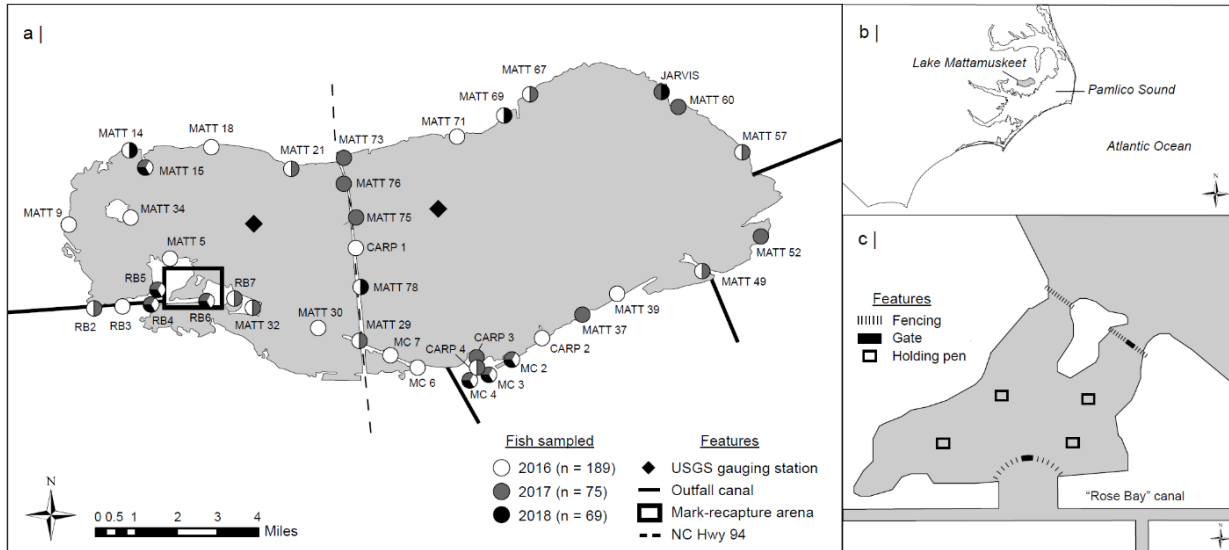
<b>Variable</b>	<b>Description</b>	<b>Estimated Value(s)</b>
$TL_{\min}$	Mimumum observed total length (mm)	316
$N_0$	Number of fish in population	971,220
$b$	Intercept of $\log_{10}$ length-weight regression	3.26
$a$	Slope of $\log_{10}$ length-weight regression	-5.67
$Age_{\max}$	Maximum observed age	7
$L_\infty$	Theorhetical maximum length (mm)	552.1
$K$	Growth coefficient	0.68
$t_0$	Theorhetical length at age-0 (mm)	0.52
$cm$	Conditional natural mortality	0.41 - 0.59
$cf$	Conditional fishing mortality	0.00 - 0.90

**Table 1.4:** Catch-per-unit-effort (CPUE) of Common Carp sampled in Lake Mattamuskeet from 2016 to 2018, shown by sampling site and latitude/longitude. Rows containing (-) were inaccessible due to low water levels, dense *Phragmites australis* coverage, or sedimentation.

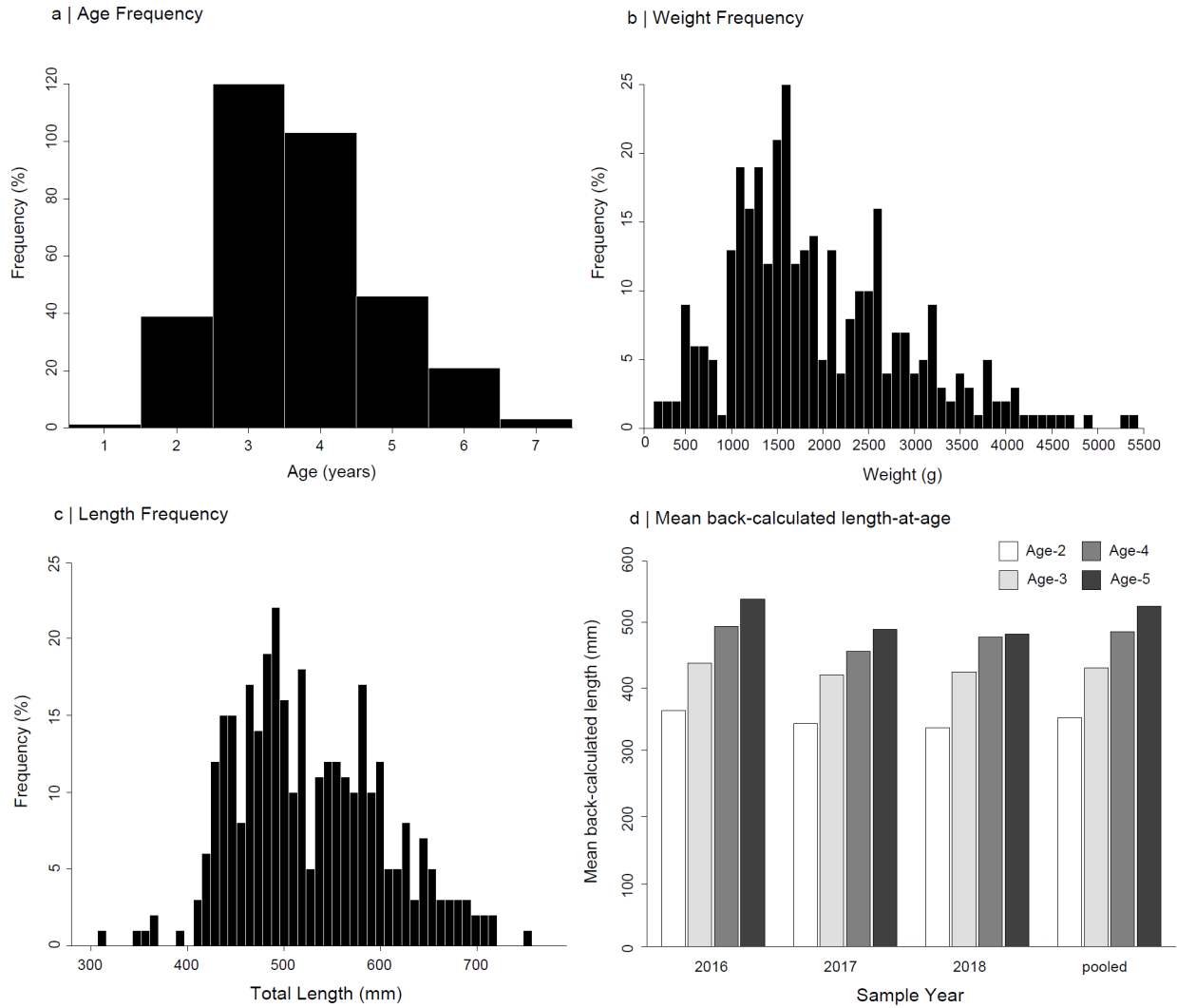
Site Name	Latitude	Longitude	CPUE (fish/hr)		
			2016	2017	2018
CARP1	35.48872	-76.21321	108	-	-
CARP2	35.46668	-76.14767	25	-	-
CARP3	35.45621	-76.17485	46	-	-
CARP4	35.45145	-76.17298	15	-	-
JARVIS	35.55400	-76.10400	0	3	101
MATT14	35.53298	-76.29417	3	-	6
MATT15	35.52750	-76.28897	24	6	4
MATT18	35.53449	-76.26514	69	20	-
MATT29	35.46578	-76.21258	56	-	0
MATT30	35.47003	-76.22729	26	0	0
MATT32	35.47710	-76.25059	6	6	0
MATT34	35.45759	-76.17048	12	0	0
MATT37	35.47140	-76.13941	0	21	0
MATT39	35.48119	-76.12392	9	0	0
MATT49	35.50259	-76.06971	6	69	-
MATT5	35.49450	-76.27994	15	0	0
MATT52	35.52029	-76.06734	-	7	-
MATT57	35.54884	-76.09915	9	23	-
MATT60	35.55971	-76.11757	-	-	0
MATT67	35.55345	-76.15182	12	-	-
MATT68	35.54477	-76.15775	-	6	-
MATT69	35.53784	-76.18581	15	-	9
MATT71	35.53332	-76.20418	3	0	0
MATT73	35.52806	-76.21929	-	53	-
MATT75	35.50860	-76.21531	-	29	-
MATT76	35.52322	-76.21805	-	33	-
MATT78	35.47877	-76.21221	33	0	75
MATT9	35.50666	-76.31599	29	-	0
MC1	35.46371	-76.14960	-	-	43
MC2	35.45864	-76.15821	36	29	72
MC3	35.45356	-76.16683	21	15	13
MC4	35.45145	-76.17298	24	6	6
MC5	35.45479	-76.18224	-	-	5
MC6	35.45793	-76.19171	-	15	-
MC7	35.46107	-76.20121	-	30	-
RB2	35.47713	-76.30686	9	-	-
RB3	35.47778	-76.29688	6	3	-
RB4	35.47857	-76.28691	15	12	6
RB5	35.47929	-76.27695	18	18	12
RB6	35.47992	-76.26697	6	9	6
RB7	35.48061	-76.25699	3	9	0



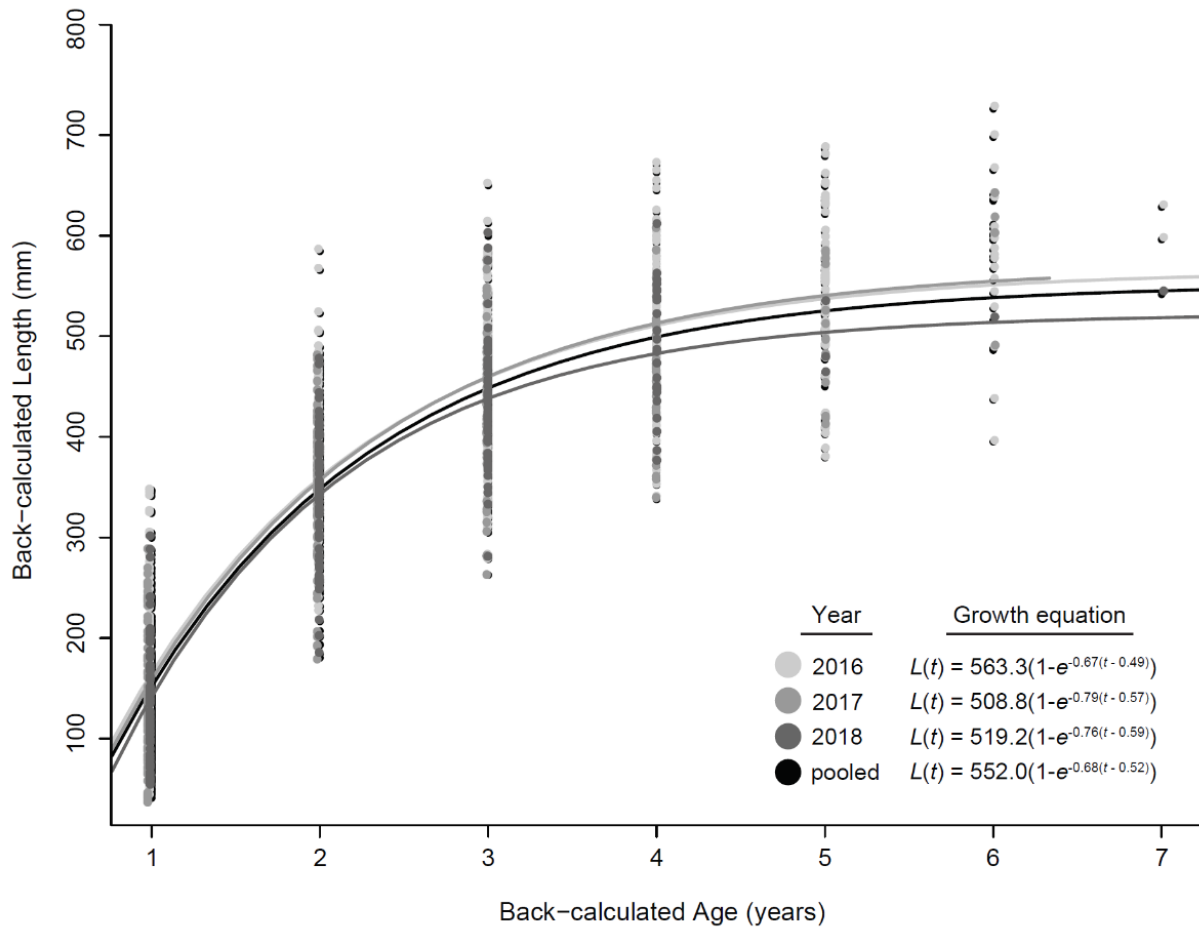
## 1.8 Figures



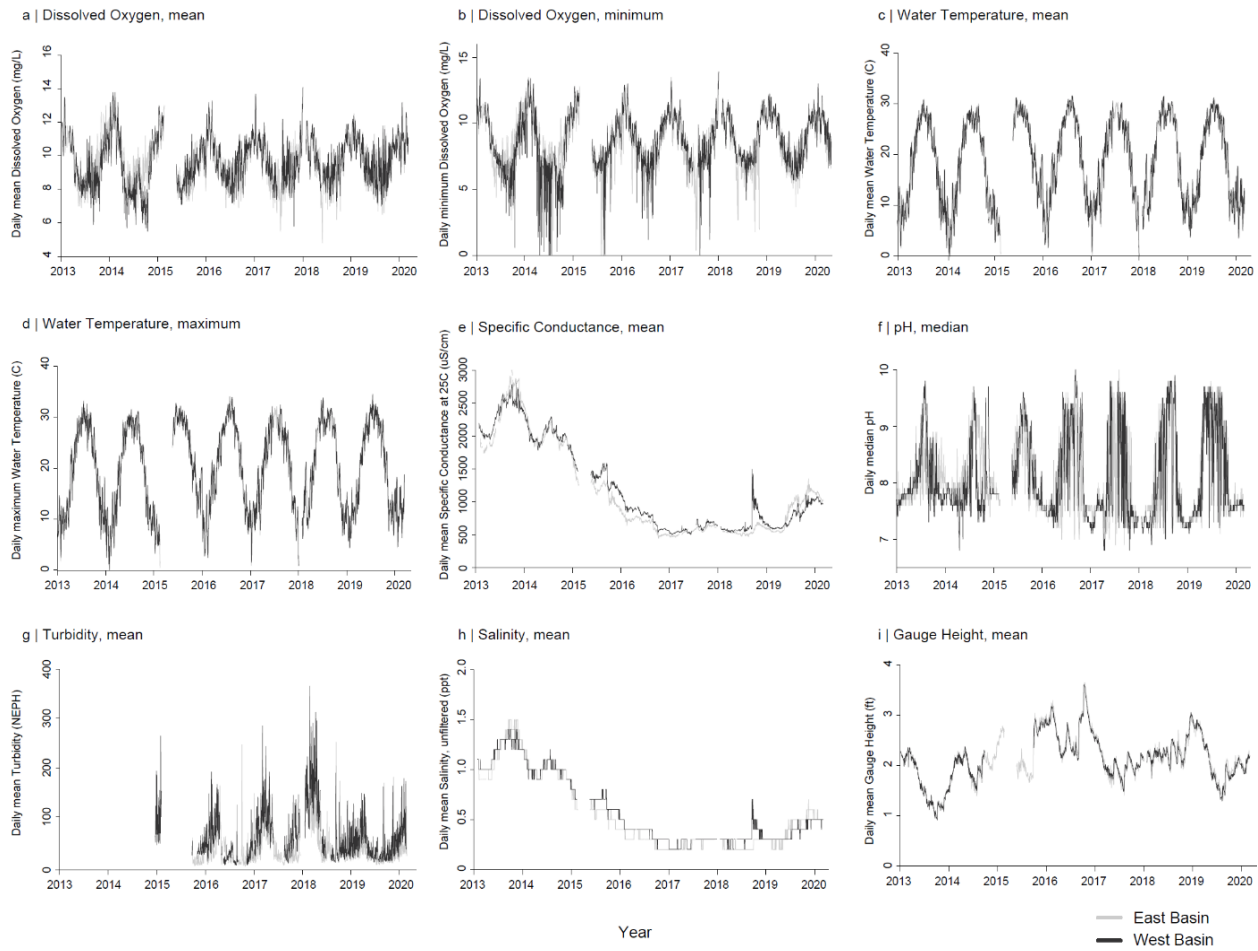
**Figure 1.1:** Map (a) and location (b) of the study area, Lake Mattamuskeet, in North Carolina. Fish sampling sites are marked with pie charts representing the year(s) Common Carp were successfully captured. Diamonds mark the locations of USGS gauging stations. The boxed region (c) represents the location and general layout of the constructed mark-recapture arena with holding pens, fences, and gates noted.



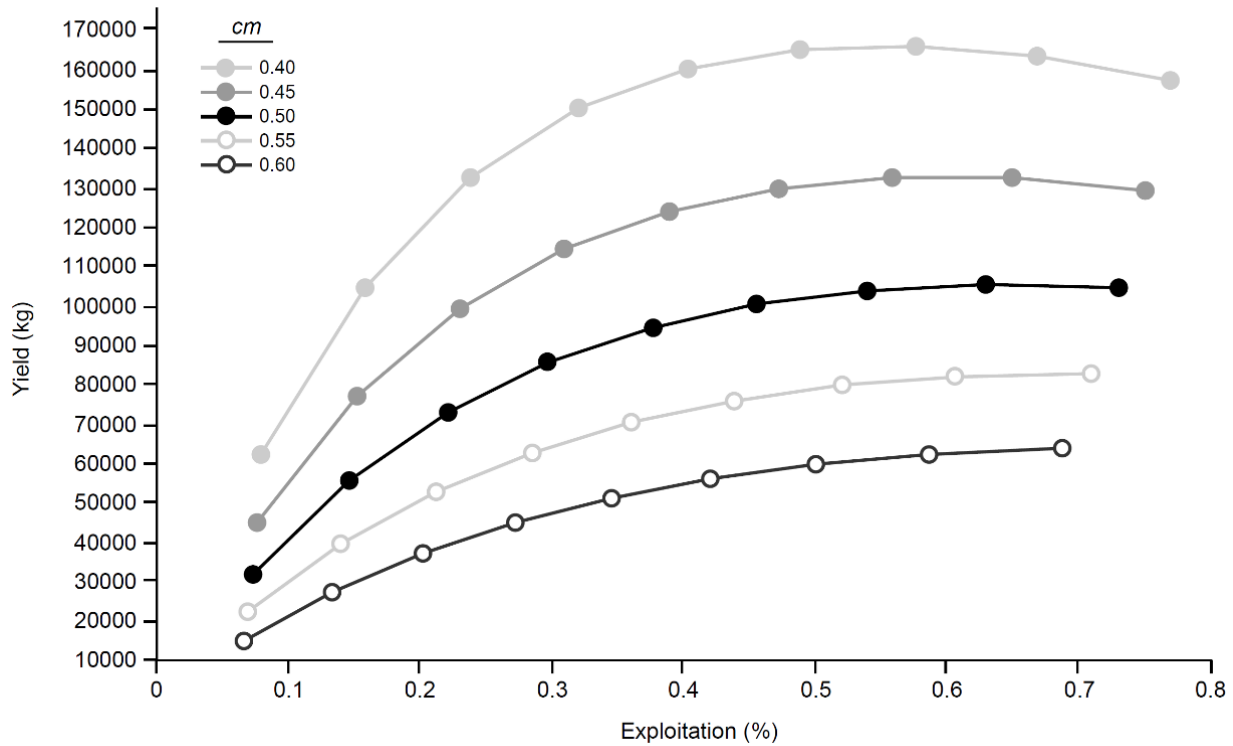
**Figure 1.2:** Age (a), weight (b), and length (c) distribution of Common Carp in Lake Mattamuskeet. Growth in fork length of Common Carp across all years (d). Curved line represents the fit von-Bertalanffy growth function. Points represent individual mean back-calculated length-at-age values.



**Figure 1.3:** Visualization of the von-Bertalanffy growth function fit to carp mean back-calculated length by capture year. Points represent individual mean back-calculated length-at-age values. Equations are given by year and follow the general format:  $L_t = L_\infty (1 - e^{-K(t-t_0)})$ .



**Figure 1.4:** Time-series plots showing variation in physiochemical parameters by basin and across years in Lake Mattamuskeet from 2013 to 2020 as recorded by USGS continuous monitoring stations. From left to right, top to bottom, parameters examined include mean daily dissolved oxygen (a), minimum daily dissolved oxygen (b), mean daily water temperature (c), maximum daily water temperature (d), mean daily specific conductance at 25C (e), median daily pH (f), mean daily turbidity (g), mean daily salinity (h), and mean daily gauge height (i).



**Figure 1.5:** Yield-per-recruit (YPR) model of Common Carp in Lake Mattamuskeet showing expected yield (y-axis) at varying levels of exploitation (x-axis) and estimated natural mortality rates ( $cm$ ). Natural mortality rates used encompass the confidence interval (CI: 0.41, 0.59) of the estimated annual mortality for Common Carp in Lake Mattamuskeet.

## **CHAPTER 2**

### **Overwinter survival and growth of transplanted submerged aquatic vegetation (SAV) in a shallow, eutrophic lake**

## 2.1 Abstract

Globally, shallow lakes and wetlands are experiencing unprecedented declines in the abundance and biodiversity of submerged aquatic vegetation (SAV). This loss is detrimental, as SAV increases ecological resilience, provides unparalleled foraging and refugia habitat for fish and waterfowl, and limits eutrophication. Declines in SAV abundance are frequently driven by changes in nutrient loading and turbidity, which disproportionately impact closed systems with high residence times and a limited capacity to self-regulate inputs. Shallow inland lakes therefore exist in one of two alternative ecological states: a clear-water state dominated by SAV, or a turbid-water state dominated by phytoplankton. Restoring shallow lakes to a clear-water state is particularly difficult once a regime shift has occurred, especially when biotic and abiotic stressors are still present. The growing consensus is that an adaptive, multifaceted approach that increases ecological resilience in addition to reducing stressors is needed for successful restoration. Transplanting SAV propagules offers one strategy that can help reestablish native species in systems where seed banks have been depleted and provide immediate habitat for larval and juvenile fish as well as invertebrates. However, transplantation success may be limited by degraded water quality, low light attenuation, and storm events. This study aims to address these uncertainties and inform SAV restoration efforts in Lake Mattamuskeet, a 16,314-ha shallow, hypereutrophic lake in eastern North Carolina that has undergone widespread declines in water quality and a total loss of SAV. Specifically, we evaluate the establishment, overwinter survival, and growth potential of three native, macrophyte species [*Vallisneria americana* (submerged), *Najas guadalupensis* (submerged), *Nymphaea odorata* (floating-leaf)] when planted alone and together, and measure localized water quality parameters that may impact transplantation success. All three species successfully established, despite several water quality parameters that failed to meet median SAV habitat requirements. Submergent taxa exhibited the highest survival (*N. guadalupensis* = 92%; *V. americana* = 83%) followed by *N. odorata* (=75%). By far, *V. americana* exhibited the greatest upward and outward growth, expanding outside of the planting area in every enclosure it was detected in. We observed only one instance of vegetation (*V. americana*) growing outside of an enclosure. Total biomass of *V. americana* captured outside of the planting area averaged 126.0-g and was significantly higher in the all species treatment (*V. americana* + *N. guadalupensis* + *N. odorata*) than when planted alone or with only *N. odorata* after we corrected for differences in initial transplant numbers between treatments.

Cumulatively, our results suggest that transplanted SAV will survive and grow under current water quality conditions when protected from uprooting and herbivory.

## **2.2 Introduction**

Submerged aquatic vegetation (SAV) is a vital component of shallow freshwater, estuarine, and saltwater ecosystems (Orth and Moore 1982; Chambers et al. 2008). Like other forms of aquatic macrophytes (e.g. emergent, floating-leaf, free-floating), SAV performs a wide range of ecosystem functions including oxygenation, carbon sequestration, nutrient cycling, wave attenuation, and sediment stabilization that improve water quality and ecosystem health (Hillman et al. 2020; Hansson et al. 2010; de Boer 2007). Established SAV beds also provide essential foraging and refugia habitat for fish, invertebrates, waterfowl, and mammals (Rozas and Odum 1988; Heck et al. 2003). Finally, SAV plays a key role in limiting phytoplankton abundance by competing for available Nitrogen and providing refugia for zooplankton, reducing the potential for eutrophication and harmful algal blooms (HABS; Wigand et al. 2000; Liu et al. 2013, Moore et al. 2008; Wiltsie et al. 2018). Natural resource managers have long recognized the economic and ecological value of these ecosystem services; but, unprecedented global declines in SAV abundance paired with the increasing occurrence and severity of HABS in recent decades highlight the need to restore SAV communities (Kahn et al. 1985; Orth and Montfrans 1990; Costanza et al. 1997; Waycott et. al 2009).

SAV is comprised of over 30 species of aquatic macrophytes which grow fully beneath the water surface and typically at depths less than 2 meters (Chambers et al. 2008; Stephan et al. 2000). Apart from depth, salinity is the primary determinant of SAV community composition (Haller et al. 1974; Hillmann et al. 2019). Freshwater and oligohaline species are typically restricted to freshwater lakes and coastal river inlets, whereas meso- and polyhaline species are found in estuaries and saltwater environments (Moore et al. 2000). SAV vary in growth morphology, reproduction, and sensitivity to external stressors; but, the availability of subsurface light in the form of photosynthesis active radiation (PAR) is the primary limiting factor for the growth of most taxa (Kemp et al. 2004). SAV communities are therefore vulnerable to processes that increase turbidity, be they anthropogenically (e.g. changes in land use/land cover) or naturally (e.g. storm events) driven (Livingston et al. 1998; Patrick et al. 2018). At the same time, these processes frequently increase nutrient loading which can strain SAV communities



and facilitate algal growth and eutrophication. Cropland, for example, has been linked to high levels of Nitrogen and Phosphorous export which can limit SAV root growth and make SAV more susceptible to uprooting and below-ground herbivory. Conversely, developed land often lacks an emergent vegetation zone which helps reduce runoff and sediment resuspension during high rainfall storm-events (van Altena et al. 2016). Further, impaired aquatic conditions may favor the establishment of homogenous stands of tolerant taxa, like the highly invasive *Hydrilla verticillata* (Waterthyme), which can suppress native SAV and cause widespread economic and ecological damage (Patrick et al. 2018; Langeland 1996; Richardson 2008). Because of their vulnerability to changes in anthropogenic stressors, SAV are frequently used as indicators of overall ecosystem health (Orth et al. 2017).

Although “SAV” is generally used to describe submerged macrophytes in coastal areas many freshwater species, such as *Vallisneria americana* (Wild Celery), are prevalent in non-tidal shallow lakes throughout North America (MacFarland 2006). Freshwater SAV beds are a highly-valued resource for inland fisheries, as they provide structures for egg deposition, refugia for larval fishes, and increase water clarity which benefits sight-feeding, sportfish like Largemouth Bass (*Micropterus salmoides*) and Bluegill (*Lepomis macrochirus*; Valley et al. 2004). The absence of SAV can be detrimental for freshwater food webs and has been linked to recruitment failure and decreased abundance of numerous fish species (Moll et al. 2017; Miller et al. 2018; Jordan et al. 2009). Shallow lakes are particularly susceptible to SAV die offs and exist almost exclusively in one of two contrasting ecological states: the clear state or turbid water state (Scheffer et al. 1993). The clear water state occurs when aquatic macrophytes dominate primary production, whereas the turbid state occurs when nutrient or light availability limits the growth of aquatic macrophytes, allowing phytoplankton to dominate primary production and causing SAV die-offs, HABS, and hypereutrophication (Carpenter et al. 1999). This two-state dynamic is referred to as alternative stable states, as the mechanisms that drive the occurrence of each state generate positive feedback loops which increase resilience to perturbations and reinforce the occupied state (Beisner et al. 2003). When resilience is lost, shallow lakes often undergo a “regime shift” from the clear water state to the turbid water state (Burdis et al. 2020). This may occur abruptly or gradually and be driven by changes in LULC, salinity, nutrient loadings, water level, or invasive species abundance (Waters et al. 2010; Schallenberg & Sorrell 2010; Patrick et al. 2018).

Restoring shallow lakes to a clear water, SAV dominated state is particularly difficult once a regime shift has occurred, especially when biotic and abiotic stressors are still present (Hansen et al. 2017). The growing consensus is that for most turbid-state systems, an adaptive, multifaceted approach aimed at increasing ecological resilience in addition to reducing or removing stressors, is needed (Geist and Hawkins 2016, Moorman et al. 2017; Pellitier et al. 2020). This may include reductions in nutrient loading, water level management, biomanipulation of invasive species, and replanting of native SAV to prevent the colonization of invasive plant species (Harwell and Havens 2003, Pinto et al. 2005, Smart et al. 1998). For example, removing Common Carp (*Cyprinus carpio*), invasive benthivores that resuspend sediment, uproot SAV, and increase nutrient availability during foraging, is an effective strategy to drastically improve water quality and clarity by breaking positive feedback loops that promote the turbid state (Schrage and Downing 2004; Weber et al. 2009; Tempero 2019). However, following removal, it may take several years for native aquatic vegetation to reestablish, leaving systems vulnerable to colonization by invasive species (Lauridsen et al. 1994). Transplanting SAV propagules following carp removal offers one avenue that can help reestablish native macrophyte species and create immediate habitat for larval and juvenile fish and invertebrates (Wu et al. 2019; Sponberg and Lodge 2005). In addition, this approach may be necessary in systems that have experienced complete losses in SAV cover where natural seed banks have been depleted or lost (Knopik and Newman 2018). Enclosures have been shown to increase establishment of SAV by protecting plants from herbivory and uprooting (Johnson et al. 2019). However, the timing of SAV transplantation, sub-optimal water quality conditions, and storm events may collectively reduce success (Orth et al. 2010). In this study, we aim to address these uncertainties and inform SAV restoration in Lake Mattamuskeet, a shallow, coastal, and hypereutrophic lake located eastern North Carolina that has recently undergone widespread declines in water quality and a total loss of SAV. Specifically, we propagate, transplant, and evaluate the establishment, overwinter survival, and growth potential of three native, macrophyte species, *Vallisneria americana* (Wild Celery), *Najas guadalupensis* (Southern Naiad), and *Nymphaea odorata* (White Waterlily) using partially-submerged enclosures. In addition, we measure localized nutrient and physical water quality parameters that may impact transplantation success.

## 2.3 Methods

### 2.3a Study system

Lake Mattamuskeet is a large (16,314-ha), shallow (~1-m) lake ecosystem located on the Albemarle–Pamlico Peninsula in eastern North Carolina (Figure 2.1a). Lake Mattamuskeet is naturally formed but underwent a series of hydrological manipulations since the early-1800's that significantly altered its natural morphology. Briefly, from 1830 - 1932, four separate attempts to drain the lake for agricultural use resulted in a ~34% reduction in total surface area, from an estimated 48,000-ha to its current size. During this period, water was actively pumped from Lake Mattamuskeet to the estuarine Pamlico Sound via four manmade outfall canals. Ultimately efforts to reclaim Lake Mattamuskeet were unsuccessful and abandoned in 1932. At that time, Lake Mattamuskeet and its surrounding wetlands were sold to the U.S. Government and established as the Mattamuskeet National Wildlife Refuge (henceforth “the Refuge”; Carson 1947). In 1945, following this acquisition, a causeway (N.C. Hwy 94) was constructed longitudinally through the center of the lake, splitting it into two distinct basins (east and west). Five culverts located along the length of the causeway link and allow water, fish, and other organisms to pass freely between the basins (Dockendorf 2014).

Precipitation and drainage represent the two primary hydrological inputs to Lake Mattamuskeet (Moorman et al. 2017). Apart from Refuge-managed impoundments, land use surrounding the lake is primarily agricultural. Cotton, soybeans, and corn are the primary crops grown (Homer et al. 2015). Historical changes in lake-ownership have allowed several farms to retain the legal right to drain or pump water into the lake through networks of canals and ditches. This occurs throughout the year but is most frequent from late winter to early spring when private impoundments are drained in preparation for the arrival of waterfowl (Winton et al. 2016). Water exits Lake Mattamuskeet through evaporation or via the outfall canals, which are outfitted with passive water control structures that allow Lake Mattamuskeet to drain to the tidal and estuarine Pamlico Sound during high precipitation events while otherwise protecting against saltwater inundation (Waters et al. 2010). This system ensures that the lake remains primarily a freshwater ecosystem within salinities averaging between 0.5 and one ppt.

Typical of shallow lakes, water quality and SAV coverage in Lake Mattamuskeet have fluctuated largely over the last century. During periods of clear water, dominant species included *Vallisneria americana* (Wild celery), *Stucknia pectinate* (Sago pondweed), *Najas guadelupensis*

(Southern naiad), and *Potamogeton perfoliatus* (Redhead grass), of which *V. americana* accounted for over 80% of total SAV biomass (Moorman et al. 2017). After the construction of Hwy 94, Lake Mattamuskeet supported two distinct alternative stable states for over 60 years, with the west basin dominated by phytoplankton and the east basin by SAV (Waters et al. 2009). In 1953, poor water quality was attributed to a high abundance of benthivorous fish, which prompted a baited removal of Common Carp, Blue Catfish (*Ictalurus furcatus*), and Channel Catfish (*Ictalurus punctatus*) in the lake, of which Common Carp were the most abundant species removed. Following these removals, water clarity reportedly improved from less than six inches to over two feet of visibility and SAV expanded to cover an estimated 6,475-ha of the lakebed (Cahoon 1953). The state of each basin however, remained stable for over 60 years (Waters et al. 2007). Then, from 1991 - 2017, Lake Mattamuskeet experienced another continual and severe SAV die off which caused the east basin to shift to phytoplankton-dominated and resulted in the total loss of SAV in both basins (North Carolina Coastal Federation 2018). Monitoring data attributed this decline to poor water quality and clarity, mainly regarding observed increases in Nitrogen and Phosphorous content followed by lake-wide eutrophication. In 2016, the N.C. Division of Water Resources listed the lake on the 303(d) list of impaired waters due to high pH and chlorophyll-a, which are key indicators for cyanotoxin-producing cyanobacteria harmful algal blooms (cyanoHABs; USEPA 2016). Further analysis confirmed that three cyanotoxins, cylindrospermopsin, microcystin, and saxitoxin are present in the lake, with cylindrospermopsin concentrations bordering federal limits for recreational contact (Moorman et al. 2017). Cumulatively, these issues prompted Refuge officials and stakeholders to implement the Lake Mattamuskeet Watershed Restoration Plan in 2019, which outlines strategies to reduce external and internal nutrient loading (North Carolina Coastal Federation 2018). Presently, the removal of Common Carp is being explored as one strategy to reduce internal nutrient loading.

### 2.3b Site selection

We conducted a visual survey of Lake Mattamuskeet to identify areas suitable for targeted SAV restoration. Several factors limited site availability. Namely, the uniformity of Lake Mattamuskeet's shoreline, which lacks the branching embayments typical of other inland lakes, made it difficult to locate sites that were protected from wind. Site selection was further limited by thick stands of invasive Common reed, *Phragmites australis*, which occur along 90%

or more of the lake shoreline and are impassable by boat and foot in most areas. Two bays in the southwestern region of the lake provided an ideal balance between logistical and financial limitations; namely they were similar in size and depth, relatively protected from wind, easily accessible in most weather conditions, and represent some of the largest possible areas (80-ha) available for restoration in the lake (Figure 2.1a). Ten restoration sites (five per bay) were randomly selected using ArcGIS (Figure 2.1b). Two geographical constraints (10-m from shore, 50-m from active Osprey nests) were applied to ensure sites did not fall within areas that could not be monitored or conflict with Refuge policies (USFWS 2008).

### *2.3c Water quality: sample collection and storage*

Two USGS continuous monitoring gauges located in the East (35°30'23", -76°11'02) and West (35°30'21", -76°15'14) basins of Lake Mattamuskeet provide access to high quality, long-term water quality monitoring data for Lake Mattamuskeet (Figure 2.1a); however, these gauges are over two kilometers away from our study area and may not be indicative of localized water quality. Therefore, to better characterize water quality within the study area, we supplemented gauging station data by measuring physicochemical parameters and chlorophyll-*a* from September 2018 - August 2019 and nutrients from April - August 2019 at each restoration site. Physicochemical parameters including water temperature (°C), dissolved oxygen (mg/L), conductivity (µS/cm), salinity (ppt), and pH, as well as Secchi depth, were measured at each site using a YSI multimeter and Secchi tube, respectively. To measure nutrient and chlorophyll-*a* concentrations, we collected surface water grab samples in 1-L, amber polypropylene bottles acid-washed in 10% hydrochloric acid (HCL) and triple rinsed with deionized water, which were brought back to the lab on ice. Both grab samples and YSI measurements were taken between the hours of 1100 and 1400 and via kayak to limit bottom disturbance. Upon arrival, 200-mL of water from each sample (in four, 50-mL aliquots) was immediately filtered and then stored at 4°C along with the remaining, unfiltered water. Of these, the first two aliquots of each sample were filtered across GF/C glass microfiber filters and promptly frozen for future chlorophyll-*a* analysis.

We measured chlorophyll-*a* concentration following the EPA method 445.0 (USEPA 1997). Specifically, chlorophyll was extracted from thawed filters using acetone and measured fluorometrically. To assess precision of chlorophyll-*a* analysis, duplicate samples were collected for each site. We measured nutrient concentrations including reactive phosphorous (PO<sub>4</sub><sup>3-</sup>), total

phosphorous (TP), nitrate ( $\text{NO}_2^-$ ), nitrite ( $\text{NO}_3^-$ ), and ionized ammonia ( $\text{NH}_4^+$ ), as well as turbidity, using a photometer (Hach DR 890 Procedure Manual). Generally, this method of testing nutrients is less precise than other methods, but in our case offered a relatively quick and inexpensive solution to testing multiple parameters monthly for over a year (Boyd 1980). Additionally, the availability of high-quality nutrient data for Lake Mattamuskeet provided in Moorman et al. (2017) gave us an established baseline with which to compare our findings. Reactive phosphorous was measured from filtered samples and all remaining nutrients were measured from unfiltered samples. In general, chlorophyll-*a* analyses were conducted 2 to 4 months after the sample collection date and nutrient analyses were conducted between 12 hours and 24 days after sample collection, according to procedure guidelines (Hach DR 890 Procedure Manual).

### 2.3d Treatment design

Aquatic macrophytes were selected based on a known-historical presence in Lake Mattamuskeet, value to waterfowl species, and biological traits that could influence successful establishment and growth in current or slightly improved lake conditions. Two submergent taxa, *Vallisneria americana* (Wild Celery) and *Najas guadalupensis* (Southern Naiad), were prioritized as they historically accounted for a majority of the SAV community in Lake Mattamuskeet and were readily available through known sources. Both species have also been shown to successfully reestablish following the removal of Common Carp (Knopik and Newman 2018). Additionally, *V. americana* was already being used as the focal species for a pilot project to test the impact of herbivory on SAV establishment in Lake Mattamuskeet, which demonstrated promising results that the species could establish when protected (Piehler unpublished). Briefly, *V. americana* is a dioecious, rooted taxa capable of reproducing sexually or asexually. Sexual reproduction typically occurs over the late-summer months via surface flowering, whereas asexual reproduction occurs year-round via cloning (Korschgen and Green 1988). Asexual reproduction is generally responsible for overwinter expansion and is considered the primary means of population growth in many systems (Catling et al. 1994; McFarland 2008). Unlike *V. americana*, *N. guadalupensis* is monocious and may be rooted or form a free-floating mat (Haynes 1979). One floating-leaf species, *Nymphaea odorata* (White Waterlily), was also selected as it may be less susceptible to stunted photosynthesis from turbid conditions and could potentially help facilitate the establishment of other species.

Six treatments were devised, consisting of one or more taxa per treatment. Treatments included: *V. americana* only (25 plants), *N. guadalupensis* only (25), *N. guadalupensis* (22) + *N. odorata* (3), *V. americana* (22) + *N. odorata* (3), and *V. americana* (12) + *N. guadalupensis* (12) + *N. odorata* (3). These combinations were selected for two primary reasons. First, taxa were planted individually and together to evaluate the impact of increased diversity on survival and growth. Additionally, *N. odorata* was paired with submergent taxa to determine whether the presence of large stems and leaves would protect SAV from wind, or stunt SAV photosynthesis via shading.

### 2.3e Aquatic vegetation procurement and propagation

Aquatic vegetation was obtained from a combination of sources. Over 90% of *V. americana* was grown at North Carolina State University from March 2018 - August 2019 using stock originally collected from Lake Mattamuskeet when it still supported dense beds of *V. americana*. Plants were grown in 4" pots and propagated by separating rosettes every 2-3 months. Plants were grown outdoors and under a shade cloth, in tubs filled with water from a local pond. A 1:4 ratio of sand to topsoil was used as the growing medium and plants were propagated by separating rosettes every 2-3 months. In August 2019, an additional 200 *V. americana*, along with all *N. guadalupensis*, were purchased from a wetland plant nursery in Edenton, North Carolina (Wetland Plants Inc.). To ensure freshness, these plants were delivered across several days and in the mornings prior to planting. Finally, all *N. odorata* was collected by hand from impoundments on the Refuge. Again, this was done in the morning by carefully digging up and rinsing tubers. All plants were stored in a water-filled pool and under shade until they could be planted. Although not measured, submergent taxa were estimated to weight no more than 20-g prior to planting.

### 2.3f Transplant methodology

In August 2019, we constructed 70, 9.3-m<sup>2</sup> transplant enclosures in the study area. Enclosures were grouped into clusters of seven and arranged in a circular formation around the ten water quality monitoring sites (Figure 2.1c). We constructed the enclosures by first securing 12-gauge galvanized steel cattle panels to "T-post style" fence posts (2.13-m) using galvanized wire clips. We then outfit each enclosure with a lid to prevent herbivory by turtles and waterfowl and uprooting by Common Carp (Figure 2.2a). Each enclosure within a cluster was planted with one of the seven treatments (including the control), which were assigned using a random block

design prior to transplantation (Figure 2.2b). To maximize the chance of the submergent taxa (*V. americana* and *N. guadalupensis*) rooting in the soft substrate, plants were hand-sewn into burlap squares and attached to a 1.2-m<sup>2</sup> fence panel (Figure 2.2c). This method has been used in varying forms in other systems and allowed us to keep an accurate account of the number of plants in each plot, submerge the entire panel of plants at once, and ensure that no plants were lost during the transplant process (Orth et al. 2006).

### 2.3f Assessing transplant survival and growth

In May 2020, we assessed overwinter survival and growth of transplanted macrophytes at 4/10 transplant sites, 28 enclosures total, using a combination of destructive and non-destructive sampling techniques. To determine survival, we utilized a line-intercept survey method and recorded the presence/absence of transplanted taxa (Madsen 1999). Transects extended the entire length of the enclosure and to 1-m outwards in one direction, with presence assessed at three points, two within the enclosure (central to and on either side of the planting panel) and one outside of the enclosure. The direction of the transect was randomized to each enclosure. We considered the submergent taxa, *V. americana* and *N. guadalupensis*, to have survived if both roots and leaves were detectable, and *N. odorata* to have survived if both tubers and stems were detectable, even if floating leaves were not visible.

To estimate percent surface coverage of *N. odorata* which may influence light attenuation, we took aerial photos above each enclosure using a Hero7 GoPro camera and extendable tripod. We removed the lid and positioned the camera on the corner post of each enclosure such that the entire planting area was captured. Images were imported into Adobe Photoshop and cropped using the perspective crop tool such that only the area within the enclosure was visible (Figure 2.3a). Percent coverage was then visually estimated by overlaying a 25 x 25-cell grid on to each image in Adobe Illustrator and measuring the number of cells which contained vegetation (Chen et al. 2010). Each cell was placed into one of four weighted categories depending on the percent cover of vegetation within that cell (i.e. 0-25% = 0.25, 25-50% = 0.50, 50-75% = 0.75, 75-100% = 1.0) and then summed.

We used expansion of taxa outside of the planting area as a proxy for plant growth. To quantify expansion, we deployed a 24 x 24-cm PVC quadrat halfway between the planting panel and exterior fence in each enclosure, in a randomized direction, and carefully removed all captured vegetation by hand. Plants were separated by species, put into a mesh bag, and spun in a



circle fifteen times to remove excess water. Above (stems and leaves) and below (roots and shoots) ground structures were then separated and weighed for each species.

### 2.3g *Statistical analyses*

All statistical analyses were conducted in R v. 3.4.3 (R Development Core Team 2018). Water quality parameters measured at the study area and west-basin USGS gauging station were summarized using the packages *wql* v. 0.4.9 and *waterData* v. 1.0.8, respectively (Stachelek 2017; Ryberg and Vecchia 2017). To compare individual monitoring sites and bays, we conducted a single factor analysis of variance (ANOVA) for each water quality parameter. Likewise, to compare the entire sample area and USGS gauging station, we summed measurements across all monitoring sites and conducted a Welch's t-test for each parameter that was measured at both locations (Table 2.1). To compare surface cover of *N. odorata* between treatments, we performed an arcsine transformation on percent cover and conducted an ANOVA. Finally, we used an ANOVA to compare mean biomass of expanded vegetation between treatments. An alpha level ( $\alpha$ ) of 0.05 was assumed for all ANOVA and t-test analyses, and when applicable we ran a Tukey's HSD test to determine specific mean to mean differences.

## 2.4 Results

### 2.4a *Water quality*

The relative percent deviation of chlorophyll-*a* was <30% for all but one pair of duplicates, so samples were pooled for comparative analyses. Water quality parameters (physiochemical, nutrient, chlor-*a*) varied throughout time but our sampling design was not robust enough to test for seasonal variation or trends, so parameters are summarized across their relative sampling period (Table 2.1). We found no significant differences in water quality parameters between monitoring sites nor bays, suggesting that water quality should influence transplanted macrophytes proportionally across restoration sites. However, several parameters including temperature ( $t = 3.51$ ;  $P = 0.05e-2$ ), salinity ( $t = 18.14$ ;  $P = 2.2e-16$ ), pH ( $t = 7.10$ ;  $P = 1.48e-11$ ), and specific conductance ( $t = 17.93$ ;  $P = 2.2e-16$ ) were statistically higher in the study area compared to the west-basin USGS gauging station (Table 2.1).

### 2.4b *SAV Survival and Growth*

All three species of transplanted taxa, along with planting panels and burlap squares, were detected within the initial planting area in May 2020. Overwinter survival varied by site,

treatment, and taxa (Table 2.2). *N. guadalupensis* exhibited the highest overall survival rate and was detected in 92% of the enclosures, followed by *V. americana* detected in 83%, and *N. odorata* detected in 75%. Despite slightly lower survival than *N. guadalupensis*, *V. americana* exhibited the greatest outward growth of all three species and was found growing outside of the planting area in every cage it was detected in (i.e. 83%), followed by *N. guadalupensis* (33%) and finally *N. odorata* (6%). We observed only one instance of vegetation growing outside of an enclosure, in the form of a single *V. americana* stolon with 3-4 rosettes that extended less than 1-m outside of the fence.

Anecdotally, *V. americana* exhibited the largest amount of upward growth in addition to outward expansion across treatments and sites. Although biomass was not quantified at this time within the planting area, *V. americana* formed dense beds of thick-leaved (5-cm+) plants that extended to the surface of 75% of enclosures it was observed in. In the remaining 25% of enclosures, *V. americana* appeared susceptible to herbivory, as large leaves were clearly “mowed” down, but stolons, rosettes, small leaves, and roots remained intact and expansive throughout the enclosures. Additionally, in 25% of the enclosures *V. americana* displayed female surface-level blooms, which were captured and counted using aerial images (Table 2.3; Figure 2.4). In 75% of enclosures, *N. guadalupensis* was detected in the form of short strands (<20-cm) of vegetation that were difficult to locate and identify. However, in the remaining 25% of cages, *N. guadalupensis* formed thick, dense rooted mats that extended to the water surface like *V. americana*. Of all three taxa, *N. odorata* were the most difficult to assess growth-wise as floating leaves were only observed in only 44% of enclosures and covered less than <3% of the enclosure surface area (Table 2.3). In addition, neither percent cover nor mean number of floating leaves were significantly different between treatments containing *N. odorata*.

*V. americana* constituted over 95% of vegetation captured outside of the planting panel, with *N. guadalupensis* and *N. odorata* captured just once each. Additionally, because *V. americana* plants grew much larger than anticipated, only 1-2 individual plants were captured in the 24 x 24-cm quadrat at each site. Even though *V. americana* was present outside of the planting area in most cases, vegetation was captured within the quadrat at 10/28 sampled enclosures so biomass was pooled across all sites for analysis. To account for the possibility of species-specific density dependent effects on growth that may have occurred from planting different initial numbers of *V. americana* per treatment, the raw biomass of each species was

corrected using the formula:  $\text{Biomass}_{\text{corrected}}(\text{species}, \text{treatment}) = \text{raw biomass}_{(\text{species})} / X_{(\text{species})}$ , where  $X$  is the number of plants of that species initially planted per treatment. Biomass was then visualized by above ground (leaves/stems), below ground (roots), below ground (stolons), and total biomass (Figure 2.5). Prior to correction, the above ground biomass of *V. americana* and *N. guadalupensis* averaged 94.8-g and 6.84-g, respectively, across all sites. No above-ground biomass was collected for *N. odorata*. Likewise, below ground biomass as roots of *V. americana*, *N. guadalupensis*, and *N. odorata* averaged 15.2-g, 0.54-g, and 3.32-g, respectively. Stolons were only quantified for *V. americana*, and averaged 16.0-g. The ratio of *V. americana* leaves to roots to stolons did not differ significantly between treatments. After correction, the total captured biomass of *V. americana* was significantly higher in the all species treatment than both the *V. americana* only ( $P = 0.003$ ) and *V. americana* + *N. odorata* treatments ( $P = 0.004$ ). Biomass did not differ significantly between the *V. americana* only and *V. americana* + *N. odorata* treatments ( $P = 0.999$ ).

## 2.5 Discussion

Global declines in SAV abundance have prompted the need to develop multifaceted restoration strategies that reduce system-specific stressors to SAV communities and improve ecological resilience (Waycott et al. 2009; Orth et al. 2017). Our study constitutes the first large-scale effort to evaluate the survival and growth capabilities of transplanted aquatic macrophytes in Lake Mattamuskeet, an expansive but hypereutrophic, coastal lake located on the Albemarle-Pamlico Peninsula in eastern North Carolina. We demonstrated that all three taxa (*V. americana*, *N. guadalupensis*, and *N. odorata*) successfully established when protected from herbivory and uprooting from Common Carp, despite high nutrient concentrations and turbidity. Additionally, we found that the *V. americana* (submergent) exhibited the greatest potential to expand outside of its initial transplant area, expanding up to a meter outward in every cage it was detected. The presence of *V. americana* blooms suggest that transplants are mature and capable of sexual reproduction, but whether this is occurring is unclear, as male, and female plants were neither distinguished nor quantified prior to planting. Meanwhile, the other two taxa expanded outside of the planting area only once each and exhibited no obvious flowering. When corrected, biomass of expanded *V. americana* was highest when planted in a multispecies treatment with both *N. guadalupensis* (submergent) and *N. odorata* (floating-leaf), but not significantly different

between the *V. americana*-only treatment and the *V. americana* + *N. odorata* treatment. The lack of *N. odorata*, which exhibited the lowest survival of all three species, at several sites may have influenced this result. However, our results support the findings by Knopik and Newman (2018), who found no evidence that transplanted SAV (including *V. americana*) grew better when planted with floating-leaf taxa following Common Carp removal. A more comprehensive sampling approach is needed to better understand the relative role of *N. odorata* and *N. guadalupensis* in regulating *V. americana* growth, as well the relationship between functional diversity and plant growth in Lake Mattamuskeet.

Several physiochemical and nutrient parameters measured in the study area, including pH, dissolved oxygen, turbidity, and total phosphorous, exceeded the water quality standards and maximum values reported by Moorman et al. (2017) for Lake Mattamuskeet from 2012 - 2015. Of these, total phosphorous differed the most dramatically, exceeding the water quality standards and reported values by 3400% and 340%, respectively. Although testing discrepancies may have influenced results, these values are not wholly unexpected based on the long-term trends for Lake Mattamuskeet presented by Moorman et al. (2017), which showed a 100% and 400% increase in total phosphorous total nitrogen, respectively, from 1983 – 2015. Due to a lack of testing resources, we were unfortunately unable to measure the primary component of total nitrogen, Kjeldahl nitrogen, which prevented us from further assessing trends in total nitrogen. However, several parameters associated with eutrophication in aquatic systems including chlorophyll-*a*, turbidity, and Secchi depth, exceeded the median habitat requirements for SAV growth and survival described by Batiuk et al. (2000). These findings are again consistent with the median summer values and significant long-term trends reported for Lake Mattamuskeet by Moorman et al. (2017), suggesting that water quality has remained largely consistent in Lake Mattamuskeet since 2015. In our case, a photometer-based nutrient analysis method offered a straightforward and cost-effective solution that allowed us to measure a suite of parameters within the study area monthly. However, as efforts to reduce nutrient loadings, Common Carp density, or lake levels are carried out on a broader scale, continued and high precision nutrient testing will be important for assessing ecosystem-wide trends in water quality.

In combination with nutrient analysis, monthly physiochemical monitoring provided several useful insights for SAV restoration in Lake Mattamuskeet. First, we determined that while the USGS gauging stations are important resources for high quality, long-term water

quality monitoring in Lake Mattamuskeet, they are not wholly indicative of water quality in other areas of the lake. This is not surprising, as both physiochemical and nutrient water quality parameters are influenced by a suite of factors, including depth, wind exposure, fetch, and sediment type, that can vary both spatially and temporally within a single system (Ling et al. 2017). In our case, the 2-ft discrepancy in depth between the study area and gauging station may have contributed to significant differences in water temperature and pH. Additionally, the close proximity of our study area to the Rose Bay canal, which links Lake Mattamuskeet to the estuarine Pamlico Sound and is recorded to have higher salinities than the main lake, likely explains the observed discrepancy in salinity (Figure 2.1a; Potoka et al. 2014). Although significant, spatial variations in water quality may not be biologically important for determining the location of SAV restoration sites in Lake Mattamuskeet, as both sets of physiochemical measurements fell within described tolerance ranges of freshwater SAV species that previously dominated the lakebed (e.g. *V. americana*; Doering et al. 2001; Haynes 1979).

Other abiotic factors not quantified in this study, such as fetch and sediment composition, may also play a role in predicting the long-term success of SAV transplantation and survival. For example, in shallow lakes, wind-driven waves penetrate the entire water column and stir up sediment, thereby driving patterns in sediment composition and transport (Vijverberg et al. 2011). Lake Mattamuskeet's unique morphology primarily consists of vast stretches of open lake with limited embayments, excluding peripheral impoundments and canal systems. We chose our study area in part because it constituted one of the most wind-protected areas in the lake, hence ideal for transplanting SAV. However, the limitation of this approach is that it fails to address the potential wind wave effects on SAV establishment and survival in Lake Mattamuskeet's majority habitat (i.e. open, unprotected). Anecdotally, we did notice slight variations in sediment composition (sand to deep muck) and wind exposure between individual restoration sites within the study area, which may have influenced plant survival. However, this was not tested.

Hurricanes and other major storm events have posed numerous challenges to large-scale SAV restoration efforts in coastal ecosystems (Orth and Moore 1983). Specifically, hurricanes increase wave attenuation and turbidity, cause rapid fluctuations in salinity, and can bury SAV tubers and rhizomes (Littles et al. 2005; Hamberg 2017). Therefore, SAV abundance regularly declines following major storm events (Frazer et al. 2006; Poirrier et al. 2017). Within a month of transplanting SAV in our enclosures, category-5 hurricane "Dorian" swept up the North

Carolina coast bringing intense rain and wind (Rey and Mulligan 2020). Astonishingly, all enclosures were intact and transplanted vegetation accounted for following the storm. The galvanized steel enclosure frames likely played a role in protecting transplants; but, both enclosures and transplants may have incurred more damage had they been placed in larger fetch areas. Additional research is needed to better understand these and other factors which may impact the species-specific establishment and survival of transplanted macrophytes.

While advances in remote sensing, drone, and underwater mapping technologies have generally increased the ability to monitor SAV over expansive areas, restoration has historically been limited to smaller water bodies and utilized preexisting stands of naturally-occurring SAV from which plants could be harvested and transplanted (Lou et al. 2016; Doyle et al. 1997; Smart and Dick 1998). This reliance is rapidly becoming problematic, as many naturally-occurring stands of SAV have dwindled or disappeared entirely in large coastal systems because of increased anthropogenic activity and severity of hurricane events (Shafer et al. 2008). For example, the Albemarle-Pamlico peninsula and estuary system (APES) along the North Carolina coast contains among the highest abundance SAV habitat in North America, upwards of 200,000-acres spread across coastal, estuarine, and freshwater waterbodies. Formatively an ideal location for harvesting SAV, recent surveys shown that increases in turbidity have caused widespread declines in freshwater, oligio- and meso-haline taxa (NCDEQ 2016). In addition, the commercial availability of SAV is limited depending on region. Cumulatively, these factors outline a need to develop alternative SAV restoration strategies that do not rely on wild SAV beds and can be applied to large areas (Shafer et al. 2008). Seed harvest and dispersal offers one cost- and labor-effective approach, but effectiveness varies by species and system, with lower success rates in highly turbid or unvegetated systems where seeds are subject to low germination rates (Moore and Jarvis 2008; Kujawski and Thompson 2000). In addition, seeding may take up to 3 years to produce viable plants, whereas our study demonstrates ability of adult transplants to quickly establish, expand, and in the case of *V. americana*, flower (Shafer et al. 2008). Finally, the deployment of artificial aquatic plants (AAB) treated with periphyton biofilms have been shown to locally improve water quality and SAV establishment by up to 50%, and may offer a promising restoration option in systems where water quality is the primary limitation to SAV establishment (Wu et al. 2019).

SAV restoration is a valuable and necessary approach to increasing ecological resilience and integrity in shallow aquatic ecosystems and can directly benefit numerous organisms (Vanausdall and Dinsmore 2018; Ruhl and Rybicki 2010). However, to reinstate healthy, diverse SAV communities, multifaceted efforts to reduce stressors to SAV communities (e.g. nutrient loadings, Common Carp, invasive plant colonization) are needed. Even still, reduction alone may not be sufficient to reinstate prior states (e.g. the clear-water state in shallow lakes) if ecological resilience has been lost, highlighting a major challenge of ecosystem-wide restoration in the Anthropocene (Hanson et al. 2017).

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## 2.7 Tables

**Table 2.1:** Water quality summary statistics for physical, nutrient, and chlorophyll-*a* parameters measured across the study area and by the west basin gauging station (USGS 0208458892) in Lake Mattamuskeet. For study area samples, physical parameters (*temperature, dissolved oxygen, specific conductance, salinity, pH, and Secchi depth*) and chlorophyll-*a* were sampled monthly from September to August 2019 and nutrients monthly from April to August 2019. Gauging station data was taken continuously and summarized from September 2018 to August 2019. Bolded values represent parameters which differed significantly between the study area and USGS gauging station assuming an alpha level ( $\alpha$ ) of 0.05.

Parameter	n	min	10%	median	mean	SD	90%	max	Method
<b>Study area</b>									
Temperature (°C)	156	7.3	11	26	<b>23</b>	7.7	30	32	YSI multimeter
Dissolved oxygen (mg/L)	150	4.2	8.0	10	10	1.6	12	18	YSI multimeter
Specific conductance at 25 C (µS/cm)	144	528	970	1157	<b>1388</b>	447	2168	2448	YSI multimeter
Salinity (ppt)	144	0.3	0.5	0.6	<b>0.7</b>	0.2	1.1	1.3	YSI multimeter
pH	143	6.5	7.5	9.3	<b>9.0</b>	1.1	10.3	11	YSI multimeter
Secchi depth (cm)	156	10	12	17	17	4.4	24	28	Secchi tube
Chlorophyll- <i>a</i> (µg/L)	312	17	33	57	59	22	89	119	EPA 445.0; fluorometer
Nitrate (µg/L)	60	0.0	0.0	15	23	22	60	70	Hach DR 890 photometer
Nitrite (µg/L)	60	0.0	0.0	4.0	3.9	3.4	7.1	16	Hach DR 890 photometer
Ammonia (µg/L)	60	0.0	10	40	48	75	60	60	Hach DR 890 photometer
Phosphorous, total (µg/L)	60	160	239	330	346	163	490	680	Hach DR 890 photometer
Phosphorous, reactive (µg/L)	60	10	36	160	165	103	379	650	Hach DR 890 photometer
Hardness, Ca + Mg (mg/L)	60	0.7	0.9	2.1	2.0	0.8	3.1	3.6	Hach DR 890 photometer
Turbidity (FAU)	60	29	36	52	53	14	74	83	Hach DR 890 photometer
<b>USGS 0208458892 (West basin)*</b>									
Temperature (°C)	396	3.7	7.0	22	<b>20</b>	8.3	30	31	USGS monitoring station
Dissolved oxygen (mg/L)	394	7.0	7.8	9.8	9.8	1.2	12	12	USGS monitoring station
Specific conductance at 25 C (µS/cm)	396	547	572	651	<b>706</b>	149	1041	1490	USGS monitoring station
Salinity (ppt)	396	0.2	0.3	0.3	<b>0.3</b>	0.1	0.4	0.7	USGS monitoring station
pH	394	7.1	7.2	8	<b>8.3</b>	1.0	9.7	9.9	USGS monitoring station
Turbidity (FAU)	383	16	19	39	<b>48</b>	29	115	197	USGS monitoring station

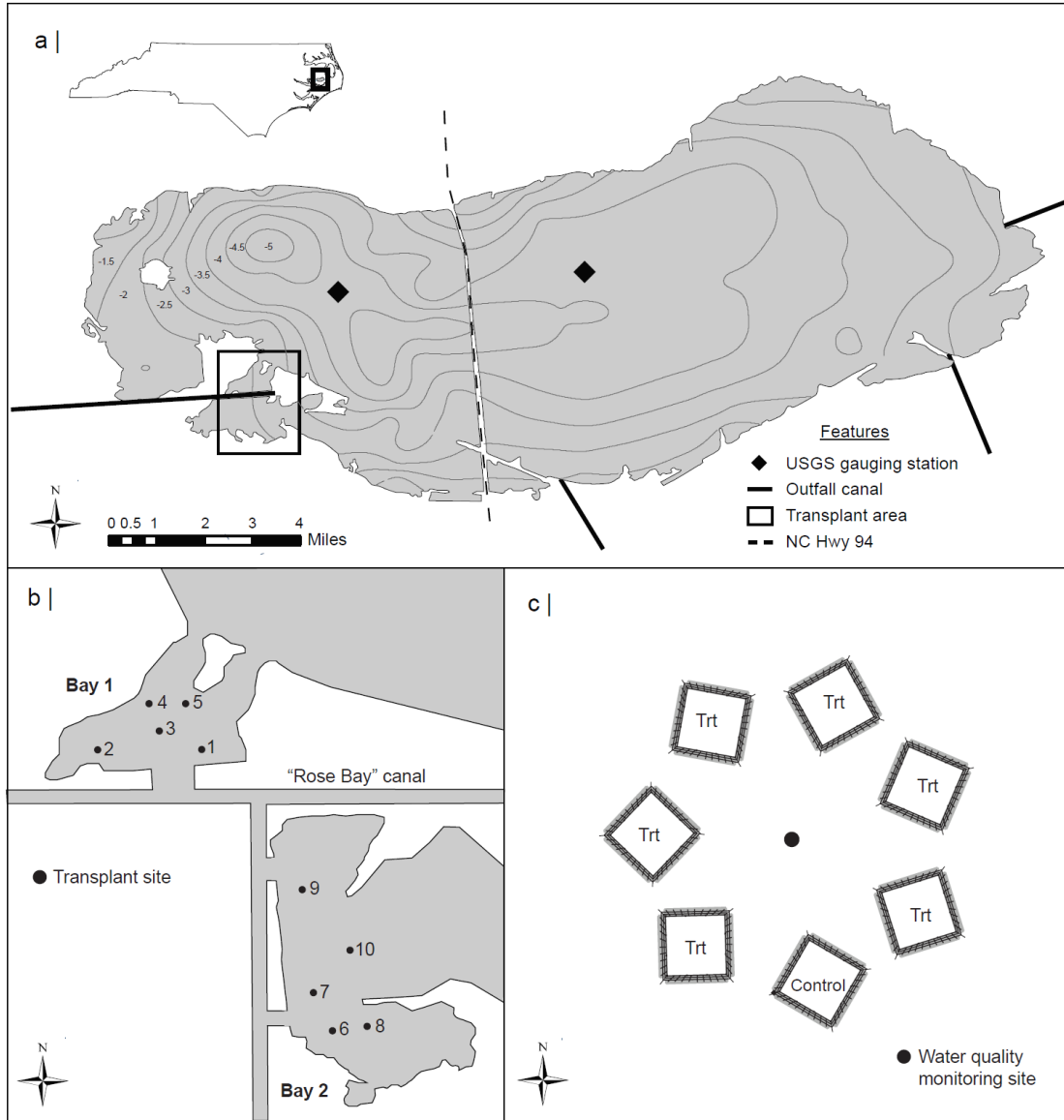
**Table 2.2:** Presence/absence of three species of aquatic macrophytes (*Vallisneria americana*, *Najas guadalupensis*, and *Nymphaea odorata*) transplanted within enclosures in Lake Mattamuskeet.

Treatment	<i>V. americana</i>				<i>N. guadalupensis</i>				<i>N. odorata</i>			
	site 2	site 3	site 7	site 8	site 2	site 3	site 7	site 8	site 2	site 3	site 7	site 8
<b>Inside panel (survival)</b>												
<i>V. americana</i>	1	1	1	1	-	-	-	-	-	-	-	-
<i>N. guadalupensis</i>	-	-	-	-	1	1	1	1	-	-	-	-
<i>N. odorata</i>	-	-	-	-	-	-	-	-	1	1	0	1
<i>V. americana</i> + <i>N. odorata</i>	1	1	0	1	-	-	-	-	1	1	1	0
<i>N. guadalupensis</i> + <i>N. odorata</i>	-	-	-	-	1	1	1	1	1	1	0	1
<i>V. americana</i> + <i>N. guadalupensis</i> + <i>N. odorata</i>	0	1	1	1	0	1	1	1	1	1	0	1
control	-	-	-	-	-	-	-	-	-	-	-	-
<b>Outside panel (growth)</b>												
<i>V. americana</i>	1	1	1	1	-	-	-	-	-	-	-	-
<i>N. guadalupensis</i>	-	-	-	-	0	0	0	1	-	-	-	-
<i>N. odorata</i>	-	-	-	-	-	-	-	-	0	0	0	0
<i>V. americana</i> + <i>N. odorata</i>	1	1	0	1	-	-	-	-	0	0	1	0
<i>N. guadalupensis</i> + <i>N. odorata</i>	-	-	-	-	0	0	1	1	0	0	0	0
<i>V. americana</i> + <i>N. guadalupensis</i> + <i>N. odorata</i>	0	1	1	1	0	0	0	1	0	0	0	0
control	-	-	-	-	-	-	-	-	-	-	-	-
<b>Outside cage (growth)</b>												
<i>V. americana</i>	0	0	0	0	-	-	-	-	-	-	-	-
<i>N. guadalupensis</i>	-	-	-	-	0	0	0	0	-	-	-	-
<i>N. odorata</i>	-	-	-	-	-	-	-	-	0	0	0	0
<i>V. americana</i> + <i>N. odorata</i>	0	0	0	0	-	-	-	-	0	0	0	0
<i>N. guadalupensis</i> + <i>N. odorata</i>	-	-	-	-	0	0	0	0	0	0	0	0
<i>V. americana</i> + <i>N. guadalupensis</i> + <i>N. odorata</i>	0	0	0	1	0	0	0	0	0	0	0	0
control	-	-	-	-	-	-	-	-	-	-	-	-

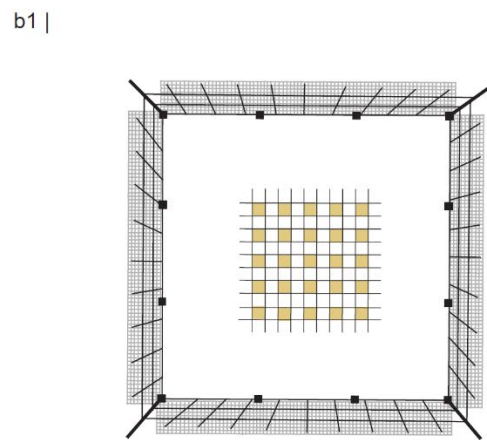
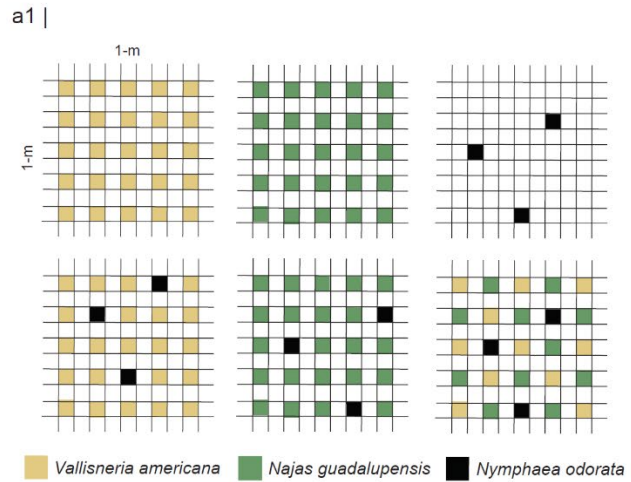
**Table 2.3:** Estimated percent surface cover of *Nymphaea odorata*, number of *N. odorata* leaves, and number of *Vallisneria americana* blooms within 9.3-m<sup>2</sup> enclosures in Lake Mattamuskeet, represented by treatment. Values are summarized by treatment across the four sampled sites.

Treatment	% cover	<i>N.odorata</i> (leaves)			<i>V. americana</i> (blooms)		
		mean	SE	max	mean	SE	max
<i>V. americana</i>	-	-	-	-	2.5	2.5	10
<i>N. guadalupensis</i>	-	-	-	-	-	-	-
<i>N. odorata</i>	0.015	6.5	3.9	16	-	-	-
<i>V. americana</i> + <i>N. odorata</i>	0.024	6.5	5.5	23	5.5	3.3	13
<i>N. guadalupensis</i> + <i>N. odorata</i>	0.016	7.8	5.7	24	-	-	-
<i>V. americana</i> + <i>N. guadalupensis</i> + <i>N. odorata</i>	0.001	2.8	2.8	11	2.8	2.8	11
control	-	-	-	-	-	-	-

## 2.8 Figures



**Figure 2.1:** Map (a) of the study area, Lake Mattamuskeet, and its location in North Carolina. Diamonds indicate the locations of USGS gauging stations and depth contours are represented in feet. The boxed region (b) highlights the region selected for restoration and shows the distribution of transplant sites across bays. Each transplant location (c) contains seven enclosures, six containing unique vegetation treatments and one control cage containing no vegetation, positioned around a centrally-located water quality monitoring site.



**Figure 2.2:** Schematic (a1) and photo (a2) showing the general layout of the six macrophyte treatments (*Vallisneria americana* only, *Najas guadalupensis* only, *Nymphaea odorata* only, *V. americana* + *N. odorata*, *N. guadalupensis* + *N. odorata*, and all species) using the planting panel and burlap squares. Plant location was randomized on each panel for the mixed-species treatments. Schematic (b1) and photo (b2) showing the construction and layout of each vegetation enclosure.

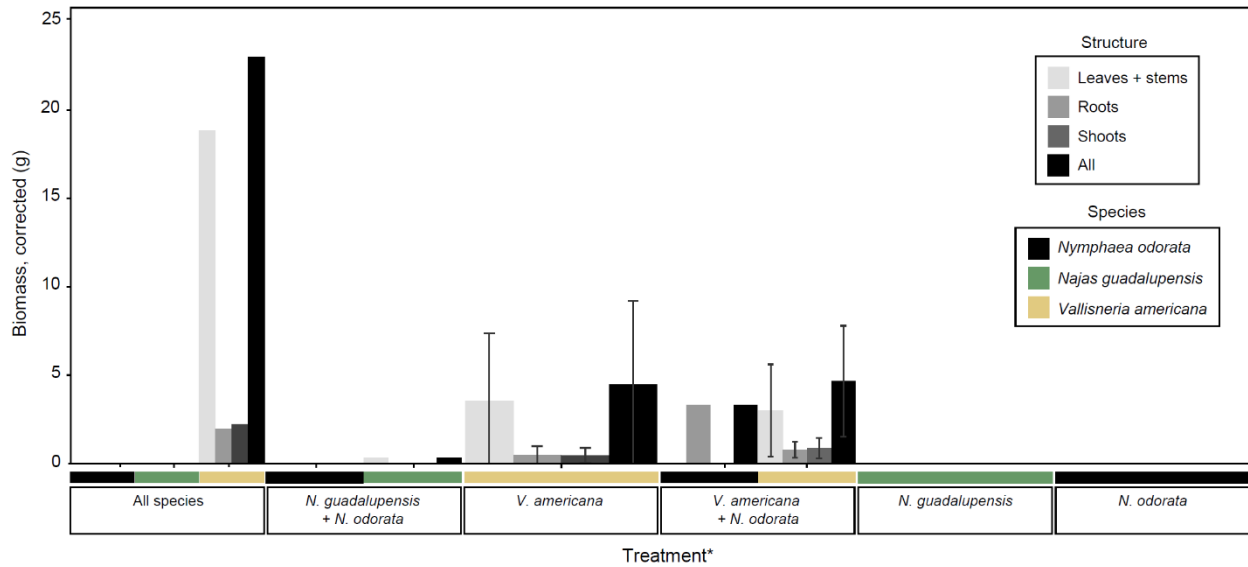
a |



b |



**Figure 2.3:** Aerial photos showing how plant growth (a) and structures (b) were estimated and identified, respectively.



**Figure 2.4:** Bar graphs showing the biomass\* of transplanted aquatic macrophytes (*Vallisneria americana*, *Najas guadalupensis*, and *N. odorata*) harvested from within a 24 x 24-cm quadrat deployed outside of the planting panel and within the enclosure. Data is from 4 of the 10 restoration sites. Above and below ground biomass was quantified for each treatment by separating plant leaves and stems, roots, and shoots and measuring the wet weight of each structure. \*To account for the possibility of density dependent effects on growth, the raw biomass of each species was divided by the number of plants of that species that were initially planted in each treatment [e.g. Biomass, corrected (*V. americana*, all species treatment) = raw biomass(*V. americana*) / 11(*V. americana*)].