RELATING DIETS AND FOOD AVAILABILITY TO LONG-TERM POPULATION TRENDS OF LESSER SCAUP WINTERING ON LAKE PONTCHARTRAIN, LOUISIANA

A Thesis

Submitted to the Graduate Faculty of the Louisiana State University and Agricultural and Mechanical College in partial fulfillment of the requirements for the degree of Master of Science

in

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by Clay Michael Stroud B.S., University of Georgia, 2013 May 2018 I would like to dedicate this thesis to my "Papa," James Larry Overstreet. From an early age, Papa taught me the value of having a strong work ethic. He would come home from working a long shift at the local paper mill only to start working around the farm, often until well after the sun went down. It was at Papa's farm where he taught me life lesson after life lesson. Papa taught me to value education and to choose a career doing something you loved. Taking this wisdom to heart is what drove me to pursue a graduate degree in wildlife. Most of my love for the wildlife and the outdoors can be traced back to Papa's farm. My first memories of hunting, driving a tractor, and simply watching the wind blow through the pine trees all occurred with Papa on his farm. The life lessons Papa imparted provided me a solid foundation to build my life and career on. I will forever be indebted to my Papa for helping me become the person I am today.

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TABLE OF CONTENTS

ACKNOWLEDGEMENTS	iii
LIST OF TABLES	vi
LIST OF FIGURES	vii
ABSTRACT	viii
CHAPTER 1. INTRODUCTION	1
1.1 Literature Cited	
CHAPTER 2. SCAUP DIETS RELATIVE TO PREY AVAILABILITY	16
2.1 Introduction	
2.2 Methods	21
2.3 Results	27
2.4 Discussion	34
2.5 Literature Cited	38
CHAPTER 3. SCAUP POPULATION RESPONSES TO PREY AVAILABILITY AND	
ENVIRONMENTAL DISTURBANCES	44
3.1 Introduction.	44
3.2 Methods.	50
3.3 Results	55
3.4 Discussion.	59
3.5 Literature Cited	64
CHAPTER 4. SUMMARIES AND CONCLUSIONS	70
4.1 Literature Cited	74
APPENDIX. MODEL SELECTION TABLES	76
VITA	78

LIST OF TABLES

Table 2.1. Percent occurrence of food items, aggregate percent dry weight, and percent occurrence of scaup from 28 scaup collected during the winter of 2016–2017	30
Table 2.2. Scaup food items consumed and their availability on Lake Pontchartrain during the winter of 2016–2017	31
Table 2.3. Selection indices and standardized selection indices for scaup food items on Lake Pontchartrain. Estimates from insects and amphipods were not included	32
Table 3.1. Rangia estimates \pm SE in the same year as a hurricane and in the year following a hurricane from 1996–2017	57
Table 3.2. Model selection table for environmental factors impacting scaup abundances on Lake Pontchartrain from 1996–2017	58
Table 3.3. Scaup estimates \pm SE in response to hurricanes and tropical storms/hurricanes from 1996–2017 and from 1977–2017	59
Table 3.4. Model selection table for environmental factors impacting scaup abundances on Lake Pontchartrain from 1977–2017	59

LIST OF FIGURES

Figure 2.1. Map of freshwater sources and tidal passes on Lake Pontchartrain, Louisiana, USA (IHNC = Inner Harbor Navigational Canal, MRGO = Mississippi River Gulf Outlet, and GIWW = Gulf Intracoastal Waterway). Map amended from Poirrier and Caputo (2015)
Figure 2.2. Map of lesser scaup (<i>Aythya affinis</i>) collection sites and benthic dredge sampling locations on Lake Pontchartrain, Louisiana, USA
Figure 2.3. Photograph of prey species consumed by lesser scaup (<i>Aythya affinis</i>) on Lake Pontchartrain, Louisiana, USA
Figure 2.4. Variance loading of principle components analysis (PCA) conducted on morphometric measurements of lesser scaup (<i>Aythya affinis</i>) collected on Lake Pontchartrain, Louisiana, USA during the winter of 2016–2017
Figure 2.5. Lesser scaup (<i>Aythya affinis</i>) body condition over time on Lake Pontchartrain, Louisiana, USA during the winter of 2016–201734
Figure 3.1. Map of freshwater sources and tidal passes on Lake Pontchartrain, Louisiana, USA (IHNC = Inner Harbor Navigational Canal, MRGO = Mississippi River Gulf Outlet, and GIWW = Gulf Intracoastal Waterway. Map amended from Poirrier and Caputo (2015)
Figure 3.2. Map of benthic invertebrate sampling locations along the East-West (EW) and North-South (NS) transects on Lake Pontchartrain, Louisiana, USA
Figure 3.3. Annual lesser scaup (<i>Aythya affinis</i>) estimates of the continental breeding population (solid line), and wintering Lake Pontchartrain population (dashed line) from 1977–2017. Scaup breeding estimates shown here are divided by 10 from the actual continental population estimates
Figure 4.1. Lesser scaup (<i>Aythya affinis</i>) and medium-sized (≥6 mm to <16 mm) rangia (<i>Rangia cuneata</i>) abundances on Lake Pontchartrain, Louisiana, USA from 1996–2017 (* denotes years that a hurricane made landfall within 150 km from the center of Lake Pontchartrain)

ABSTRACT

Lake Pontchartrain provides wintering habitat for a continentally-significant proportion of lesser scaup (Aythya affinis). Mid-winter aerial surveys indicate dramatic variation in annual scaup abundance (0–1,194,907), though the mechanisms driving fluctuations have not been previously investigated. In response to natural and anthropogenic disturbances, species composition, abundance, and size structure of benthic invertebrate populations in Lake Pontchartrain exhibit drastic variability among years. Given that wintering scaup feed primarily on mollusks, environmental disturbances have the potential to influence scaup dynamics on the estuary by altering the benthic community. To diagnose trophic linkages and variation in scaup abundance, we collected ducks (n=60) and benthic samples (n=6) from the field to evaluate diet preferences, and then used this information to guide analyses using pre-existing long-term datasets on scaup and benthic populations. The most common prey species was the common rangia (Rangia cuneata), accounting for 43% of the total number of food items consumed and 60% of the aggregate dry weight ingested. Rangia was also highly preferred by scaup relative to availability. Medium-size classes (≥6 mm to <11 mm and ≥11 mm to <16 mm) of rangia appear to be particularly important, as they represented 71% of the total number and 91% of the aggregate dry weight of rangia consumed by scaup. Moreover, my long-term analyses revealed that scaup populations on Lake Pontchartrain were significantly influenced by the abundances of these medium-size classes. In agreement with prior studies, I found that rangia abundances were impacted by hurricanes; clam populations were greatly reduced in the same year as a hurricane, but significantly increased the following year. Scaup abundances also declined in the same year a hurricane occurred and increased the subsequent year. Thus, hurricanes appear to drive a bottom-up trophic cascade that ultimately affects scaup populations over multiple years on Lake

Pontchartrain. My results provide valuable information on trophic linkages in an estuarine system that is particularly prone to increases in hurricane intensity predicted with climate change.

CHAPTER 1. INTRODUCTION

Since 1955, the Waterfowl Breeding Population and Habitat Survey (BPOP) has been conducted annually through a cooperative effort by the United States Fish and Wildlife Service and the Canadian Wildlife Service. The primary purpose of the BPOP is to provide population trend data for North American waterfowl species, a subset of which are used to set annual hunting regulations and identify at-risk species. Because lesser scaup (Aythya affinis) and greater scaup (Aythya marila) cannot be distinguished during aerial surveys, the BPOP combines population estimates into a single "scaup" estimate. Scaup populations have fluctuated since the BPOP began (Smith 1995): population trends are characterized by a decline in the 1960s, an increase in the 1970s and early 1980s, and a decline beginning in the mid-1980s (Afton and Anderson 2001). Most other North American duck species exhibited similar declines beginning in the mid-1980s (Nichols et al. 1995); however, when most waterfowl species rebounded in the early 1990s, scaup numbers continued a downward trend. Scaup populations reached an all-time low of 3.25 ± 0.17 million in 2006 (USFWS 2017). Despite a recent increase in scaup numbers, the 2017 estimate of 4.37 ± 0.23 million is still 13% below the long-term average of 5.02 ± 0.04 million (USFWS 2017). Scaup population declines are concerning to biologists, sportsmen, and conservationists.

Uncertain of the cause of their prolonged declines, the U.S. Fish and Wildlife Service listed both lesser scaup and greater scaup as "focal species of concern" (USFWS 2011). The combined range of lesser and greater scaup is more widespread than any other diving duck species in North America. Lesser scaup breed primarily in the boreal forest and prairie pothole region, whereas greater scaup mainly breed in the tundra, although some breed in the boreal forest. Both species winter along the Atlantic and Pacific Oceans, the Gulf of Mexico, and the

Great Lakes, though lesser scaup are more likely to winter on inland lakes. The largest declines in scaup populations have occurred in the boreal forest, which is the core breeding area for lesser scaup; numbers in the prairie pothole region have also declined (Afton and Anderson 2001). However, scaup numbers in the tundra, the main breeding ground for greater scaup, have been stable or slightly increasing since the 1970s. Because lesser scaup are experiencing the largest population declines and account for approximately 89% of the scaup population, lesser scaup (hereafter, scaup) are the primary species of concern (Afton and Anderson 2001).

Scaup recruitment and female survival rates have declined since 1978, contributing to the continental scaup decline (Afton and Anderson 2001). Nutrient reserves acquired at wintering or spring migration areas are important predictors of scaup reproductive success and survival (Afton 1984, Afton and Ankney 1991, Pace III and Afton 1999, Anteau and Afton 2004). Although scaup use exogenous nutrients, endogenous lipid reserves are critical for clutch formation and incubation (Afton and Ankney 1991, Afton and Paulus 1992, Esler et al. 2001). For example, while endogenous protein reserves were stable during egg formation (Afton and Ankney 1991, Esler et al. 2001), lipid reserves declined 0.7 g for every gram of lipid deposited in in eggs (Esler et al. 2001). Therefore, endogenous lipids have the potential to influence nesting propensity, egg quality, clutch size, hatchability, and eventual recruitment (Afton and Ankney 1991, Esler et al. 2001, Anteau and Afton 2004). These ideas were formalized in the Spring Condition Hypothesis (SCH), which postulates that reproductive success has declined because female scaup are arriving on breeding grounds in poorer body condition than in the past. Afton and Anderson (2001) hypothesized poorer body condition was a result of reduced availability and/or quality of food resources on wintering, spring migration, and/or breeding areas, resulting

in decreased recruitment because females are unable to build sufficient lipid reserves required for breeding.

Consistent with the SCH, food resources have declined at many spring staging areas, particularly in the upper Midwest (Anteau and Afton 2006, 2008*a*). Amphipods are the most important food source for spring migrating scaup in the upper Midwest (Rogers and Korschgen 1966, Afton and Hier 1991, Afton et al. 1991, Strand 2005, Anteau 2006). However, studies indicate that scaup consumption of amphipods has exhibited a decadal decline. Amphipod consumption by scaup was lower in the 2000s compared to the 1980s (Anteau and Afton 2006, 2008*b*). Similarly, amphipod consumption declined in the 1980s relative to historic levels from the 1960s (Rogers and Korschgen 1966, Bartonek and Hickey 1969, Swanson and Duebbert 1989, Afton and Hier 1991, Afton et al. 1991). Studies have speculated that less consumption of amphipods is a direct result of declines in amphipod densities throughout the upper Midwest (Anteau and Afton 2004, 2006, 2008*a*, 2008*a*).

Scaup diets have also shifted towards mollusks in the upper Midwest (Anteau and Afton 2006, 2008*b*). However, mollusks have lower gross energy, protein, and lipid content than amphipods (Jorde and Owen 1988, Ballard et al. 2004). Mollusks also provide lower true metabolizable energy to waterfowl than amphipods (Jorde and Owen 1988, Ballard et al. 2004). Because scaup are more efficient at retaining energy from amphipods than other ducks (Jorde and Owen 1988, Ballard et al. 2004), scaup may be specially adapted to forage on amphipods. Thus, scaup diet shifts from amphipods to mollusks is likely to have negative consequences. Anteau and Afton (2006, 2008*b*) concluded that forage quality in Iowa and Minnesota had declined because of decadal scaup diet shifts from amphipods to mollusks. Moreover, scaup lipid reserves in Minnesota and Manitoba were nearly 30% lower in the early 2000s as compared

to the 1980s, providing further support to the SCH (Anteau and Afton 2004). Because of declines in foraging quality at spring migration areas in the upper Midwest, major wintering areas may be increasingly important for accumulation of nutrient reserves (Austin et al. 2006). However, studies investigating changes to prey availability and diet composition on wintering grounds are lacking.

The Mississippi Flyway, which winters approximately 40% of the continental scaup population, is experiencing the largest population declines (Afton and Anderson 2001). Louisiana winters 91% of the scaup in the Mississippi Flyway (Afton and Anderson 2001), and one area in Louisiana that hosts large numbers of scaup is Lake Pontchartrain (Kinney 2004). However, annual scaup estimates on Lake Pontchartrain fluctuate drastically. The highest estimate was over a million birds (1,194,907) in December 2006 while zero scaup have been estimated twice, in January 2006 and December 2012 (unpublished data).

One potential source for this variation in scaup abundance is coincident variation in food availability on Lake Pontchartrain. The importance of mollusks as the primary food source for wintering scaup is well-documented (Harmon 1962, Perry and Uhler 1982, Hoppe et al. 1986, Custer and Custer 1996). Furthermore, many of the dominant mollusk species found in Lake Pontchartrain are principal diet components for scaup at many wintering areas (Harmon 1962, Bowman 1973, Perry and Uhler 1982, Perry et al. 2007). In the only diet study on Lake Pontchartrain, Bowman (1973) found that common rangia clams (*Rangia cuneata*) (hereafter, rangia) and dark false mussels (*Mytilopsis leucophaeta*) were the main prey species consumed by scaup, accounting for 81% and 14% of scaup diets, respectively. Scaup exhibit species- and size- specific prey selection of mollusks (Custer and Custer 1996, Richman and Lovvorn 2004). Numerous studies indicate that scaup and other diving ducks consume mollusk sizes based on

handling times, meat-to-shell ratios which affect nutrients relative to passage rate, and risk avoidance of very large prey (Draulans 1982, Bustnes and Erikstad 1990, de Leeuw and van Eerden 1992, Bustnes 1998, Hamilton et al. 1999, Richman and Lovvorn 2004).

Benthic communities in oligohaline estuaries like Lake Pontchartrain have low species richness (Remane and Schleiper 1971). These benthic communities are influenced more by abiotic variables than biotic interactions (Gunter 1960, Boesch and Rosenberg 1981). Benthic communities on Lake Pontchartrain exhibit extreme fluctuations in overall abundance, biomass, and species and size diversity among years due environmental conditions and disturbances (Sikora and Sikora 1982, Poirrier et al. 2009, Poirrier and Caputo 2015). Shell dredging, salt water intrusion, hurricanes, spillway openings, and La Niña-driven droughts have all been documented to impact water quality and benthic invertebrate populations in Lake Pontchartrain (Abadie and Poirrier 2000, 2001*a*, 2001*b*, Brammer et al. 2007, Poirrier et al. 2008, Poirrier et al. 2009, Poirrier and Caputo 2015).

For example, Lake Pontchartrain has an extensive history of shell dredging dating back to the 1930s. Sikora and Kjerfve (1985) asserted that 4 million m³ of rangia fossil shells were dredged annually until operations ended in 1990. Shell dredging disturbed bottom sediments, increased turbidity, and decreased densities of large rangia clams ≥ 21 mm (Chew 1987, Abadie and Poirrier 2000, 2001a). Because high salinity bottom water flows along depth contours, channels created by shell dredging likely increase distribution of water containing low levels of dissolved oxygen, thereby exacerbating the impacts of other disturbances (Poirrier et al. 2009). Indeed, Poirrier et al. (2008) suggested that effects from Hurricane Katrina may have been amplified in areas disturbed by shell dredging as compared to those areas not exposed to these operations.

After shell dredging ceased, densities of large rangia increased to historic levels throughout much of the estuary (Abadie and Poirrier 2000), and water clarity also increased at most locations (Francis and Poirrier 1999). However, water clarity and densities of large rangia did not increase in an area roughly 250 km² located along the southern shore (Francis and Poirrier 1999, Abadie and Poirrier 2000, 2001a, 2001b). Reduced water clarity and densities of large rangia along the southern shore was attributed to salinity stratification caused by saline water entering through the Inner Harbor Navigation Canal (IHNC) via the Mississippi River Gulf Outlet (MRGO), a shipping canal completed in 1968. Anoxia and hypoxia is typical at the mouth of the IHNC (Poirrier 1978, Junot et al. 1983). Furthermore, hypoxia has been observed regularly at a site 17 km from the mouth of the IHNC, and periodically at a site 24 km from the mouth of the IHNC, underscoring the extensive area influenced by salt water intrusion from the MRGO (Poirrier et al. 2009). Low species diversity and the absence of large rangia is typical in this area, which has become known as the "dead zone" (Poirrier et al. 2009). The MRGO also exacerbated the storm surge produced from Hurricane Katrina (Shaffer et al. 2009), one of the primary reasons for its closure in 2009. After closure of the MRGO, episodic hypoxia no longer occurs from salt water intrusion near the mouth of the IHNC (Poirrier 2013).

Numerous studies have shown that hurricanes impact benthic invertebrates, both directly and indirectly (Poirrier et al. 2008, Engle et al. 2009, Ray 2009, Poirrier and Caputo 2015). Flocks et al. (2009) found that the top 1 m of sediments are fundamentally reworked after major storms. Instead of being transported out of Lake Pontchartrain, sediments settle rapidly along the estuary bottom due to slow flushing rates (Flowers and Isphording 1990). Sediment deposits can cause benthic invertebrates to be displaced and buried, ultimately causing death (Poirrier et al. 2008, Poirrier et al. 2013). Indirect effects include declines in benthic invertebrate diversity,

abundance, and biomass, possibly resulting from a nonmixing stratified layer with increased salinity and low dissolved oxygen along the estuary bottom (Poirrier et al. 2008, Poirrier et al. 2009).

Hurricane Katrina, a Category 3 storm that made landfall near eastern Lake Pontchartrain on August 29, 2005, caused salinity stratification and low dissolved oxygen at multiple locations, as well as an estuary-wide increase in salinity from storm surge (Poirrier et al. 2008). Species diversity of benthic invertebrates declined at most sites (Poirrier et al. 2008). Densities of rangia and two hydrobiid snails that lack common names (*Probythinella protera* and *Texadina sphinctoma*), all of which usually rank among the most abundant benthic invertebrates on Lake Pontchartrain, were greatly reduced (Poirrier et al. 2008, Engle et al. 2009, Poirrier et al. 2009). Moreover, Hurricane Katrina resulted in the complete loss of rangia and other dominant benthic species at depths greater than 3.7 m, which accounts for approximately half the estuary (Poirrier et al. 2008, Poirrier et al. 2009).

Hurricanes Ike and Gustav in 2008 and Isaac in 2012 also decreased densities of rangia on Lake Pontchartrain (Ray 2009, Poirrier and Caputo 2015). Poirrier and Caputo (2015) found that density changes in 6–20 mm clams accounted for most of rangia declines following hurricanes, possibly because smaller clams are likely to have greater sensitivity to the direct physical damage caused by hurricanes relative to larger clams. Poirrier and Caputo (2015) also reported that 6–20 mm rangia significantly increased in years without hurricanes due to recruitment and fast growth rates.

Opening the Bonnet Carré Spillway, an emergency floodway designed to divert water from the Mississippi River to Lake Pontchartrain to prevent flooding in New Orleans, can drastically affect water quality and the benthic community in Lake Pontchartrain (Sikora and

Sikora 1982, Day 1998, Brammer et al. 2007). Since its completion in 1931, the spillway has been opened 11 times, mostly during the spring. The volume of freshwater discharge from the Spillway during a single flood event can exceed the total estuarine volume (Swenson 1980). Spillway openings have been shown to decrease salinity and increase turbidity (Poirrier and Mulino 1977, Sikora and Sikora 1982, Day 1998, Brammer et al. 2007). Massive introductions of nutrients have also been reported, resulting in harmful cyanobacterial blooms (Day 1998). The rate of change and recovery of salinity and turbidity during a spillway opening depends on the volume and duration of the discharge, local precipitation, and tidal exchanges (Brammer et al. 2007).

After the 1979 Spillway opening, Sikora and Sikora (1982) found that the abundance of most species declined, including rangia, dwarf surf clams, and dark false mussels. However, the study concluded that *T. sphinctostoma* did not differ in abundance, and numbers of *P. protera* increased. Brammer et al. (2007) found that macrofaunal species diversity and abundances, as well as rangia abundance and biomass, significantly declined following the 1997 Spillway opening. Brammer et al. (2007) did not pinpoint the exact causes of the negative impacts on benthic communities following the 1997 opening, though the study speculated that reduced salinity, cyanobacteria blooms, and bottom water hypoxia/anoxia were probable factors.

La Niña-driven droughts also affect water quality and benthic communities in Lake Pontchartrain (Poirrier et al. 2009, Poirrier and Caputo 2015). A shift from a historic El Niño to a strong La Niña occurred between 1997 and 2001 (Zheng et al. 2003), resulting in a drought across southern Louisiana from 1999–2001 (Poirrier et al. 2009). Subsequently, salinity increased to post-Hurricane Katrina levels across the estuary (Poirrier et al. 2009). Overall rangia densities declined, though abundances of clams between 6–15 mm remained the same

(Poirrier and Caputo 2015). The drought promoted the hooked mussel (*Ischadium recurvum*) and other high salinity species, leading to increased species diversity characteristic of higher salinity systems (Poirrier et al. 2009, Poirrier and Caputo 2015). Changes to the benthic community composition lasted multiple years, underscoring the effects caused by La Niña-driven droughts (Poirrier et al. 2009, Poirrier and Caputo 2015).

Given that wintering scaup feed primarily on mollusks (often of a particular species or size), it seems likely that the variation in scaup populations observed on Lake Pontchartrain is somehow tied to the variation in benthic communities, though these relations may be complex and perhaps variable among years because of the dynamic nature of benthic assemblages in the estuary. Therefore, I designed a two-component study that integrated field work and retrospective analyses of long-term population and environmental data. The overall objective of the project was to identify potential drivers of annual changes to scaup populations on Lake Pontchartrain. In Chapter 1, the specific objectives were to: 1) determine diet composition (both by species and size class) of scaup collected from Lake Pontchartrain, 2) estimate concurrent prey availability on the estuary, and 3) assess dietary preferences by comparing prey consumption to availability. After determining the preferred prey of scaup wintering on Lake Pontchartrain, my objectives in Chapter 2 were to: 1) build on previous work identifying how environmental conditions and disturbances affect preferred prey populations, 2) determine if changes to food sources, in response to environmental conditions and disturbances, impact annual scaup abundances. By identifying the drivers of scaup population changes on Lake Pontchartrain, I was able to address the effects of food variability on wintering waterfowl distributions, which is poorly known for most species and geographies. Identification of the proximate drivers of scaup abundances on Lake Pontchartrain also should increase our capacity

to predict scaup populations over short-term (i.e. are conditions favorable for scaup this year?) and long-term (i.e. how will climatic shifts in hurricane frequency and intensity impact scaup abundance?) scales.

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CHAPTER 2. SCAUP DIETS RELATIVE TO PREY AVAILABILITY

2.1 Introduction

Since 1955, the Waterfowl Breeding Population and Habitat Survey (BPOP) has been conducted annually through a cooperative effort by the United States Fish and Wildlife Service and the Canadian Wildlife Service. The primary purpose of the BPOP is to provide population trend data for North American waterfowl species, a subset of which are used to set annual hunting regulations and identify at-risk species. Because lesser scaup (Aythya affinis) and greater scaup (Aythya marila) cannot be distinguished during aerial surveys, the BPOP combines population estimates into a single "scaup" estimate. Scaup populations have fluctuated since the BPOP began (Smith 1995): population trends are characterized by a decline in the 1960s, an increase in the 1970s and early 1980s, and a decline beginning in the mid-1980s (Afton and Anderson 2001). Most other North American duck species exhibited similar declines beginning in the mid-1980s (Nichols et al. 1995); however, when most waterfowl species rebounded in the early 1990s, scaup numbers continued a downward trend. Scaup populations reached an all-time low of 3.25 ± 0.17 million in 2006 (USFWS 2017). Despite a recent increase in scaup numbers, the 2017 estimate of 4.37 ± 0.23 million is still 13% below the long-term average of 5.02 ± 0.04 million (USFWS 2017). Scaup population declines are concerning to biologists, sportsmen, and conservationists.

Uncertain of the cause of their prolonged declines, the U.S. Fish and Wildlife Service listed both lesser scaup and greater scaup as "focal species of concern" (USFWS 2011). The combined range of lesser and greater scaup is more widespread than any other diving duck species in North America. Lesser scaup breed primarily in the boreal forest and prairie pothole region, whereas greater scaup mainly breed in the tundra, although some breed in the boreal

forest. Both species winter along the Atlantic and Pacific Oceans, the Gulf of Mexico, and the Great Lakes, though lesser scaup are more likely to winter on inland lakes. The largest declines in scaup populations have occurred in the boreal forest, which is the core breeding area for lesser scaup; numbers in the prairie pothole region have also declined (Afton and Anderson 2001). However, scaup numbers in the tundra, the main breeding ground for greater scaup, have been stable or slightly increasing since the 1970s. Because lesser scaup are experiencing the largest population declines and account for approximately 89% of the scaup population, lesser scaup (hereafter, scaup) are the primary species of concern (Afton and Anderson 2001).

Scaup recruitment and female survival rates have declined since 1978, contributing to the continental scaup decline (Afton and Anderson 2001). Nutrient reserves acquired at wintering or spring migration areas are important predictors of scaup reproductive success and survival (Afton 1984, Afton and Ankney 1991, Pace III and Afton 1999, Anteau and Afton 2004). Although scaup use exogenous nutrients, endogenous lipid reserves are critical for clutch formation and incubation (Afton and Ankney 1991, Afton and Paulus 1992, Esler et al. 2001). For example, while endogenous protein reserves were stable during egg formation (Afton and Ankney 1991, Esler et al. 2001), lipid reserves declined 0.7 g for every gram of lipid deposited in in eggs (Esler et al. 2001). Therefore, endogenous lipids have the potential to influence nesting propensity, egg quality, clutch size, hatchability, and eventual recruitment (Afton and Ankney 1991, Esler et al. 2001, Anteau and Afton 2004). These ideas were formalized in the Spring Condition Hypothesis (SCH), which postulates that reproductive success has declined because female scaup are arriving on breeding grounds in poorer body condition than in the past. Afton and Anderson (2001) hypothesized poorer body condition was a result of reduced availability and/or quality of food resources on wintering, spring migration, and/or breeding areas, resulting

in decreased recruitment because females are unable to build sufficient lipid reserves required for breeding.

Consistent with the SCH, food resources have declined at many spring staging areas, particularly in the upper Midwest (Anteau and Afton 2006, 2008*a*). Amphipods are the most important food source for spring migrating scaup in the upper Midwest (Rogers and Korschgen 1966, Afton and Hier 1991, Afton et al. 1991, Strand 2005, Anteau 2006). However, studies indicate that scaup consumption of amphipods has exhibited a decadal decline. Amphipod consumption by scaup was lower in the 2000s compared to the 1980s (Anteau and Afton 2006, 2008*b*). Similarly, amphipod consumption declined in the 1980s relative to historic levels from the 1960s (Rogers and Korschgen 1966, Bartonek and Hickey 1969, Swanson and Duebbert 1989, Afton and Hier 1991, Afton et al. 1991). Studies have speculated that less consumption of amphipods is a direct result of declines in amphipod densities throughout the upper Midwest (Anteau and Afton 2004, 2006, 2008*a*, 2008*a*).

Scaup diets have also shifted towards mollusks in the upper Midwest (Anteau and Afton 2006, 2008*b*). However, mollusks have lower gross energy, protein, and lipid content than amphipods (Jorde and Owen 1988, Ballard et al. 2004). Mollusks also provide lower true metabolizable energy to waterfowl than amphipods (Jorde and Owen 1988, Ballard et al. 2004). Because scaup are more efficient at retaining energy from amphipods than other ducks (Jorde and Owen 1988, Ballard et al. 2004), scaup may be specially adapted to forage on amphipods. Thus, scaup diet shifts from amphipods to mollusks is likely to have negative consequences. Anteau and Afton (2006, 2008*b*) concluded that forage quality in Iowa and Minnesota had declined because of decadal scaup diet shifts from amphipods to mollusks. Moreover, scaup lipid reserves in Minnesota and Manitoba were nearly 30% lower in the early 2000s as compared

to the 1980s, providing further support to the SCH (Anteau and Afton 2004). Because of declines in foraging quality at spring migration areas in the upper Midwest, major wintering areas may be increasingly important for accumulation of nutrient reserves (Austin et al. 2006). However, studies investigating changes to prey availability and diet composition on wintering grounds are lacking.

The Mississippi Flyway, which winters approximately 40% of the continental scaup population, is experiencing the largest population declines (Afton and Anderson 2001). Louisiana winters 91% of the scaup in the Mississippi Flyway (Afton and Anderson 2001), and one area in Louisiana that hosts large numbers of scaup is Lake Pontchartrain (Kinney 2004). However, annual scaup estimates on Lake Pontchartrain fluctuate drastically. The highest estimate was over a million birds (1,194,907) in December 2006 while zero scaup have been estimated twice, in January 2006 and December 2012 (unpublished data).

One potential source for this variation in scaup abundance is coincident variation in food availability on Lake Pontchartrain. The importance of mollusks as the primary food source for wintering scaup is well-documented (Harmon 1962, Perry and Uhler 1982, Hoppe et al. 1986, Custer and Custer 1996). Furthermore, many of the dominant mollusk species found in Lake Pontchartrain are principal diet components for scaup at many wintering areas (Harmon 1962, Bowman 1973, Perry and Uhler 1982, Perry et al. 2007). In the only diet study on Lake Pontchartrain, Bowman (1973) found that common rangia clams (*Rangia cuneata*) (hereafter, rangia) and dark false mussels (*Mytilopsis leucophaeta*) were the main prey species consumed by scaup, accounting for 81% and 14% of scaup diets, respectively. Scaup exhibit species- and size- specific prey selection of mollusks (Custer and Custer 1996, Richman and Lovvorn 2004). Numerous studies indicate that scaup and other diving ducks consume mollusk sizes based on

handling times, meat-to-shell ratios which affect nutrients relative to passage rate, and risk avoidance of very large prey (Draulans 1982, Bustnes and Erikstad 1990, de Leeuw and van Eerden 1992, Bustnes 1998, Hamilton et al. 1999, Richman and Lovvorn 2004).

However, other prey sources have been documented as important food bases for scaup wintering in Louisiana (Rogers and Korschgen 1966, Afton et al. 1991, Moore et al. 1998).

Scaup from Lake Borgne and Grand Chenier ate primarily fish, with sheepshead minnow (Cyprinodon variegatus) and unidentified fish fragments accounting for 42% of the total volume of food consumed (Rogers and Korschgen 1966). Sawgrass (Cladium jamaicense), bulrushes (Scirpus spp.), widgeon grass (Ruppia maritima), filamentous algae and unidentified plant fragments and seeds represented 36% of the total volume of food consumed (Rogers and Korschgen 1966). Various crustaceans also represented a sizeable portion of the scaup diets from Lake Borgne and Grand Chenier, accounting for 17% of the total volume consumed (Rogers and Korschgen 1966). In contrast, on Catahoula Lake, scaup consumed mostly plant seeds, particularly from bearded sprangletop (Leptochloa fusca fascicularis) and an unidentified millet species (Echinochloa sp.), (Moore et al. 1998). Finally, on Rockefeller Wildlife Refuge in southwest Louisiana, midge larvae (Chironomidae) were the most consumed prey item, though bulrush seeds also represented a major portion of scaup diets (Afton et al. 1991).

Given the disparity in scaup diets in Louisiana, my goal was to determine important diet items in scaup wintering on Lake Pontchartrain, especially in relation to their availability in the benthic substrate. Therefore, my objectives were to: 1) determine diet composition (prey species and size class) of scaup collected from Lake Pontchartrain, 2) estimate concurrent prey availability in the estuary, and 3) assess dietary preferences by comparing prey consumption to availability.

2.2 Methods

2.2.1 Study Area

Located in southeastern Louisiana, Lake Pontchartrain is a 1,630 km² oligohaline estuarine lagoon with an average salinity of 3.9 parts per thousand (ppt), an average depth of 3.7 m, and a maximum depth of 5 m (Sikora and Kjerfve 1985). From the north and west, Lake Pontchartrain receives freshwater discharges from the Tangipahoa River, the Tchefuncte River, and Pass Manchac, which connects to Lake Maurepas to the west (Figure 2.1). Lake Pontchartrain also receives freshwater input from numerous bayous, outfall canals from the south shore, and periodic openings and leakage from the Bonnet Carré Spillway. There are two narrow, natural tidal passes on the eastern portion of the estuary: the Rigolets leading into Lake Borgne/Western Mississippi Sound and Chef Menteur, which opens into Lake Borgne. The Inner Harbor Navigation Canal (IHNC), located in the southeastern side of the estuary, serves as a third tidal pass and opens into the Gulf Intracoastal Waterway. The Mississippi River Gulf Outlet (MRGO) also connected Lake Pontchartrain to the Gulf of Mexico via the IHNC from 1968 until its closure in 2009. Higher salinity water enters from the east through these three tidal passes. The combination of freshwater discharges from the west and saline influxes from the east creates a salinity gradient that increases from west to east (Sikora and Kjerfve 1985).

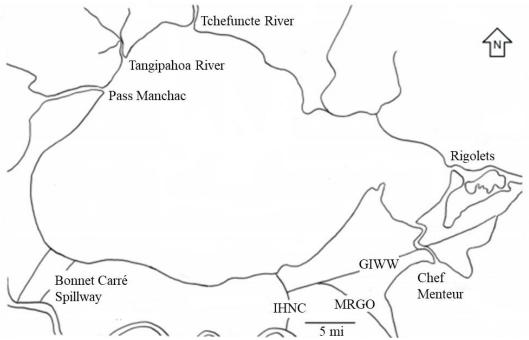


Figure 2.1. Map of freshwater sources and tidal passes on Lake Pontchartrain, Louisiana, USA (IHNC = Inner Harbor Navigational Canal, MRGO = Mississippi River Gulf Outlet, and GIWW = Gulf Intracoastal Waterway). Map amended from Poirrier and Caputo (2015).

2.2.2 Scaup Collections

Scaup begin to arrive in the Lake Pontchartrain area between late October and the middle of November (Baldassare 2014). We attempted collections on Lake Pontchartrain between November 2016 and January 2017, weather permitting. Scaup were collected from boats using semi-automatic 12-gauge shotguns firing #2 steel shot, as permitted under United States Fish and Wildlife Service scientific collecting permit MB74481B-0, Louisiana Department of Wildlife and Fisheries scientific collecting permit LNHP-15-074, and Louisiana State University (LSU) AgCenter Animal Care and Use Committee protocol A2015-20. Flocks were located using binoculars and ranged in size from dozens to several thousands of individuals. After confirming individuals within flocks were foraging, we accelerated the boat to full speed (~60 km/hr) heading at approximately a 45-degree angle in relation to the flock. We maneuvered the boat around the birds in a circular pattern getting progressively closer. Once the boat was within

~200 m of the flock, most of the birds would flush. However, many individuals (often several hundred) would remain on the water, and it was evident that the remaining birds were reluctant to take flight. After we approached within ~75 m of swimming flocks, all remaining birds flushed. We then turned the boat directly toward the scaup, often allowing for shooting opportunities at birds before or slightly after taking flight.

Some individuals resorted to diving rather than flight as an escape mechanism. In these circumstances, the boat was positioned over top the last place the bird was spotted before diving. Once below surface, birds would usually swim 15–75 m in an unpredictable direction and were generally under water for 30–45 seconds. After surfacing, scaup were generally only above water for a split-second, making collection difficult; repositioning the boat several times was often required for successful collection.

2.2.3 Field and Laboratory Procedures Post-collection

Immediately after collection in the field, I injected scaup with 10% buffered formalin to prevent further digestion (Afton et al. 1991). Scaup were then placed in individual freezer bags and placed in a cooler to be brought back to LSU, where birds were dried using box fans for 12 h. After drying, I identified the sex and age of scaup by examining rectrices and wing plumage (Carney 1992). Next, body mass (with ingesta) and morphometric measurements were taken, including body length, culmen length and width, tarsometatarsus length, wing chord length, and longest rectrix width (Afton and Ankney 1991, Hohman et al. 1995). Ingesta mass was not subtracted from total body mass (Hine et al. 1996, Austin et al. 1998, Vest et al. 2006).

I removed the esophagus and proventriculus (with ingesta) and placed them into containers filled with 10% buffered formalin (Afton et al. 1991). The gizzard, small intestines,

and large intestines were removed, and the carcasses were placed in a freezer for a separate study. Next, I used a dissecting microscope to sort esophageal and proventricular contents by species into 5 mm size classes based on length: 0 to < 6 mm, \ge 6 mm to < 11 mm, \ge 11 mm to < 16 mm, and \ge 16 mm to < 21 mm. Esophageal and proventricular contents were combined for analysis to maximize sample size (Sugden 1973, Afton et al. 1991). I excluded contents from the gizzard and intestines, because the gizzard imposes a sampling bias by retaining harder food items (Dirschl 1969, Swanson and Bartonek 1970). After sorting, I counted the number of diet items in each species and size class, placed them into tin cups, and dried them in an oven for 24 h at 60° C (Afton et al. 1991). After drying, I determined the dry mass of each species and size class to the nearest 0.1 mg.

With the assistance of M. Poirrier and C. Caputo, three replicate dredge samples were taken at 6 locations (4 at scaup collection sites and 2 at long-term benthic sampling locations near scaup collection sites) using a 15 cm² petite Ponar dredge (Abadie and Poirrier 2000, Brammer et al. 2007, Poirrier et al. 2008). Samples were rinsed and sieved using a Wildco 12 L, 0.6 mm sieve bucket, and then preserved in 10% Borax-buffered formalin with rose Bengal stain (Abadie and Poirrier 2000, Brammer et al. 2007, Poirrier et al. 2008). In the laboratory, samples were rinsed in a 0.5 mm sieve (Abadie and Poirrier 2000, Brammer et al. 2007, Poirrier et al. 2008). Under a dissecting microscope, benthic invertebrates were sorted and counted by species into 5 mm size classes based on length (Abadie and Poirrier 2000, Brammer et al. 2007, Poirrier et al. 2008). These counts were then used to estimate the number of individuals/m² by extrapolating from the surface area sampled by the petite Ponar dredge (225 cm²) (Abadie and Poirrier 2000, Brammer et al. 2007, Poirrier et al. 2008). Food availability was calculated by averaging benthic invertebrate abundances across the 6 benthic sampling locations.

2.2.4 Statistical Analyses

I used linear regression to determine whether food consumption varied by sex, age, time of collection, and collection date. All scaup were included in these analyses, including those that consumed zero food items. For scaup that consumed more than 5 food items (Reinecke and Owen 1980), I described consumption using three different metrics (Swanson et al. 1974, Prevett et al. 1979). First, I defined percent occurrence as the percentage of the total number of food items consumed that each item represented. Aggregate percent dry weight was defined as the percentage of total dry weight that a particular food item represented. Lastly, I defined percent occurrence of scaup as the percentage of feeding individuals that consumed a particular food item. The equations for these three expressions are listed below.

- 1) $A_i = \sum F_i / \sum F_j$, where A_i is the percent occurrence of food item i, F_i is the quantity of food item i in the sample, and F_i is the quantity of all food items in the sample.
- 2) $C_i = \sum W_i / \sum W_j$, where C_i is the aggregate percent dry weight for food item i, W_i is the dry weight of food item i in the sample, and W_j is the dry weight of all food items in the sample.
- 3) $D_i = \sum n_i / N$, where D_i is the percent occurrence of scaup for food item i, n_i is the number of scaup that consumed food item i in the sample, and N is the total number of scaup in the sample.

Selection indices and standardized selection indices were calculated to assess dietary preferences (Krebs 1999, Manly et al. 1993). Both indices were calculated using food

consumption aggregated across all scaup that consumed more than 5 food items, thus ensuring all birds were weighted equally by preventing a few individuals that gorge themselves on rare food items from skewing the data (Swanson et al. 1974). Selection index values ranged from 0 to ∞ ; values greater than 1.0 indicated scaup preferentially consumed a prey species relative to its availability (Krebs 1999). I defined the selection index as:

4) $\widehat{w}_i = \widehat{o}_i / \widehat{p}_i$, where \widehat{w}_i is the selection index for food item i, \widehat{o}_i is the proportion of species i in the diet, and \widehat{p}_i is the proportion of species i available on Lake Pontchartrain.

Manly et al. (1993) suggested using selection indices as standardized ratios that sum to 1.0 for all available prey species. Standardized selection indices are interpreted as the estimated probability that prey species *i* would be the next prey item selected if all food sources were equally available (Manly et al. 2002). A standardized selection index equal to 1 divided by the number of prey species indicates no preference (Krebs 1999). Scaup consumed a total of 10 different food items; rangia size classes were analyzed independently, and so were treated as unique food items. Therefore, values equal to 0.1 (1/10) indicate no preference for my analyses. Values below 0.1 indicate relative avoidance, while values above indicate relative preference (Krebs 1999). I defined the standardized selection index as:

5) $\hat{B}_i = \hat{w}_i / \sum_{i=1}^n \hat{w}_i$, where \hat{B}_i is the standardized selection index for food item i and \hat{w}_i is the selection index for species i.

I also conducted a principal component analysis (PCA) of the correlation matrix for all morphometric measurements (Afton and Ankney 1991, Hohman et al. 1995). This PCA

collapsed all morphometric variables into an aggregate measure of body size. Males and females were combined to increase sample size. I regressed scores for the first principal component (PC1) against body mass and used the residuals from this regression as an index of body condition (Afton and Ankney 1991, Anteau and Afton 2004). Linear regression was used to test effects of sex, age, and collection date on variation in body condition.

2.3 Results

2.3.1 Scaup Collections

I collected 60 scaup on Lake Pontchartrain across five days between December 7, 2016 and January 20, 2017 at 40 locations (Figure 2.2). Successful collection attempts were limited to days with calm winds and seas, with slightly foggy and overcast conditions improving collection success. I collected 53 males and seven females composed of 42 adults and 18 juveniles.

Twenty-eight individuals (24 males, 4 females; 20 adults, 8 juveniles) consumed more than 5 food items.

2.3.2 Scaup Diets

Sex, age, and time of collection did not affect the quantity or dry weight of overall food consumption or of individual prey species or size classes (of rangia) (all p > 0.05). However, scaup ate significantly more food later in the season, both in terms of quantity and dry weight. Using collection data as a continuous predictor variable, the number of food items consumed increased on average by 0.6 prey items per day through the season (p < 0.05). Similarly, scaup ingested 36.4 mg more of dry weight per day as the season progressed (p < 0.01). Using collection data as a factor variable, I found that scaup food consumption increased by 24.8 items

on the last collection date (p < 0.05). Scaup also consumed significantly more total dry weight on the last two collection dates, with an increase of 1.2 g and 1.4 g on January 3 and January 20, respectively (both p < 0.05).

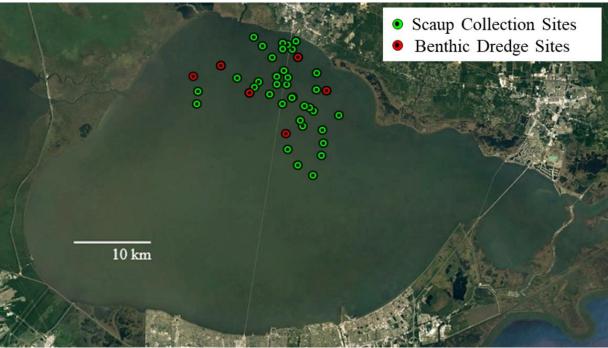


Figure 2.2. Map of lesser scaup (*Aythya affinis*) collection sites and benthic dredge sampling locations on Lake Pontchartrain, Louisiana, USA.

Five species of mollusks comprised 98% of the total number of food items and nearly 100% of the aggregate dry weight consumed (Figure 2.3). Rangia was the dominant food item eaten, accounting for 43% of the total number of food items ingested (Table 2.1). Scaup consumed 353.2 g of rangia (Table 2.2), which represented 60% of the dry weight for all food items consumed. Twenty-five out of 28 individuals (89%) that had food items in the upper digestive tract consumed rangia. Medium-size classes (\geq 6 mm to <11 mm and \geq 11 mm to <16 mm) were the most commonly consumed size classes of rangia. Over half (51%) of the rangia eaten belonged to \geq 6 mm to <11 mm size class, which accounted for 22% of the quantity of all food items ingested. Although rangia in the \geq 11 mm to <16 mm size class accounted for only

8% of the total number of food items consumed, the size class represented 36% of the aggregate dry weight ingested. Combined, the medium-size classes of rangia represented 55% of the aggregate dry weight for all food items consumed. The dark false mussel, *Mytilopsis leucophaeta*, was the second most consumed species, accounting for 26% of total number of food items and 37% of the total dry weight ingested. Furthermore, dark false mussels were consumed by 23 individuals (82%).

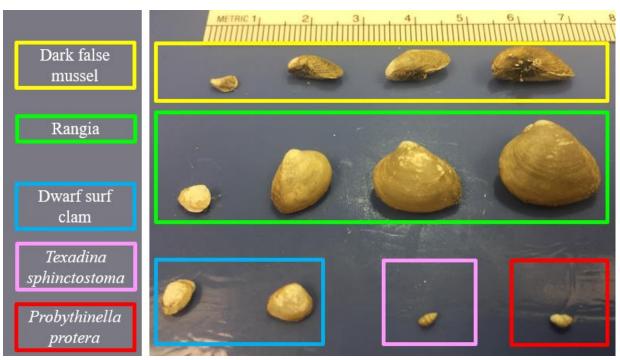


Figure 2.3. Photograph of prey species consumed by lesser scaup (*Aythya affinis*) on Lake Pontchartrain, Louisiana, USA.

Texadina sphinctostoma and Probythinella protera, aquatic snail species, represented 9% and 17% of the total number of food items ingested (Table 2.1). Although both species were consumed, they were not common prey species in all individuals. Only 6 individuals (21%) consumed *T. sphinctostoma*, with 1 individual accounting for approximately half of the total number of *T. sphinctostoma* eaten. Similarly, only 10 scaup (36%) ingested *P. protera*, with 4

individuals representing 91% of the total quantity of *P. protera* ingested. Furthermore, because of their extremely small size (both species have lengths of 2–3 mm and weigh 0.2–0.3 mg) (Sikora and Sikora 1982), *T. sphinctostoma* and *P. protera* only accounted for less than 1% and 1.5% of the aggregate dry weight consumed, respectively.

Table 2.1. Percent occurrence of food items, aggregate percent dry weight, and percent occurrence of scaup from 28 scaup collected during the winter of 2016–2017.

Food Item	% Occurrence of Food Items ^a	Aggregate % Dry Weight ^b	% Occurrence of Scaup ^c
Rangia (0 to <6 mm)	12.3	3.9	64.3
Rangia (≥6 to <11 mm)	21.9	19.1	89.3
Rangia (≥11 to <16 mm)	8.4	35.6	67.9
Rangia (≥16 to <21 mm)	0.1	1.3	3.6
Rangia total	42.6	59.9	89.3
Dwarf surf clam	2.8	1.2	57.1
Dark false mussel	25.5	36.8	82.1
Texadina sphinctostoma	9.3	0.6	21.4
Probythinella protera	17.3	1.5	35.7
Insecta ^d	2.4	0.0	14.3
Amphipoda	0.1	0.0	3.6

- a) Obtained from equation 1 in Methods
- b) Obtained from equation 2 in Methods
- c) Obtained from equation 3 in Methods
- d) Values for Coleoptera and Diptera combined

Other prey items included dwarf surf clams, insects, and one amphipod. Although 57% of scaup consumed dwarf surf clams (*Mulinia lateralis*), the prey species only represented 3% of the total number of food items and 1% of the aggregate dry weight consumed (Table 1). Insects from the Orders Coleoptera and Diptera combined to account for 2% of the total number of food items eaten and less than 1% of the aggregate dry weight consumed. Insects and amphipods were not identified below Order because they represented such a small component of the diet.

Five individuals also consumed trace amounts of plant material; this material was not included in analysis because it only represented 0.01% of the aggregate dry weight consumed.

Table 2.2. Scaup food items consumed and their availability on Lake Pontchartrain during the winter of 2016–2017.

Food item	Number of food items consumed	Dry weight consumed (g)	Number of food items available (per m²)		
Rangia total	497	353.2	274.7 ± 36.0		
Rangia (0 to <6 mm)	143	23.1	145.7 ± 34.1		
Rangia (≥6 to <11 mm)	255	112.6	71.7 ± 15.2		
Rangia (≥11 to <16 mm)	98	209.7	52.6 ± 21.6		
Rangia (≥16 to <21 mm)	1	7.9	4.8 ± 3.3		
Dwarf surf clam	33	7.2	7.2 ± 5.2		
Dark false mussel	298	217.1	38.2 ± 14.7		
Texadina sphinctostoma	108	3.5	805.1 ± 158.2		
Probythinella protera	202	8.6	250.8 ± 67.2		
Insecta ^a	28	0.2	Not estimated		
Amphipoda	1	0.0	Not estimated		
Total	1167	589.6	1376.0 ± 355.3		

a) Values for Coleoptera and Diptera combined

2.3.3 Prey Availability

 $T.\ sphinctostoma$ was the most abundant prey species detected in the benthic dredge samples, representing 59% of the total number of food items available (Table 2.3). Rangia was the second most abundant species; abundance among rangia size classes decreased with increasing size groups (Table 2.2). $P.\ protera$ was also abundant with 250.8 ± 67.2 per m² individuals estimated. Compared to other prey species, dark false mussels and dwarf surf clams were relatively rare in the benthic dredge samples, with both species accounting for <4% of the total number of food items available. Though represented at low levels in scaup diets, insects and amphipods were not effectively sampled using standard benthic dredge techniques.

2.3.4 Selection Indices and Standardized Selection Indices

Using selection index and standard selection index values, dark false mussels were the most preferred prey source, followed by dwarf surf clams. However, large selection index and standard selection index values for these species were partially an artifact of their relative rarity in the dredge samples (Table 2.2). Using selection index values, scaup preferentially selected rangia as a species and the three smallest size classes (0 to <6 mm, ≥6 mm to <11 mm, and ≥11 mm to <16 mm) (Table 2.3). However, only the ≥6 mm to <11 mm size class was preferred according to standardized selection index values, and small rangia in the 0 to <6 mm size class were avoided. Both selection index and standardized selection index values indicated that scaup did not prefer *T. sphinctostoma* or *P. protera*.

Table 2.3. Selection indices and standardized selection indices for scaup food items on Lake Pontchartrain. Estimates from insects and amphipods were not included.

Food Item	Proportion Consumed (o _i)	Proportion Available (p _i)	Selection Index (w _i) ^a	Standardized Selection Index (B _i) ^b
Rangia (0 to <6 mm)	0.12	0.11	1.16	0.05
Rangia (≥6 to <11 mm)	0.22	0.05	4.20	0.18
Rangia (≥11 to <16 mm)	0.08	0.04	2.20	0.09
Rangia (≥16 to <21 mm)	0.00	0.00	0.25	0.01
Rangia total	0.43	0.20	2.13	0.09
Dwarf surf clam	0.03	0.01	5.43	0.23
Dark false mussel	0.26	0.03	9.19	0.39
Texadina sphinctostoma	0.09	0.59	0.16	0.01
Probythinella protera	0.17	0.18	0.95	0.04
Total	0.98	1.00	23.53	1.00

- a) Obtained from equation 4 in Methods; values above 1.0 indicate preference
- b) Obtained from equation 5 in Methods; values above 0.1 indicate preference

2.3.5 Principle Components Analysis

Our Principle Components Analysis collapsed several co-varying measurements of scaup structural morphology into an aggregated metric of body size. Principle component 1 (PC1) explained 82.0% of the variance and loaded strongly on body length (Figure 2.4). Principle component 2 (PC2) explained 12.9% of the variance and loaded strongly on wing cord. I regressed PC1 values against empirical scaup body mass to obtain an index of mass corrected for structural size (i.e., body condition). Body condition index did not vary by age or sex (p > 0.05). Collection date also did not affect the body condition index (Figure 2.5).

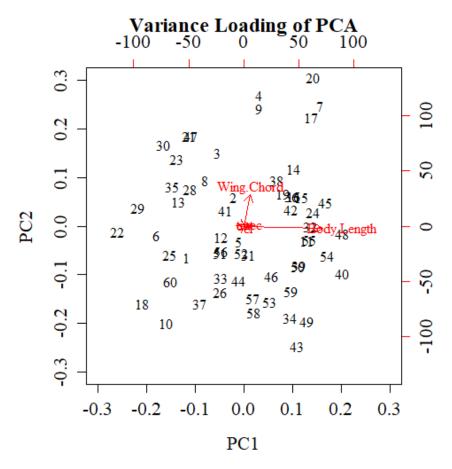


Figure 2.4. Variance loading of principle components analysis (PCA) conducted on morphometric measurements of lesser scaup (*Aythya affinis*) collected on Lake Pontchartrain, Louisiana, USA during the winter of 2016–2017.

2.4 Discussion

Scaup ate significantly more food later in the season, especially on the last two collection dates. It seems plausible that scaup increase food consumption as spring migration nears; however, body condition did not increase later in the season. Consistent with my results, Anteau and Afton (2004) found that lipid reserves did not change from mid- to late-winter in Louisiana. While small sample size and temporal resolution limits the scope of my conclusions, it is possible that the lower nutrient density of mollusks compared to other prey species (such as amphipods commonly consumed during migration [Rogers and Korschgen 1966, Afton and Hier 1991, Afton et al. 1991, Anteau 2006]) prevents scaup from building lipid reserves, even as they consume higher numbers of prey later in the wintering season.

Scaup body condition over time

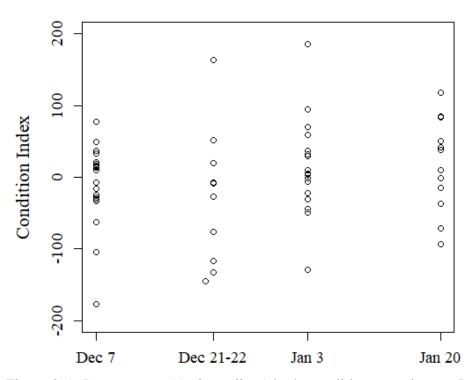


Figure 2.5. Lesser scaup (*Aythya affinis*) body condition over time on Lake Pontchartrain, Louisiana, USA during the winter of 2016–2017.

Wintering scaup primarily feed on mollusks, often of a particular species or size (Afton et al. 1991, Custer and Custer 1996, Richman and Lovvorn 2004). My results show that scaup

wintering on Lake Pontchartrain fed almost exclusively on mollusks, in accordance with previous work conducted by Bowman (1973). Other food sources, such as plant material, insects, and amphipods, do not seem to be important food items for scaup wintering on Lake Pontchartrain. Although Moore et al. (1998) reported plant material represented a major component of diets of scaup wintering on Catahoula Lake, Louisiana, only five individuals consumed trace amounts of plant material on Lake Pontchartrain. Combined, plant material from these five birds represented only 0.01% of the dry weight of all food consumed. Insects from the Orders Coleoptera and Diptera combined represented less than 1% of the total dry weight ingested. Furthermore, only 4 individuals consumed these insects, with 1 individual accounting for 68% of the total insect consumption. Thus, mollusks seem to be the only significant food sources for scaup on Lake Pontchartrain.

Rangia and dark false mussels were the dominant prey species consumed by scaup on Lake Pontchartrain during the winter of 2016–2017. Rangia accounted for large percentages of the total number of food items and dry weight consumed. Bowman (1973) also found rangia were the most consumed prey species, comprising 81% of the total number of food items consumed. Rangia is often a dominant species in the benthic community on Lake Pontchartrain (Sikora and Sikora 1982, Poirrier et al. 2009), making it likely that the species represents a large component of annual scaup diets on the estuary. Dark false mussels were the second most important prey species, accounting for over a quarter of the total quantity of food items eaten and 37% of the aggregate dry weight consumed. Bowman (1973) also found dark false mussels were the second most consumed food source, representing 14% of the total number of food items. Dark false mussels attach to hard surfaces, such as rocks, artificial reefs, walls, or pilings (Oliver

et al. 1998, Bamber and Taylor 2002), all of which are found on Lake Pontchartrain. Thus, it is possible that dark false mussels provide scaup with an easy food source at known locations.

Studies have shown that larger clams contain more nitrogen, lipids, and energy (kJ) than smaller clams (Richman and Lovvorn 2004). Therefore, it is intuitive to expect scaup to maximize the size of prey items consumed. However, several studies have shown that scaup and other diving ducks more commonly select small- or intermediate-sized clams, possibly because of differing handling times, effects of meat-to-shell ratios on nutrients digested relative to passage rate, and risk avoidance of very large prey (Draulans 1982, Bustnes and Erikstad 1990, de Leeuw and van Eerden 1992, Bustnes 1998, Hamilton et al. 1999, Richman and Lovvorn 2004). For example, clams <12 mm long comprised 90% of scaup diets in the San Franscisco Bay (Richman and Lovvorn 2004). Similarly, I found that 80% of rangia ingested by scaup on Lake Pontchartrain were <11 mm long. Rangia in the ≥ 6 mm to <11 mm size class represented roughly one-fifth of both the total number of food items and the aggregate dry weight consumed. This size class was also highly preferred relative to availability. Although scaup ate considerably smaller quantities of rangia in the ≥11 mm to <16 size class, this group comprised consumed 59% of the total rangia dry weight ingested. Furthermore, this size class represented 36% of the dry weight of all food items consumed.

Despite being a preferred food source based on selection index and standardized selection index values, dwarf surf clams accounted for a very small percentage of food consumption.

These clams represented less than 1% of the total food available during the winter of 2016–2017, likely limiting their biological importance to scaup diets during our study. However, it is well-documented that wintering scaup often consume substantial amounts of dwarf surf clams if they are available (Cronan Jr. 1957, Harmon 1962, Perry and Uhler 1982). For example, in southwest

Louisiana, dwarf surf clams represented over 99% of the total number of food items consumed (Harmon 1962). Thus, is likely that that the species would comprise a much higher percentage of scaup diets on Lake Pontchartrain in years when the species is more abundant.

T. sphinctostoma and P. protera accounted for sizable percentages of the total number of food items consumed. However, only a small percentage of scaup consumed each species. Selection index and standardized selection index values indicate that both species are avoided by scaup. Also, because of their small size, the nutritional value of T. sphinctostoma or P. protera is likely insignificant compared to other food sources. Therefore, neither species should be viewed as important food sources on Lake Pontchartrain.

I found that dark false mussels were preferred by scaup relative to their abundance in the benthic dredge surveys. However, it is likely that dark false mussels are poorly sampled in these dredge surveys. With bridge pilings, a seawall along the southern portion of the lake, and other artificial structures found throughout the lake, it is likely that dark false mussels attach to these structures and are much more prevalent than indicated through the traditional benthic dredge surveys. As such, selection index and standardized selection index estimates reported here for dark false mussels are likely inflated due to sampling bias. Since standardized selection indices are a comparison among prey items, inflated values for dark false mussels would reduce the index scores of other food sources, possibly causing rangia in the ≥11 mm to <16 size class and rangia as a species to be inaccurately classified as slightly avoided according to standardized selection indices.

Because benthic invertebrate diversity is low on Lake Pontchartrain, it seems plausible that the community of mollusks mentioned here constitute the majority of scaup diets. However, given the extreme annual changes in the benthic community, diet composition is likely to change

from year to year. On Lake Pontchartrain, hooked mussel (*Ischadium recurvum*) abundance is usually low but the species can become extremely numerous in years of higher salinity on the estuary (Poirrier and Caputo 2015). Although no scaup consumed the hooked mussel in my study, scaup are known to consume the species at other wintering locations (Perry et al. 2007). Thus, it seems likely that scaup may feed on hooked mussels when the salinity is high on the estuary. Dwarf surf clams, another species well-documented as a favored food source for scaup in other wintering areas, are also likely to constitute a greater percentage of scaup diets when more abundant. Although *T. sphinctostoma* or *P. protera* often dominate benthic invertebrate assembles on Lake Pontchartrain, neither species seems likely to be important food items because of their extremely small size. Finally, our results indicate that rangia, especially medium-size classes, and dark false mussels seem to be the most important food sources for scaup wintering on Lake Pontchartrain.

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CHAPTER 3. SCAUP POPULATION RESPONSES TO PREY AVAILABILITY AND ENVIRONMENTAL DISTURBANCES

3.1 Introduction

Continental scaup populations, which include lesser scaup (*Aythya affinis*) and greater scaup (*Aythya marila*), have been declining since the 1980s (Afton and Anderson 2001). However, lesser scaup are experiencing the largest population declines and account for approximately 89% of the scaup population; therefore, lesser scaup (hereafter, scaup) are the primary species of concern (Afton and Anderson 2001). The Mississippi Flyway, which winters approximately 40% of the continental scaup population, is experiencing the largest population declines (Afton and Anderson 2001). Louisiana winters 91% of the scaup in the Mississippi Flyway (Afton and Anderson 2001), and one area in Louisiana that hosts large numbers of scaup is Lake Pontchartrain (Kinney 2004). However, annual scaup estimates on Lake Pontchartrain fluctuate drastically. The highest estimate was over a million birds (1,194,907) in December 2006 while zero scaup have been estimated twice, in January 2006 and December 2012 (unpublished data).

One potential source for this variation in scaup abundance is coincident variation in food availability on Lake Pontchartrain. The importance of mollusks as the primary food source for wintering scaup is well-documented (Harmon 1962, Perry and Uhler 1982, Hoppe et al. 1986, Custer and Custer 1996). Furthermore, many of the dominant mollusk species found in Lake Pontchartrain are principal diet components for scaup at many wintering areas (Harmon 1962, Bowman 1973, Perry and Uhler 1982, Perry et al. 2007). In the only diet study on Lake Pontchartrain, Bowman (1973) found that common rangia clams (*Rangia cuneata*) (hereafter, rangia) and dark false mussels (*Mytilopsis leucophaeta*) were the main prey species consumed by scaup, accounting for 81% and 14% of scaup diets, respectively. Scaup exhibit species- and

size- specific prey selection of mollusks (Custer and Custer 1996, Richman and Lovvorn 2004). Numerous studies indicate that scaup and other diving ducks consume mollusk sizes based on handling times, meat-to-shell ratios which affect nutrients relative to passage rate, and risk avoidance of very large prey (Draulans 1982, Bustnes and Erikstad 1990, de Leeuw and van Eerden 1992, Bustnes 1998, Hamilton et al. 1999, Richman and Lovvorn 2004).

Benthic communities in oligohaline estuaries like Lake Pontchartrain have low species richness (Remane and Schleiper 1971). These benthic communities are influenced more by abiotic variables than biotic interactions (Gunter 1960, Boesch and Rosenberg 1981). Benthic communities on Lake Pontchartrain exhibit extreme fluctuations in overall abundance, biomass, and species and size diversity among years due environmental conditions and disturbances (Sikora and Sikora 1982, Poirrier et al. 2009, Poirrier and Caputo 2015). Shell dredging, salt water intrusion, hurricanes, spillway openings, and La Niña-driven droughts have all been documented to impact water quality and benthic invertebrate populations in Lake Pontchartrain (Abadie and Poirrier 2000, 2001*a*, 2001*b*, Brammer et al. 2007, Poirrier et al. 2008, Poirrier et al. 2009, Poirrier and Caputo 2015).

For example, Lake Pontchartrain has an extensive history of shell dredging dating back to the 1930s. Sikora and Kjerfve (1985) asserted that 4 million m^3 of rangia fossil shells were dredged annually until operations ended in 1990. Shell dredging disturbed bottom sediments, increased turbidity, and decreased densities of large rangia clams ≥ 21 mm (Chew 1987, Abadie and Poirrier 2000, 2001a). Because high salinity bottom water flows along depth contours, channels created by shell dredging likely increase distribution of water containing low levels of dissolved oxygen, thereby exacerbating the impacts of other disturbances (Poirrier et al. 2009). Indeed, Poirrier et al. (2008) suggested that effects from Hurricane Katrina may have been

amplified in areas disturbed by shell dredging as compared to those areas not exposed to these operations.

After shell dredging ceased, densities of large rangia increased to historic levels throughout much of the estuary (Abadie and Poirrier 2000), and water clarity also increased at most locations (Francis and Poirrier 1999). However, water clarity and densities of large rangia did not increase in an area roughly 250 km² located along the southern shore (Francis and Poirrier 1999, Abadie and Poirrier 2000, 2001a, 2001b). Reduced water clarity and densities of large rangia along the southern shore was attributed to salinity stratification caused by saline water entering through the Inner Harbor Navigation Canal (IHNC) via the Mississippi River Gulf Outlet (MRGO), a shipping canal completed in 1968. Anoxia and hypoxia is typical at the mouth of the IHNC (Poirrier 1978, Junot et al. 1983). Furthermore, hypoxia has been observed regularly at a site 17 km from the mouth of the IHNC, and periodically at a site 24 km from the mouth of the IHNC, underscoring the extensive area influenced by salt water intrusion from the MRGO (Poirrier et al. 2009). Low species diversity and the absence of large rangia is typical in this area, which has become known as the "dead zone" (Poirrier et al. 2009). The MRGO also exacerbated the storm surge produced from Hurricane Katrina (Shaffer et al. 2009), one of the primary reasons for its closure in 2009. After closure of the MRGO, episodic hypoxia no longer occurs from salt water intrusion near the mouth of the IHNC (Poirrier 2013).

Numerous studies have shown that hurricanes impact benthic invertebrates, both directly and indirectly (Poirrier et al. 2008, Engle et al. 2009, Ray 2009, Poirrier and Caputo 2015). Flocks et al. (2009) found that the top 1 m of sediments are fundamentally reworked after major storms. Instead of being transported out of Lake Pontchartrain, sediments settle rapidly along the estuary bottom due to slow flushing rates (Flowers and Isphording 1990). Sediment deposits can

cause benthic invertebrates to be displaced and buried, ultimately causing death (Poirrier et al. 2008, Poirrier et al. 2013). Indirect effects include declines in benthic invertebrate diversity, abundance, and biomass, possibly resulting from a nonmixing stratified layer with increased salinity and low dissolved oxygen along the estuary bottom (Poirrier et al. 2008, Poirrier et al. 2009).

Hurricane Katrina, a Category 3 storm that made landfall near eastern Lake Pontchartrain on August 29, 2005, caused salinity stratification and low dissolved oxygen at multiple locations, as well as an estuary-wide increase in salinity from storm surge (Poirrier et al. 2008). Species diversity of benthic invertebrates declined at most sites (Poirrier et al. 2008). Densities of rangia and two hydrobiid snails that lack common names (*Probythinella protera* and *Texadina sphinctoma*), all of which usually rank among the most abundant benthic invertebrates on Lake Pontchartrain, were greatly reduced (Poirrier et al. 2008, Engle et al. 2009, Poirrier et al. 2009). Moreover, Hurricane Katrina resulted in the complete loss of rangia and other dominant benthic species at depths greater than 3.7 m, which accounts for approximately half the estuary (Poirrier et al. 2008, Poirrier et al. 2009).

Hurricanes Ike and Gustav in 2008 and Isaac in 2012 also decreased densities of rangia on Lake Pontchartrain (Ray 2009, Poirrier and Caputo 2015). Poirrier and Caputo (2015) found that density changes in 6–20 mm clams accounted for most of rangia declines following hurricanes, possibly because smaller clams are likely to have greater sensitivity to the direct physical damage caused by hurricanes relative to larger clams. Poirrier and Caputo (2015) also reported that 6–20 mm rangia significantly increased in years without hurricanes due to recruitment and fast growth rates.

Opening the Bonnet Carré Spillway, an emergency floodway designed to divert water from the Mississippi River to Lake Pontchartrain to prevent flooding in New Orleans, can drastically affect water quality and the benthic community in Lake Pontchartrain (Sikora and Sikora 1982, Day 1998, Brammer et al. 2007). Since its completion in 1931, the spillway has been opened 11 times, mostly during the spring. The volume of freshwater discharge from the Spillway during a single flood event can exceed the total estuarine volume (Swenson 1980). Spillway openings have been shown to decrease salinity and increase turbidity (Poirrier and Mulino 1977, Sikora and Sikora 1982, Day 1998, Brammer et al. 2007). Massive introductions of nutrients have also been reported, resulting in harmful cyanobacterial blooms (Day 1998). The rate of change and recovery of salinity and turbidity during a spillway opening depends on the volume and duration of the discharge, local precipitation, and tidal exchanges (Brammer et al. 2007).

After the 1979 Spillway opening, Sikora and Sikora (1982) found that the abundance of most species declined, including rangia, dwarf surf clams, and dark false mussels. However, the study concluded that *T. sphinctostoma* did not differ in abundance, and numbers of *P. protera* increased. Brammer et al. (2007) found that macrofaunal species diversity and abundances, as well as rangia abundance and biomass, significantly declined following the 1997 Spillway opening. Brammer et al. (2007) did not pinpoint the exact causes of the negative impacts on benthic communities following the 1997 opening, though the study speculated that reduced salinity, cyanobacteria blooms, and bottom water hypoxia/anoxia were probable factors.

La Niña-driven droughts also affect water quality and benthic communities in Lake Pontchartrain (Poirrier et al. 2009, Poirrier and Caputo 2015). A shift from a historic El Niño to a strong La Niña occurred between 1997 and 2001 (Zheng et al. 2003), resulting in a drought

across southern Louisiana from 1999–2001 (Poirrier et al. 2009). Subsequently, salinity increased to post-Hurricane Katrina levels across the estuary (Poirrier et al. 2009). Overall rangia densities declined, though abundances of clams between 6–15 mm remained the same (Poirrier and Caputo 2015). The drought promoted the hooked mussel (*Ischadium recurvum*) and other high salinity species, leading to increased species diversity characteristic of higher salinity systems (Poirrier et al. 2009, Poirrier and Caputo 2015). Changes to the benthic community composition lasted multiple years, underscoring the effects caused by La Niña-driven droughts (Poirrier et al. 2009, Poirrier and Caputo 2015).

Given that wintering scaup feed primarily on mollusks (often of a particular species or size), it seems likely that the variation in scaup populations observed on Lake Pontchartrain is somehow tied to the variation in benthic communities. Nevertheless, these relationships may be complex and perhaps variable among years because of the dynamic nature of benthic assemblages on the estuary. After determining the food sources used by scaup on Lake Pontchartrain in Chapter 1, my objectives in Chapter 2 were to: 1) build on previous work to identify how environmental conditions and disturbances affect benthic invertebrate populations, 2) diagnose how environmental disturbances and variation in food abundance affects annual scaup abundances. By identifying the drivers of scaup population changes on Lake Pontchartrain, my results can begin to address the effects of food variability on wintering waterfowl distributions, which is poorly known for most species and geographies. Identification of the proximate drivers of scaup abundances on Lake Pontchartrain also should increase our capacity to predict scaup populations over short-term (i.e. are conditions favorable for scaup this year?) and long-term (i.e. how will climatic shifts in hurricane frequency and intensity impact scaup abundance?) scales.

3.2 Methods

3.2.1 Study Area

Located in southeastern Louisiana, Lake Pontchartrain is a 1,630 km² oligohaline estuarine lagoon with an average salinity of 3.9 parts per thousand (ppt), an average depth of 3.7 m, and a maximum depth of 5 m (Sikora and Kjerfve 1985). From the north and west, Lake Pontchartrain receives freshwater discharges from the Tangipahoa River, the Tchefuncte River, and Pass Manchac, which connects to Lake Maurepas to the west (Figure 3.1). Lake Pontchartrain also receives freshwater input from numerous bayous, outfall canals from the south shore, and periodic openings and leakage from the Bonnet Carré Spillway. There are two narrow, natural tidal passes on the eastern portion of the estuary: the Rigolets leading into Lake Borgne/Western Mississippi Sound and Chef Menteur, which opens into Lake Borgne. The Inner Harbor Navigation Canal (IHNC), located in the southeastern side of the estuary, serves as a third tidal pass and opens into the Gulf Intracoastal Waterway. The Mississippi River Gulf Outlet (MRGO) also connected Lake Pontchartrain to the Gulf of Mexico via the IHNC from 1968 until its closure in 2009. Higher salinity water enters from the east through these three tidal passes. The combination of freshwater discharges from the west and saline influxes from the east creates a salinity gradient that increases from west to east (Sikora and Kjerfve 1985).

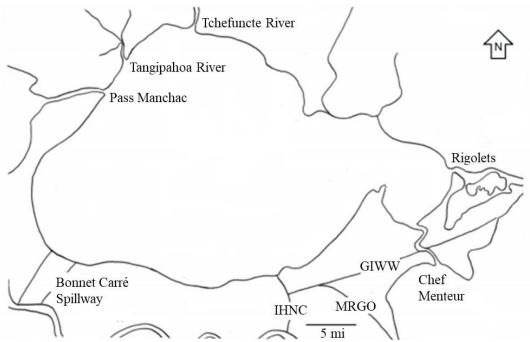


Figure 3.1. Map of freshwater sources and tidal passes on Lake Pontchartrain, Louisiana, USA (IHNC = Inner Harbor Navigational Canal, MRGO = Mississippi River Gulf Outlet, and GIWW = Gulf Intracoastal Waterway). Map amended from Poirrier and Caputo (2015).

3.2.2 Benthic Surveys

To estimate benthic invertebrate abundances, I used data collected from points along fixed transects 1996–2017 (Figure 3.2). Generally, benthic surveys occurred from October through December, just prior to or during the time period scaup would be found on the estuary. However, collections from 2000, 2001, 2002, and 2007 occurred between April and August. Exploratory analyses excluding these years indicated similar trends to results when these years were included. Furthermore, using some of the same data as in my study, Poirrier and Caputo (2015) combined monthly estimates to obtain an average yearly estimate, citing no statistical differences between uncombined monthly estimates and the averaged yearly estimates.

Therefore, I chose to include these four years of summer sampling in my analysis.

In all years except 1996 and 2007, benthic estimates from 7 sampling locations (5 locations along the east-west transect and 2 locations from the north-south transect) were used in analyses.

Data were only available for the 5 east-west transect sites in 1996 and 2007. To address this discrepancy, I compared benthic availability estimates between the 5 east-west sites and the 7 overall sampling locations (the 5 east-west sites and the 2 north-south locations) within the same year (1996 and 2007 were excluded from this comparison). These comparisons revealed a 92% correlation of rangia estimates (p < 0.01), and all size classes of rangia were significantly correlated between the 5 east-west sites and the 7 overall locations (84% correlation, p < 0.01). Dark false mussel estimates were also highly correlated (83%, p < 0.01). Therefore, because estimates of rangia and dark false mussels, the two most important food sources for scaup on Lake Pontchartrain, were highly correlated within the same year between the 5 east-west sites and the 7 overall locations, I chose to include estimates from all 7 benthic sampling location when possible.

At each sampling location, three replicate dredge samples were taken using a 15 cm² petite Ponar dredge (Abadie and Poirrier 2000, Brammer et al. 2007, Poirrier et al. 2008).

Samples were rinsed and sieved using a Wildco 12 L, 0.6 mm sieve bucket, and then preserved in 10% Borax-buffered formalin with rose Bengal stain (Abadie and Poirrier 2000, Brammer et al. 2007, Poirrier et al. 2008). In the laboratory, samples were rinsed in a 0.5 mm sieve (Abadie and Poirrier 2000, Brammer et al. 2007, Poirrier et al. 2008). Under a dissecting microscope, benthic invertebrates were sorted and counted by species into 5 mm size classes based on length (Abadie and Poirrier 2000, Brammer et al. 2007, Poirrier et al. 2008). Next, the quantity of benthic invertebrates of each species/size class were then used to estimate the number of individuals/m² by extrapolating from the surface area sampled by the petite Ponar dredge (225 cm²) (Abadie and Poirrier 2000, Brammer et al. 2007, Poirrier et al. 2008). Estimates for all

three replicates at each sampling site were then averaged to obtain estuary-wide abundances for each benthic invertebrate species.

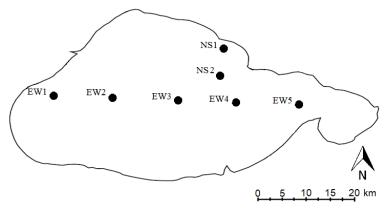


Figure 3.2. Map of benthic invertebrate sampling locations along the East-West (EW) and North-South (NS) transects on Lake Pontchartrain, Louisiana, USA.

3.2.3 Aerial Surveys

The Louisiana Department of Wildlife and Fisheries (LDWF) conducted aerial surveys along 6 fixed transects from 1977 to 2017 to estimate scaup abundance on Lake Pontchartrain.

These surveys were generally conducted in both December and January each winter. However, because scaup are among the last waterfowl species to migrate south for the winter (Anteau et al. 2014), only January estimates were included in our analyses. January surveys were not conducted in 1980, 1981, or 1988, so December estimates from these winters were used instead. No aerial surveys were conducted in 1982, 1989, and 1990. Two observers (pilot not included as an observer) counted and recorded all data for each transect. Densities of scaup (scaup/km²) along the 6 transects were multiplied by the total km² of Lake Pontchartrain to obtain scaup estimates for the entire estuary.

3.2.4 Statistical Analyses

I used linear regression to model the effects of prey abundance on scaup populations. I constructed a fully-saturated model including all prey items and predictor variables, and used the drop1 procedure in R to eliminate uninformative parameters based on AIC score. I also used linear regression to test the effects of environmental disturbance on prey abundance from 1996– 2017. These disturbances included hurricanes, tropical storms, and Bonnet Carré Spillway openings. I identified tropical storm years as those in which a tropical cyclone (a tropical storm or hurricane) made landfall within 150 km from the center of Lake Pontchartrain (Fearnley et al. 2009). I also parsed the effects of hurricanes (at least a Category 1 or greater) and major hurricanes (at least a Category 2 or greater). Finally, I investigated lag effects (i.e. subsequent years after a disturbance) of these disturbances. However, year of disturbances and lag effects could not be included in the same model because the presence of a hurricane automatically issues a value of 0 as a lag effect for that same year. I also used linear models to directly test the effects environmental disturbance on scaup abundances over two intervals: 1) a "short-term" time period concurrent with our analyses on prey abundance (1996–2017) and 2) a "long-term" interval using scaup aerial survey data from all available years (1977–2017). Linear models were also used to evaluate the relationship between continental breeding scaup populations (obtained from the BPOP surveys) and scaup estimates on Lake Pontchartrain.

I selected linear regression (Gaussian error structure) for my analyses because it provided the best fit to the data. While Poisson or negative binomial error structures are commonly used for analyses of count data, they were inappropriate for the data presented here. Lake Pontchartrain population data on both mollusks and scaup are highly variable, such that every year becomes a leverage point. After examining regression diagnostic plots, Poisson and

negative binomial models had a much poorer fit to the data, and so I determined that a Gaussian distribution and linear regression was the most appropriate construct for data analysis.

3.3 Results

3.3.1 Scaup Population Responses to Prey Availability

I found that scaup estimates on Lake Pontchartrain, while highly variable did not show a significant directional change over either time period (1977–2017 and 1996–2017) analyzed (both p > 0.05). Also, scaup numbers on Lake Pontchartrain were not correlated to the scaup breeding population estimates in either time period (Figure 3.3) (both p > 0.05), suggesting that causes unrelated to the continental population are driving annual scaup fluctuations on Lake Pontchartrain.

Scaup populations on Lake Pontchartrain 1996–2017 were significantly affected by food availability. The model containing dwarf surf clams and two size classes of rangia (\geq 11 mm to <16 mm and \geq 16 mm to <21 mm) was the most competitive model of scaup populations. In this model, scaup numbers (shown here as beta estimates \pm SE): increased by 192.7 \pm 74.8 individuals with increasing dwarf surf clam abundance (p < 0.05), increased by 3,494.4 \pm 434.4 birds for increasing abundance of rangia in the \geq 11 mm to <16 mm size class (p < 0.001), and decreased by -2,268.4 \pm 1,051.1 individuals for increasing abundance of rangia in the \geq 16 mm to <21 mm size class (p < 0.05).

Scaup Populations

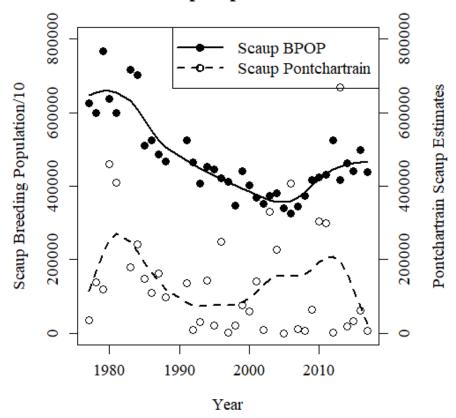


Figure 3.3. Annual lesser scaup (*Aythya affinis*) estimates of the continental breeding population (solid line), and wintering Lake Pontchartrain population (dashed line) from 1977–2017. Scaup breeding estimates shown here are divided by 10 from the actual continental population estimates.

3.3.2 Prey Species and Scaup Responses to Environmental Disturbances

Rangia, the most consumed prey species on Lake Pontchartrain, was significantly affected by hurricanes, declining by -357.4 ± 164.6 individuals in the same year of a hurricane and increasing by 635.1 ± 176.1 clams in the year immediately after a hurricane (Table 3.2). The effect of hurricanes varied among rangia size classes. Hurricanes did not significantly affect rangia in the ≥ 16 to < 21 mm size class, either in the year of or in subsequent years. The other three size classes (0 to < 6 mm, ≥ 6 mm to < 11 mm, and ≥ 11 mm to < 16 mm) declined in the year of a hurricane, though only declines in the ≥ 6 mm to < 11 mm size class reached our alpha threshold for statistical significance (Table 3.1). All three of these rangia size classes

significantly increased in the year after a hurricane (Table 3.1). Parsing tropical cyclone effects by severity of the storm resulted in reduced power to predict clam populations and effects became non-significant. Spillway openings did not affect overall rangia populations or those in any size class (all p > 0.05).

T. sphinctostoma, P. protera, and dwarf surf clams were not significantly affected by any environmental disturbance (all p > 0.05). The presence of at least a tropical storm (either a tropical storm or hurricane) was the only environmental model that significantly affected dark false mussels. In years that a tropical storm or hurricane occurred, dark false mussels declined by -95.6 \pm 44.0 individuals (p < 0.05). However, this significance was lost when only accounting for hurricanes or major hurricanes in the model (p > 0.05).

Table 3.1. Rangia estimates \pm SE in the same year as a hurricane and in the year following a hurricane from 1996–2017.

	Year of Hurri	cane	Year After Hurricane		
	Estimate ± SE	р	Estimate ± SE	р	
Rangia 0 to <6 mm	-108.22 ± 62.17	0.097	240.162 ± 73.90	0.005	
Rangia ≥6 mm to <11 mm	-189.78 ± 87.71	0.043	319.34 ± 90.69	0.003	
Rangia ≥11 mm to <16 mm	-46.18 ± 24.14	0.070	68.58 ± 27.22	0.024	
	$-357.37 \pm$				
Rangia	164.58	0.042	635.08 ± 176.06	0.003	

Over the short-term interval (1996–2017), scaup abundance on Lake Pontchartrain was affected by environmental disturbances. The model that included the presence of a hurricane provided the best fit to the data (Table 3.2); scaup numbers declined in the same year as a hurricane but increased in the year after a hurricane (both p < 0.05) (Table 3.3). While lagged environmental models were a poorer fit to the data, scaup numbers still significantly increased by $229,331 \pm 100,603$ individuals in the year immediately after a tropical storm/hurricane (p < 0.05). The lag effects from the presence of a hurricane and a tropical storm/hurricane were

limited to the immediate year following a hurricane. Major hurricanes and spillway openings did not significantly impact scaup abundances immediately or in subsequent years (all p > 0.05).

Table 3.2. Model selection table for environmental factors impacting scaup abundances on Lake Pontchartrain from 1996–2017.

Model	K	-2LL	AIC c	Δ AIC $_{c}$	Wi
Hurricane	3	-293.767	594.9	0.00	0.656
TS/Hurricane	3	-295.176	597.7	2.82	0.160
Major Hurricane	3	-295.434	598.2	3.34	0.124
Spillway	3	-296.266	599.9	5.00	0.054
TS/Hurricane Lag Effects	6	-293.345	604.3	9.42	0.006
Hurricane Lag Effects	8	-290.516	608.1	13.24	0.001

Scaup population responses to environmental disturbances were also detected over my long-term time period (1977–2017). Again, including the presence of a hurricane was the best supported model (Table 3.4). Scaup numbers declined in the same year as a hurricane but increased in the year after a hurricane (both p < 0.01) (Table 3.3). Though not detected in the short-term interval, the presence of a tropical storm/hurricane resulted in a significant decrease in scaup numbers during the same year as the disturbance in our long-term time period (p < 0.05). Scaup numbers increased in the year immediately after the presence of a tropical storm/hurricane (p < 0.05). As in the short-term interval, major hurricanes and spillway openings did not affect scaup populations in the long-term time period (all p > 0.05).

Table 3.3. Scaup estimates \pm SE in response to hurricanes and tropical storms/hurricanes from 1996–2017 and from 1977–2017.

	Short-term Interval (1996-2017)	Long-term Interval (1977-2017)		
	Scaup ± SE	Scaup ± SE		
Year of Hurricane	$-178,870 \pm 76,503$	$-144,496 \pm 51,003$		
Year of Tropical Storm/Hurricane	$-113,115 \pm 72,954$	$-109,374 \pm 49,055$		
Year After Hurricane	297,720 ± 102,753	$203,990 \pm 66,998$		
Year After Tropical Storm/Hurricane	229,331 ± 100,603	$167,522 \pm 66,264$		

Table 3.4. Model selection table for environmental factors impacting scaup abundances on Lake Pontchartrain from 1977–2017.

Model	K	-2LL	AICc	ΔAICc	Wi
Hurricane	3	-503.866	1014.4	0.00	0.722
TS/Hurricane	3	-505.232	1017.2	2.73	0.184
Major Hurricane	3	-506.256	1019.2	4.78	0.066
Spillway	3	-507.537	1021.8	7.34	0.018
Hurricane Lag Effects	8	-501.448	1023.9	9.42	0.006
TS/Hurricane Lag Effects	7	-503.896	1025.5	11.09	0.003

3.4 Discussion

3.4.1 Scaup Population Responses to Prey Availability

Food availability significantly impacted scaup populations on Lake Pontchartrain.

Rangia, particularly the ≥11 mm to <16 mm size class, seems to be particularly important indicators of scaup populations on Lake Pontchartrain. Scaup diet composition results from Chapter 2 showed that the ≥11 mm to <16 mm size class accounted for the largest percentage of rangia dry weight consumption. Selection index values also indicate that scaup preferred rangia in the ≥11 mm to <16 mm size class relative to availability. Therefore, the ≥11 mm to <16 mm

of rangia should be viewed as the primary food source driving scaup abundances on Lake Pontchartrain.

Scaup numbers marginally increased with increasing dwarf surf clam abundance. Based on these results, it seems likely that the low amount of dwarf surf clams represented in scaup diets in the winter of 2016–2017 was a product of extremely low densities that year. Given that dwarf surf clams were highly preferred relative to their availability in my study and the species is known to an important scaup food source in other areas of Louisiana (Harmon 1962), significant increases in scaup estimates in years that dwarf surf clams are abundant provides further evidence that the species is an important food source for scaup on Lake Pontchartrain.

Rangia in the \geq 16 mm to <21 mm size class was also an important predictor of scaup populations. Scaup abundances declined as the quantity of rangia in the \geq 16 mm to <21 mm size class increased. Scaup and other diving ducks have been documented to consume small- or intermediate- size classes of clams over larger ones, possibly as in response to different handling times, effects of meat-to-shell ratios on nutrients digested relative to passage rate, and risk avoidance of very large prey (Draulans 1982, Bustnes and Erikstad 1990, de Leeuw and van Eerden 1992, Bustnes 1998, Hamilton et al. 1999, Richman and Lovvorn 2004). My results from Chapter 2 are consistent with other research indicating that clams \geq 16 mm long are not important food sources for scaup (Custer and Custer 1996, Richman and Lovvorn 2004). Therefore, once rangia reach lengths \geq 16 mm, they are likely no longer profitable for scaup to consume, and thus, are avoided. This avoidance, usually in combination with environmental disturbance, leads to declines of scaup numbers on Lake Pontchartrain when clams \geq 16 mm to <21 mm dominate the rangia population.

Although scaup numbers were not correlated with abundances of dark false mussels or the two smallest size classes of rangia (0 to <6 mm and ≥6 mm to <11 mm), these results should be viewed with caution. Dark false mussels accounted for sizable percentages of both the total number and dry weight consumed by scaup on Lake Pontchartrain (see Chapter 2). Because dark false mussels attach to hard surfaces, such as rocks, artificial reefs, walls, or pilings (Oliver et al. 1998, Bamber and Taylor 2002), it is likely that the species is much more prevalent than indicated through the traditional benthic dredge surveys. This probable under-representation could explain why scaup populations were not significantly affected by abundances of dark false mussels. Rangia in the 0 to <6 mm and ≥6 mm to <11 mm size classes accounted for a large percentage of the total quantity of food items ingested (Chapter 2). Both size classes were also preferred by scaup relative to availability. Therefore, dark false mussels and the two smallest size classes of rangia are clearly important food sources used by scaup on Lake Pontchartrain.

3.4.2 Prey Species and Scaup Responses to Environmental Disturbances

Although hurricane effects can differ based on storm track and the coastal morphology where landfall occurs (Chen et al. 2008), hurricanes often result in increased salinity, salinity stratification, and low dissolved oxygen on Lake Pontchartrain (Poirrier et al. 2008, Poirrier et al. 2013, Poirrier and Caputo 2015). Storm surges and wave energy from hurricanes causes bottom sediments to be disturbed (Flocks et al. 2009). Sediment disturbance can cause rangia to be displaced and buried beneath the sediment; after Hurricanes Katrina and Isaac, dead rangia were commonly found on Lake Pontchartrain, apparently dying from the direct effects of these storms (Poirrier et al. 2008, Poirrier et al. 2013).

Several studies have shown the negative impacts of hurricanes on rangia populations on Lake Pontchartrain, though most focused on clams too large for scaup to consume. However, Poirrier and Caputo (2015) found rangia between 6-20 mm declined in the same year as a hurricane. I also detected significant declines in rangia <21 mm long in the same year that a hurricane occurred, though the ≥6 mm to <11 mm size class accounted for most of this decline. Scaup populations also declined in the same year as a hurricane. Given my results that scaup populations are highly dependent on the abundance of rangia (particularly the medium-size classes), scaup declines in the year of a hurricane are presumably driven by declines in rangia abundance.

However, hurricanes can also lead to increased reproduction of rangia in increase prey availability for scaup the following year. Cain (1975) showed that rangia spawn in response to changes in salinity shifts of ± 5 ppt at temperatures above 15°C. Given rangia growth rates on the estuary have been reported to be 20 mm in the first year of life (Fairbanks 1963), salinity shifts following major storms likely lead to increased abundances of clams <21 mm in the subsequent year. Indeed, I detected significant increases in the abundance of all rangia size classes <21 mm in the year immediately after a hurricane, in accordance with results from Poirrier and Caputo (2015). In response to rangia increases, scaup populations also increased in the year immediately after a hurricane, suggesting hurricanes create a lagged, bottom-up trophic cascade on Lake Pontchartrain. Given that populations of rangia and scaup have similar responses to hurricanes, coupled with the fact that scaup estimates are significantly influenced by rangia abundances, I propose that rangia populations, particularly the medium-size classes, seem to be the most important proximate drivers of scaup numbers on the estuary.

3.4.3 Future Implications

The frequency of future tropical cyclones in the twenty-first century is predicted to decline in the Atlantic basin (Bender et al. 2010, Knutson et al. 2013, 2015). Colbert et al. (2013) also predicted a decrease in westward tracks and an increase in recurving tracks, suggesting a decrease in rates of North American landfall, independent of overall changes in tropical cyclone frequency. However, despite a decline in frequency, the average intensity (which is determined by a storm's wind speed using the Saffir-Simpson Hurricane Scale), storm size, and rainfall for tropical cyclones are predicted to increase (Bender et al. 2010, Knutson et al. 2013, 2015). Storm surge is also predicted to increase, partly in response to rising sea levels (Lin et al. 2012, Woodruff et al. 2013, Knutson et al. 2015). An obvious question is, how will changes to hurricane frequency and intensity affect the benthic community, and ultimately scaup populations, on Lake Pontchartrain?

While forecasts predict that tropical cyclones may impact Lake Pontchartrain less frequently, increases in intensity could have more severe impacts to rangia, and consequently scaup populations, when a tropical cyclone does strike. For example, because storm surge leads to rangia mortality by burial in the sediment (Poirrier et al. 2008, Poirrier et al. 2013), it seems likely that increases in storm surge could cause higher mortality rates to rangia. Compared to previous tropical cyclones, increases in storm surge would likely result in more severe salinity stratification and lower dissolved oxygen in a larger portion of the estuary. Consequently, the area with hypoxic and anoxic conditions following hurricanes would be expected to increase, limiting rangia populations in those areas. Barrier islands and wetlands along southeastern Louisiana are being lost at a significant rate because of sea level rise and subsidence (Penland et al. 2001, Couvillion et al. 2011). The continued loss of these islands and wetlands, which serve

as buffers from tropical cyclones, will likely further exacerbate the effects of storm events on rangia populations. Thus, it seems likely that rangia declines immediately after a hurricane will be more pronounced in the future. Tracking rangia abundances, scaup populations would likely also exhibit greater immediate declines in response to future hurricanes.

Although my results show that rangia populations increase in the year after a hurricane, there may be a tipping point in which future conditions prevent rangia abundances from rebounding. Poirrier and Caputo (2015) suggested that rising sea levels, barrier island loss, wetland loss, and possible enlargement of tidal passes (Li et al. 2009) could soon create environmental conditions in which rangia populations on Lake Pontchartrain are unable to recover following a hurricane. A lack of recovery for rangia populations could have devastating consequences to scaup populations on Lake Pontchartrain. However, Poirrier and Caputo (2015) also suggested that the benthic community could shift towards higher salinity species, such as the hooked mussel. Possible declines in rangia populations could be offset as hooked mussels and other higher salinity mollusks could serve as alternate food sources for scaup, though the impacts to scaup body conditions and lipid reserves following this hypothetical diet shift is uncertain. Regardless, projected environmental conditions and increases in tropical cyclone intensity will likely decrease rangia populations, which could ultimately have negative impacts on scaup populations on Lake Pontchartrain.

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CHAPTER 4. SUMMARIES AND CONCLUSIONS

My diet analyses confirm that mollusks are the primary food source for scaup wintering on Lake Pontchartrain. These results add to the extensive literature documenting mollusks as a vital component of wintering scaup diets (Harmon 1962, Perry and Uhler 1982, Hoppe et al. 1986, Custer and Custer 1996, Richman and Lovvorn 2004). Consistent with Custer and Custer (1996) and Richman and Lovvorn (2004), I also found that scaup consumed mollusks based on species and size.

Rangia, particularly medium-size classes (≥ 6 mm to ≤ 11 mm and ≥ 11 mm to ≤ 16 mm), seem to be the most important food sources for scaup on Lake Pontchartrain. Diet analyses revealed that these two size classes combined to represent 71% of the total quantity and 91% of the aggregate dry weight of rangia consumed by scaup during the winter of 2016–2017. Selection indices also indicated that scaup preferred both size classes relative to their availability during our study. The importance of the medium-size classes is best demonstrated by their representation of nearly one-third of the total number of food items eaten and over half the aggregate dry weight consumed. My analyses also reveal that scaup estimates were highly correlated with abundances of the ≥11 mm to <16 mm size class of rangia; scaup populations significantly increased as medium-size classes of rangia increased. Abundances of both scaup and rangia in the >6 mm to <11 mm size class substantially declined in the year of a hurricane, indicating that scaup populations are likely driven by declines in this size class when a hurricane strikes. Therefore, my results suggest that the ≥ 6 mm to < 11 mm and the ≥ 11 mm to < 16 mm size classes of rangia are the primary drivers of scaup populations on Lake Pontchartrain (Figure 4.1).

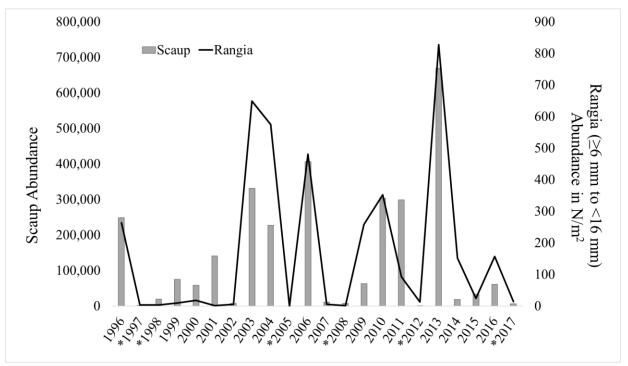


Figure 4.1. Lesser scaup (*Aythya affinis*) and medium-sized (≥6 mm to <16 mm) rangia (*Rangia cuneata*) abundances on Lake Pontchartrain, Louisiana, USA from 1996–2017 (* denotes years that a hurricane made landfall within 150 km from the center of Lake Pontchartrain).

Other prey sources, namely dwarf surf clams and rangia in the ≥11 mm to <16 mm size class, also significantly affected scaup populations on Lake Pontchartrain; however, these two prey sources affected scaup very differently. Scaup numbers marginally increased with increasing abundances of dwarf surf clams. Dwarf surf clams are known to an important scaup food source in other areas of Louisiana (Harmon 1962). Moreover, I found that dwarf surf clams were highly preferred by scaup relative to their availability in the winter of 2016–2017. Thus, it seems that extremely low densities (<10 individuals/m²) were the reason that dwarf surf clams represented only a small component of scaup diets in my study.

Scaup abundance declined as the abundance of rangia in the ≥16 mm to <21 mm size class increased. Scaup and other diving ducks have been documented to consume small- or intermediate- size classes of clams over larger ones, possibly as in response to different handling

times, effects of meat to shell ratios on nutrients digested relative to passage rate, and risk avoidance of very large prey (Draulans 1982, Bustnes and Erikstad 1990, de Leeuw and van Eerden 1992, Bustnes 1998, Hamilton et al. 1999, Richman and Lovvorn 2004). Our results from Chapter 2 are consistent with other research indicating that clams ≥ 16 mm long are not important food sources for scaup (Custer and Custer 1996, Richman and Lovvorn 2004). Therefore, once rangia reach lengths ≥ 16 mm, they are likely no longer profitable for scaup to consume, and thus, are avoided. Moreover, because these larger classes are more likely to persist in the year of a hurricane, this manifests as a decline of scaup populations on Lake Pontchartrain when the clams ≥ 16 mm dominate the rangia population.

Dark false mussels were an important food source for scaup during my study, accounting for 25.5% of total number of food items and 36.8% of the total dry weight ingested. Although scaup populations were not significantly influenced by the abundance of dark false mussels, these results may not be entirely accurate because dark false mussels are likely under-represented in the benthic dredge surveys. Dark false mussels attach to hard surfaces, such as rocks, artificial reefs, walls, or pilings (Oliver et al. 1998, Bamber and Taylor 2002). With bridge pilings, a seawall along the southern portion of the lake, and other artificial structures found throughout the lake, it is likely that dark false mussels are much more prevalent than indicated through the traditional benthic dredge surveys. Although it is not apparent if scaup populations are influenced by the abundance of dark false mussels, it is clear that dark false mussels are an important food source for scaup on Lake Pontchartrain, as evidenced by my diet analyses and Bowman (1973).

My results revealed that hurricanes significantly affected rangia populations in the same year that a hurricane occurred and in the subsequent year, though these effects are distinctly

different. In the year of a hurricane, rangia abundances drastically declined, with the ≥6 mm to <11 mm size class accounting for most of this decline. Rangia declines following a hurricane can be caused by both direct and indirect effects (Poirrier et al. 2008, Engle et al. 2009, Ray 2009, Poirrier and Caputo 2015). Regardless of the underlying mechanisms, rangia declines in the year of a hurricane appear to create a cascading food-web effect, with scaup populations declining by well over 100,000 individuals in those same years. Hurricanes also resulted in increased abundances of both rangia and scaup in the year immediately after a hurricane. Hurricanes can cause salinity shifts required by rangia to spawn. Rangia spawning events following these hurricane-induced salinity shifts result in increased abundances of clams <16 mm long. These spawning events cause a lagged, bottom-up trophic cascade, with increased abundances of rangia leading to increased scaup numbers on the estuary in the year following a hurricane. Given that populations of rangia and scaup have similar responses to hurricanes, coupled with the fact that scaup estimates are significantly influenced by rangia abundances, I conclude that rangia populations, particularly the medium-size classes, seem to be the most important proximate drivers of scaup numbers on the estuary.

In the face of changing environmental conditions and more intense tropical cyclones, responses by rangia populations are likely to also change. Rangia are likely to exhibit even greater declines in the same year as future hurricanes, causing scaup declines to be more pronounced. Moreover, rangia populations may reach a tipping point that populations are unable to recover following a hurricane. A lack of recovery for rangia populations could have devastating consequences to scaup populations on Lake Pontchartrain. Possible declines in rangia populations could be offset as hooked mussels and other higher salinity mollusks could serve as alternate food sources for scaup, though the impacts to scaup body conditions and lipid

reserves following this hypothetical diet shift is uncertain. Regardless, projected environmental conditions and increases in tropical cyclone intensity will likely decrease rangia populations, which could ultimately have negative impacts on scaup populations on Lake Pontchartrain.

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APPENDIX. MODEL SELECTION TABLES

Table A.1. Model selection table for environmental factors impacting Rangia 0 to <6 mm on Lake Pontchartrain 1996–2017.

Model	K	-2LL	AIC c	Δ AIC $_{c}$	Wi
Hurricane	3	-137.231	281.8	0.00	0.408
TS/Hurricane	3	-137.620	282.6	0.78	0.277
Major Hurricane	3	-138.325	284.0	2.19	0.137
Spillway	3	-138.675	284.7	2.89	0.096
TS/Hurricane Lag Effects	6	-133.803	285.2	3.41	0.074
Hurricane Lag Effects	8	-131.295	289.7	7.87	0.008

Table A.2. Model selection table for environmental factors impacting Rangia ≥6 mm to <11 mm on Lake Pontchartrain 1996–2017.

Model	K	-2LL	AICc	ΔAICc	Wi
Hurricane	3	-144.804	296.9	0.00	0.494
Hurricane Lag Effects	8	-135.799	298.7	1.73	0.208
Major Hurricane	3	-146.148	299.6	2.69	0.129
Spillway	3	-146.528	300.4	3.45	0.088
TS/Hurricane	3	-146.666	300.7	3.72	0.077
TS/Hurricane Lag Effects	6	-144.484	306.6	9.63	0.004

Table A.3. Model selection table for environmental factors impacting Rangia ≥11 mm to <16 mm on Lake Pontchartrain 1996–2017.

Model	K	-2LL	AIC c	Δ AIC $_{c}$	Wi
Hurricane	3	-116.421	240.2	0.00	0.548
Major Hurricane	3	-117.512	242.4	2.18	0.184
Spillway	3	-117.914	243.2	2.99	0.123
TS/Hurricane	3	-118.041	243.4	3.24	0.108
Hurricane Lag Effects	8	-109.318	245.7	5.54	0.034
TS/Hurricane Lag Effects	6	-116.813	251.2	11.05	0.002

Table A.4. Model selection table for environmental factors impacting all Rangia <21 mm on Lake Pontchartrain 1996–2017.

Model	K	-2LL	AICc	ΔAICc	Wi
Hurricane	3	-158.649	324.6	0.00	0.564
Major Hurricane	3	-160.11	327.6	2.92	0.131
Hurricane Lag Effects	8	-150.392	327.9	3.23	0.112
TS/Hurricane	3	-160.325	328.0	3.35	0.105
Spillway	3	-160.614	328.6	3.93	0.079
TS/Hurricane Lag Effects	6	-157.722	333.0	8.41	0.008

VITA

Clay Michael Stroud, born in Jesup, Georgia in 1990, graduated from the Warnell School of Forestry and Natural Resources at the University of Georgia in December 2013 with a Bachelor of Science in Forest Resources (Fisheries and Wildlife Major – Wildlife Sciences Area of Concentration). He worked nearly two years at Fort Stewart Army Installation before heading to the School of Renewable Natural Resources at Louisiana State University. Following graduation, Clay plans to transition from a Pathways intern to a full-time employee with Wildlife Services in the United States Department of Agriculture's Animal and Plant Health Inspection Service.