

THE FLORIDA STATE UNIVERSITY

COLLEGE OF ARTS AND SCIENCES

ECOLOGICAL RELATIONSHIPS OF TURTLES IN NORTHERN FLORIDA LAKES: A
STUDY OF OMNIVORY AND THE STRUCTURE OF A LAKE FOOD WEB

By

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A Dissertation submitted to the
Department of Biological Science
in partial fulfillment of the
requirements for the degree of
Doctor of Philosophy

Degree Awarded:
Spring Semester, 2005

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For my parents,
Salvatore and Barbara Aresco
and
my grandparents,
Joseph and Dorothy DiMauro

ACKNOWLEDGMENTS

I thank the following for providing access to study ponds and lakes: Michael Hill and Chuck Goodheart – Lake Piney Z; Jeff Phipps - Orchard Pond; Tall Timbers Research Station – Lake Iamonia and Gannett Pond; Curtis Watkins and the City of Tallahassee – Chapman Pond, McCord Pond, and Waverly Pond; Max Gunzburger and Janet Peterson – Lake Tom John; Apalachicola National Forest – Trout Pond, Clear Lake, Moore Lake, Andrew Lake, and Lofton Ponds. I also especially thank Jim Cox and Todd Engstrom of the Tall Timbers Research Station for allowing me to conduct the experiment in Gannett Pond. I thank Dean Hansen, Mike Brezin, and Bob Walker who helped collect turtles at McCord Pond. Mark Endries provided instruction and help with GIS. I thank Alice Winn for the generous use of her microbalance and Anna Deyle and Kristin Dormsjo for helping with sample preparation for stable isotope analysis. I thank Marcel Holyoak for first suggesting the method of stable isotope analyses for this study and Whit Gibbons and Chris Romanek for providing helpful discussions regarding this research. Tyler Macmillan of the Northwest Florida Water Management District always provided help with my work at Lake Jackson and we have become good friends as a result. I thank Dale Jackson for being a friend and mentor and for always providing his expertise and good lively discussion on my research ideas and on the natural history of turtles in north Florida. Dale and his wife Ghislaine Guyot also helped with the Lake Jackson Ecopassage project.

I thank the Florida Fish and Wildlife Conservation Commission for providing funding for this research under a Nongame Wildlife Program contract (Project Number NG01-011), especially David Cook and Michael Evans.

I thank the James and Travis labs for all of their advice and support, especially Eric Walters, Julie Jo Walters, Matt Schrader, Paul Richards, Chuck Hess, Becky Fuller, Becca Hale, Katie McGhee, Jeff Birdsley, and Brian Storz. I especially thank my good friend Eric Walters who helped me in many ways throughout my time at FSU, not only giving help, support, and advice with my research but also with the Lake Jackson Ecopassage project. Eric and Julie Jo Walters monitored my drift fences and collected road-killed animals on U.S. 27 at Lake Jackson several times in my absence.

I thank my committee for all of their help and support. Tom Miller really peaked my interest and knowledge of community ecology early on in his Community Ecology course. This is where some of my first ideas about omnivory were formulated. He also challenged my ideas about omnivory with his preliminary exam questions. I especially thank Joe Travis for his advice and time spent discussing, not only my research, but also baseball, local politics, and conservation issues. Joe supported me on a Research Assistantship for four years that allowed me the time to accomplish both my dissertation research and the Lake Jackson Ecopassage project. Joe was a great mentor and friend to me. I will always remember our days out sampling *Heterandria* as some of the best times I had at FSU.

I really thank Fran for being a great major professor and for always being there for me since bringing me into her bird lab as turtle biologist. I also appreciate her support of my conservation work and the Lake Jackson Ecopassage, although at times I am sure it seemed like those projects were taking time away from my dissertation work. Fran taught me a lot about the right way to do conservation biology and I certainly feel honored to be her last student. When I came to FSU, I was just a herpetologist but Fran helped to make me into an ecologist and conservation biologist.

I especially thank my parents, grandparents, and two brothers for their support of my chosen field. They may not have always understood exactly what I was doing in my research, but they understood how important it was to me. Since I was a very young boy learning about nature in the rolling hills and woods of central Connecticut, my parents always encouraged and cultivated my passion for natural history, biology, and studying reptiles and amphibians. They put me on a path at an early age that allowed me to end up where I am today and, for that, I am grateful.

Lastly, I want to thank Margaret Gunzburger. She is my best friend and without her caring and unwavering support, I know that this accomplishment would not have been possible. Margaret always provided advice on my research and helped me to better express my ideas. She has been with me through everything I have done over the last 8 years and am very glad that she is still with me today.

TABLE OF CONTENTS

List of Tables	vii
List of Figures	x
Abstract	xv
INTRODUCTION	1
1. ENVIRONMENTAL CORRELATES OF THE ABUNDANCES OF THREE SPECIES OF TURTLES IN LAKES IN NORTHERN FLORIDA	7
2. OMNIVORY AND COMPETITION BETWEEN TWO FRESHWATER TURTLES	52
3. TROPHIC STRUCTURE AND SOURCES OF PRIMARY PRODUCTION IN A NORTHERN FLORIDA LAKE	70
CONCLUSION	121
REFERENCES	126
BIOGRAPHICAL SKETCH	141

LIST OF TABLES

Table 1.1: Summary data of lake area, primary substrate, and primary productivity as measured by open water nutrients and chlorophyll <i>a</i> , periphyton, and macrophyte biomass and percent area covered by macrophytes (PAC) for 17 study lakes in Leon County, northern Florida. Environmental variables were measured at each lake between May and September 2003. The lakes are ordered by size.	25
Table 1.2: Environmental variables (and abbreviations) measured at 17 lakes in Leon County, Florida between May and September 2003.	27
Table 1.3: Catch per unit effort (CPUE) (no./day) of turtles trapped at lakes and ponds in Leon County, Florida, 2002-2003. At each lake two unbaited hoop traps and 30-m lead nets were set at each site for a total of 192 trap hours per lake (8 trap days). Numbers in parentheses are actual numbers of turtles trapped.	28
Table 1.4: Comparison of relative abundance of 3 turtle species captured in Leon County, Florida by trapping during a 5-day period with 2 unbaited hoop traps and 30-m lead nets (“Trapped”) vs. overall relative abundance determined by hand-capture, trapping, and mechanical excavation (“Actual” Full Count) at 3 ponds during complete drawdown and sediment removal (Waverly Pond, March 2004; Chapman Pond, September 2003; McCord Pond, October 1999 - March 2000).	29
Table 1.5: Summary data of secondary productivity as measured by abundance (no./1.25 m ²) of littoral zone macroinvertebrates (excluding snails and chironomids), fish, snails, and chironomids for 17 study lakes in Leon County, northern Florida. The abundance of macrofauna was determined from May to September 2003 using a 0.25-m ² aluminum box sampler at 5 haphazard locations in the littoral zone of each lake where turtles typically forage (water depth 0.4 -1 m).	30
Table 1.6: Spearman rank correlations (r_s) among 14 continuous environmental variables measured at 17 lakes in Leon County, Florida. The critical correlation coefficient was corrected for simultaneous tests and significant correlations ($r_s > 0.538$) are indicated in bold.	32
Table 1.7: Component loadings from principal components analysis performed on 6 environmental variables from 17 lakes. Percentages below axis number represent the proportion of the total variance associated with that axis. Eigenvalues are shown in parentheses.	34
Table 1.8: Pearson correlations (r) of DF 1 scores (from a discriminant function analysis of physiographic region and 6 environmental variables) and the original 6 environmental variables. An asterisk indicates a significant correlation at $P < 0.05$	35

Table 1.9: Pearson correlations (<i>r</i>) of DF 1 and DF 2 scores (from a discriminant function analysis of substrate type and 6 environmental variables) and the original 6 environmental variables. An asterisk indicates a significant correlation at $P < 0.05$	36
Table 1.10: Results of Mantel tests on comparisons of distance matrices of abundances of three species of turtles and environmental variables at 17 lakes in Leon Co., Florida.	37
Table 1.11: Results of a Mantel test on distance matrices of total turtle abundance and environmental variables at 17 lakes in Leon Co., Florida.	38
Table 2.1: Summary statistics among 4 treatments in a 13-month field experiment designed to test equivalence of interspecific and intraspecific competition between juveniles of <i>Trachemys scripta</i> and <i>Pseudemys floridana</i> . The experiment was conducted from 11 July 2002 to 3 August 2003 at Gannett Pond, a 21-ha lake, Leon County, Florida. Data reported are mean growth rate (mm/yr), mean number of insects in gut contents at final sampling, and mean percent of turtles with algae in gut contents at final sampling. Sample size indicates the number of replicates of each treatment and SD is indicated in parentheses.	65
Table 3.1: Baseline $\delta^{15}\text{N}$ values to estimate trophic position of vertebrates at Lake Jackson (LJ = Lake Jackson, LLJ = Little Lake Jackson). Macroalgae was collected during November 2001 – June 2004 ($n = 29$) at northwestern Lake Jackson and during October 2001– August 2003 ($n = 17$) at Little Lake Jackson. Algae samples were collected from mats in the littoral zone, from stems of maidencane grass and water lilies (periphyton), and from shells of live turtles (green algae, <i>Bacillaria</i> sp.). Unionid clams ($n = 3$) were collected from Porter Sink at Lake Jackson on 14 February 2003.	93
Table 3.2: Mean (\pm SE) $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isotope values ($^0/_{00}$) for primary producers, invertebrates, fish, reptiles, amphibians, birds, and mammals collected at Lake Jackson, Leon County, in northwestern Florida.	94
Table 3.3: Percentage of 42 animal taxa with 95% confidence intervals of mean $\delta^{13}\text{C}$ isotope values within confidence intervals of each category of basal resources in the Lake Jackson food web, Leon County, Florida.	101
Table 3.4: Frequency of occurrence of diet items in gut contents of fish ($n = 83$) collected at Porter Sink, Lake Jackson, Leon County, Florida on 20 December 2002 and 14 February 2003. All fish were collected by dip-net as water flowed into the sinkhole.	102
Table 3.5: Mean (\pm SE) trophic position of reptiles and amphibians in the Lake Jackson food web, Leon County, Florida. Isotope samples were obtained from muscle of road-killed individuals on U.S. Highway 27 bisecting Lake Jackson, dead individuals recovered during a dredging operation, and claw clips of live individuals. Trophic position of turtles, snakes, alligators, and frogs was calculated relative to the baseline $\delta^{15}\text{N}$ value with the equation $\text{TP} = ((\delta^{15}\text{N} - \delta^{15}\text{N}_{\text{baseline}}) / 2.3) + 1$, where TP is trophic position and $2.3^0/_{00}$ is the mean enrichment of $\delta^{15}\text{N}$ between trophic levels as determined in the laboratory experiment. Trophic position of sirens and amphiumas was estimated relative to the baseline $\delta^{15}\text{N}$ value with the equation $\text{TP} =$	

$((\delta^{15}\text{N} - \delta^{15}\text{N}_{\text{baseline}}) / 3.4) + 1$, where $3.4^{0/00}$ is the mean enrichment of $\delta^{15}\text{N}$ between trophic levels. For turtles, different letters denote significant differences between mean TP of adults of *P. floridana*, *T. scripta*, *A. ferox*, *S. odoratus*, and *C. serpentina* demonstrated with ANOVA and Bonferonni pairwise comparisons..... 103

Table 3.6: Percent occurrence of food items in the diet of juvenile ($n = 14$) and adult ($n = 36$) *Apalone ferox*, juvenile ($n = 18$) and adult ($n = 38$) *Trachemys scripta*, and juvenile ($n = 21$) and adult *Pseudemys floridana* ($n = 35$) at northwestern Lake Jackson and Little Lake Jackson, Leon County, Florida collected during March-October 2001-2003. Data from stomachs of road-killed individuals ($n = 15$) and fecal samples ($n = 97$) are combined, as there were no differences between these samples. Juvenile *Apalone ferox* were <120 mm plastron length and juvenile *Trachemys scripta* and *Pseudemys floridana* were < 100 mm plastron length. ... 105

LIST OF FIGURES

Figure 1.1: Location of 17 study lakes in Leon County, Florida. Dark line indicates separation of the Tallahassee Red Hills and Munson Sandhills physiographic regions. 1 = Coolview Pond, 2 = Chapman Pond, 3 = Waverly Pond, 4 = McCord Pond, 5 = Andrew Lake 6 = Trout Pond, 7 = Lake Tom John, 8 = Megginnis Arm, 9 = Clear Lake, 10 = Lofton Ponds, 11 = Gannett Pond, 12 = Little Lake Jackson, 13 = Moore Lake, 14 = Lake Piney Z, 15 = Orchard Pond, 16 = Lake Jackson, 17 = Lake Iamonia..... 39

Figure 1.2: Comparison of abundance (standardized to catch per unit effort [CPUE]) (no./day) of *Trachemys scripta*, *Pseudemys floridana*, and *Apalone ferox* trapped at 17 lakes and ponds in Leon County, Florida, 2002-2003. Two unbaited hoop traps and 30-m lead nets were set at each site for a total of 192 trap hours per lake (8 trap days). 40

Figure 1.3: Mean catch per unit effort (CPUE) of *Trachemys scripta*, *Pseudemys floridana*, and *Apalone ferox* in the Tallahassee Red Hills lakes ($n = 12$) and the Munson Sandhills lakes ($n = 5$) trapped in Leon County, Florida, 2002-2003. Two unbaited hoop traps and 30-m lead nets were set at each site for a total of 192 trap hours per lake (8 trap days). Error bars = 1 standard error. Different letters denote a significant difference in abundance between regions. 41

Figure 1.4: Mean catch per unit effort (CPUE) of *Trachemys scripta*, *Pseudemys floridana*, and *Apalone ferox* trapped in lakes with mud ($n = 4$), muck ($n = 8$), and sand substrates ($n = 5$) in Leon County, Florida, 2002-2003. Two unbaited hoop traps and 30-m lead nets were set at each site for a total of 192 trap hours per lake (8 trap days). Error bars = 1 standard error. Different letters denote a significant difference in abundance between substrates. 42

Figure 1.5. Plot of percent surface area covered by macrophytes (PAC) and periphyton productivity ($\text{g}/\text{m}^2/\text{y}$) at 17 lakes in Leon County in northern Florida. Numbers follow Fig. 1.1: 1 = Coolview Pond, 2 = Chapman Pond, 3 = Waverly Pond, 4 = McCord Pond, 5 = Andrew Lake 6 = Trout Pond, 7 = Lake Tom John, 8 = Megginnis Arm, 9 = Clear Lake, 10 = Lofton Ponds, 11 = Gannett Pond, 12 = Little Lake Jackson, 13 = Moore Lake, 14 = Lake Piney Z, 15 = Orchard Pond, 16 = Lake Jackson, 17 = Lake Iamonia. 43

Figure 1.6: Plot of the first and second principal components axes of environmental variables of 17 lakes in Leon County, northern Florida. Sizes of the circles indicate the abundance of *Trachemys scripta* at each lake. 44

Figure 1.7: Plot of the first and second principal components axes of environmental variables of 17 lakes in Leon County, northern Florida. Sizes of the circles indicate the abundance of *Pseudemys floridana* at each lake. 45

Figure 1.8: Plot of the first and second principal components axis of environmental variables of 17 lakes in Leon County, northern Florida. Sizes of the circles indicate the abundance of *Apalone ferox* at each lake. 46

Figure 1.9: Plot of the discriminant functions of three substrate types (mud, sand, and muck) at 17 lakes in Leon County, northern Florida. 47

Figure 1.10: Plot of Euclidean distances between 3 environmental variables and abundance of all three species for all pairwise comparisons of 17 lakes in Leon County, northern Florida. A significant correlation (Mantel r) between the abundance matrix and the environmental matrix demonstrates that lakes similar in abundance of turtles are similar in environmental characteristics. 48

Figure 1.11: Plot of Euclidean distances between 5 environmental variables and abundance of *Pseudemys floridana* for all pairwise comparisons of 17 lakes in Leon County, northern Florida. A significant correlation (Mantel r) between the abundance matrix and the environmental matrix demonstrates that lakes similar in abundance of turtles are similar in environmental characteristics. 49

Figure 1.12: Plot of Euclidean distances between 5 environmental variables and abundance of *Trachemys scripta* for all pairwise comparisons of 17 lakes in Leon County, northern Florida. A significant correlation (Mantel r) between the abundance matrix and the environmental matrix demonstrates that lakes similar in abundance of turtles are similar in environmental characteristics. 50

Figure 1.13: Plot of Euclidean distances between 5 environmental variables and abundance of *Apalone ferox* for all pairwise comparisons of 17 lakes in Leon County, northern Florida. A significant correlation (Mantel r) between the abundance matrix and the environmental matrix demonstrates that lakes similar in abundance of turtles are similar in environmental characteristics. 51

Figure 2.1: Location of Gannett Pond on Tall Timbers Research Station in northern Leon County, Florida where a 13-month field experiment was conducted to evaluate competitive interactions among juvenile *Trachemys scripta* and *Pseudemys floridana*. The location of 6 experimental blocks (3 cage treatments per block) is shown in the southwestern part of the pond. 66

Figure 2.2: Comparison of percent animal prey (*Belostoma lutarium*, libellulid odonate naiads, grass shrimp and fish carrion of *Heterandria formosa*), and duckweed eaten by hatchling *Trachemys scripta* and *Pseudemys floridana* in a laboratory experiment. The experiment was conducted in the laboratory in August 2001 in 55-L experimental containers (glass aquaria). Turtles were hatched from eggs collected in northern Florida and were not fed between hatching and the start of the experiment. Error bars equal ± 1 SD. 67

Figure 2.3: Differences in growth of *Trachemys scripta* and *Pseudemys floridana* among 4 treatments in a 13-month field experiment conducted from 11 July 2002 to 3 August 2003 at Gannett Pond, a 21-ha lake on Tall Timbers Research Station located near Lake Iamonia, Leon County, Florida. Mean growth (in plastron length) of *Trachemys scripta* in combination with

Pseudemys floridana was significantly greater than growth of *Trachemys scripta* under intraspecific competition ($P = 0.029$, $F = 5.98$, $df 1, 14$). 68

Figure 2.4: Differences in the number of insects found in fecal samples of *Trachemys scripta* and *Pseudemys floridana* among 4 treatments at the end of the field experiment ($P = 0.11$). The 13-month field experiment was conducted from 11 July 2002 to 3 August 2003 at Gannett Pond, a 21-ha lake on Tall Timbers Research Station located near Lake Iamonia, Leon County, Florida. 69

Figure 3.1: Study area at Lake Jackson, Leon County, Florida. 1 = Megginis Arm, 2 = Little Lake Jackson, 3 = Northwest Lake Jackson, 4 = Porter Sink. 106

Figure 3.2: Comparison of stable isotope values of claw and muscle tissue from *Trachemys scripta* ($n = 17$) and *Pseudemys floridana* ($n = 11$) collected from road-killed individuals on U.S. Highway 27 at Lake Jackson, Leon County, Florida (2001-2002). There were no significant differences between claw and muscle for $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ in either species. 107

Figure 3.3: Comparison of stable isotope values ($\delta^{15}\text{N}$ and $\delta^{13}\text{C}$) among wild ($n = 18$), captive ($n = 7$), and wild-captive (6 months) ($n = 3$) juvenile *Trachemys scripta* and commercial food (Wardleys™ TEN Reptile food sticks) ($n = 2$ aggregate samples of 20 sticks). Wild turtles were collected at Lake Jackson, Leon County, Florida and captives were hatched from eggs collected at the same location. Fractionation between food and captive turtles is 2.3 for $\delta^{15}\text{N}$ and 0.23 for $\delta^{13}\text{C}$. A diet switch from wild to captive diet required 6 months to be detected by a change in the $\delta^{15}\text{N}$ isotope and 12 months to be detected by a change in the $\delta^{13}\text{C}$ isotope. 108

Figure 3.4: Mean $\delta^{15}\text{N}$ vs. mean $\delta^{13}\text{C}$ (± 1 SE) of C3 macrophytes ($n = 30$), particulate organic matter (POM) ($n = 6$), and macroalgae ($n = 32$) from the littoral zone of northwestern Lake Jackson, Leon County, Florida. Floating, submerged, and emergent macrophytes were collected during February 2002 - August 2003. Macroalgae (periphyton and filamentous algae) were collected during November 2001 – June 2004. Particulate organic matter (POM), a mix of phytoplankton, macroalgae, and detritus, was collected during May - August 2003. 109

Figure 3.5: Mean $\delta^{15}\text{N}$ vs. mean $\delta^{13}\text{C}$ (± 1 SE) for primary consumers in the shallow littoral zone and pelagic zone at Lake Jackson, Leon County, Florida. Open water zooplankton ($n = 10$ aggregate) was collected at northwestern Lake Jackson using a 250-um zooplankton tow net during August 2002 – November 2003. Unionid clams (paper pondshell [*Utterbackia imbecillis*]) ($n = 3$) were collected at Porter Sink, Lake Jackson in December 2002 – February 2003. Snails (*Aminicola*), chironomids, amphipods, and tadpoles of *Rana sphenocephala* were collected by dipnet in 2002 and 2003. 110

Figure 3.6: Comparison of mean $\delta^{15}\text{N}$ vs. mean $\delta^{13}\text{C}$ (± 1 SE) (± 1 SE) of juvenile and adult *Trachemys scripta*, *Pseudemys floridana*, and *Apalone ferox*, and adult *Sternotherus odoratus* and *Chelydra serpentina* and C4 macrophytes, particulate organic matter (POM), and macroalgae from the littoral zone of Lake Jackson, Leon County, Florida. LLJ = samples were collected from Little Lake Jackson and LJ = samples were collected from northwest Lake Jackson and reflect stable isotope from these respective sites. 111

Figure 3.7: Mean stable isotope values (± 1 SE) of snakes, frogs, alligators, and aquatic salamanders at Lake Jackson, Leon County, Florida. Isotope samples were collected in 2001-2004 from muscle of road-killed individuals on U.S. Highway 27 bisecting Lake Jackson, dead individuals recovered during a dredging operation, and claw clips of live individuals. Trophic position of snakes, alligators, and frogs was calculated relative to the baseline $\delta^{15}\text{N}$ value with the equation $\text{TP} = ((\delta^{15}\text{N} - \delta^{15}\text{N}_{\text{baseline}}) / 2.3) + 1$, where TP is trophic position and $2.3^{0/00}$ is the mean enrichment of $\delta^{15}\text{N}$ between trophic levels as determined in the laboratory experiment. Trophic position of sirens and amphiumas was estimated relative to the baseline $\delta^{15}\text{N}$ value with the equation $\text{TP} = ((\delta^{15}\text{N} - \delta^{15}\text{N}_{\text{baseline}}) / 3.4) + 1$, where $3.4^{0/00}$ is the mean enrichment of $\delta^{15}\text{N}$ between trophic levels. 112

Figure 3.8: Trophic position (± 1 SE) of turtles at Lake Jackson, Leon County, Florida. Isotope samples were collected in 2001-2004 from muscle of road-killed individuals on U.S. Highway 27 bisecting Lake Jackson and claw clips of live individuals. Trophic position of turtles was calculated relative to the baseline $\delta^{15}\text{N}$ value with the equation $\text{TP} = ((\delta^{15}\text{N} - \delta^{15}\text{N}_{\text{baseline}}) / 2.3) + 1$, where TP is trophic position and $2.3^{0/00}$ is the mean enrichment of $\delta^{15}\text{N}$ between trophic levels as determined in the laboratory experiment. 113

Figure 3.9: Trophic position vs. plastron length of *Pseudemys floridana*. Mean trophic position of adults and juveniles is 2.3 (SE = 0.06) at Lake Jackson, Leon County, Florida. Isotope samples were collected in 2001-2004 from muscle of road-killed individuals on U.S. Highway 27 bisecting Lake Jackson and claw clips of live individuals. Trophic position of turtles was calculated relative to the baseline $\delta^{15}\text{N}$ value with the equation $\text{TP} = ((\delta^{15}\text{N} - \delta^{15}\text{N}_{\text{baseline}}) / 2.3) + 1$, where TP is trophic position and $2.3^{0/00}$ is the mean enrichment of $\delta^{15}\text{N}$ between trophic levels as determined in the laboratory experiment. Dashed lines denote theoretical TP of a strict “Primary Consumer”(TP = 2.0), “Secondary Consumer” (TP = 3.0), and “Tertiary Consumer” (TP = 4.0). 114

Figure 3.10: Trophic position vs. plastron length of *Trachemys scripta* at Lake Jackson, Leon County, Florida. Isotope samples were collected in 2001-2004 from muscle of road-killed individuals on U.S. Highway 27 bisecting Lake Jackson and claw clips of live individuals. Trophic position of turtles was calculated relative to the baseline $\delta^{15}\text{N}$ value with the equation $\text{TP} = ((\delta^{15}\text{N} - \delta^{15}\text{N}_{\text{baseline}}) / 2.3) + 1$, where TP is trophic position and $2.3^{0/00}$ is the mean enrichment of $\delta^{15}\text{N}$ between trophic levels as determined in the laboratory experiment. Dashed lines denote theoretical TP of a strict “Primary Consumer”(TP = 2.0), “Secondary Consumer” (TP = 3.0), and “Tertiary Consumer” (TP = 4.0). 115

Figure 3.11: Trophic position vs. plastron length of *Apalone ferox* at Lake Jackson, Leon County, Florida. Mean trophic position of adults and juveniles is 3.6 (SE = 0.09). Isotope samples were collected in 2001-2004 from muscle of road-killed individuals on U.S. Highway 27 bisecting Lake Jackson and claw clips of live individuals. Trophic position of turtles was calculated relative to the baseline $\delta^{15}\text{N}$ value with the equation $\text{TP} = ((\delta^{15}\text{N} - \delta^{15}\text{N}_{\text{baseline}}) / 2.3) + 1$, where TP is trophic position and $2.3^{0/00}$ is the mean enrichment of $\delta^{15}\text{N}$ between trophic levels as determined in the laboratory experiment. Dashed lines denote theoretical TP of a strict “Primary

Consumer”(TP = 2.0), “Secondary Consumer” (TP = 3.0), and “Tertiary Consumer” (TP = 4.0).
 116

Figure 3.12: Combined plot of trophic position vs. plastron length of all three species with 75% confidence ellipses. Isotope samples were collected in 2001-2004 from muscle of road-killed individuals on U.S. Highway 27 bisecting Lake Jackson and claw clips of live individuals. Trophic position of turtles was calculated relative to the baseline $\delta^{15}\text{N}$ value with the equation $\text{TP} = ((\delta^{15}\text{N} - \delta^{15}\text{N}_{\text{baseline}}) / 2.3) + 1$, where TP is trophic position and $2.3^{0/00}$ is the mean enrichment of $\delta^{15}\text{N}$ between trophic levels as determined in the laboratory experiment. Dashed lines denote theoretical TP of a strict “Primary Consumer”(TP = 2.0), “Secondary Consumer” (TP = 3.0), and “Tertiary Consumer” (TP = 4.0).
 117

Figure 3.13: Mean stable isotope values (± 1 SE) of fish at Lake Jackson, Leon County, Florida. Fish were collected at Porter Sink, Lake Jackson on 20 December 2002 and 14 February 2003 and in the shallow, littoral zone of northwestern Lake Jackson during May to August 2002-2003.
 118

Figure 3.14: Trophic position (± 1 SE) of fish at Lake Jackson, Leon County, Florida. Trophic position of deep-water zooplankton is shown for reference as a primary consumer on phytoplankton and a diet source of some fish. Fish were collected at Porter Sink, Lake Jackson on 20 December 2002 and 14 February 2003 and in the shallow, littoral zone of northwestern Lake Jackson during May to August 2002-2003. Trophic positions were estimated relative to the baseline $\delta^{15}\text{N}$ value with the equation $\text{TP} = ((\delta^{15}\text{N} - \delta^{15}\text{N}_{\text{baseline}}) / 3.4) + 1$, where $3.4^{0/00}$ is the mean enrichment of $\delta^{15}\text{N}$ between trophic levels. 119

Figure 3.15: Food web diagram of Lake Jackson, Leon County, Florida based on trophic position. Direction of arrows indicates direction of energy flow. 120

ABSTRACT

Lakes in the southeastern United States support a high diversity of reptiles and amphibians, including many species of turtles. Reptilian omnivores are abundant and their role in lake food webs must be important. The objectives of this study were to determine the environmental correlates of abundance of the predominant turtle species, the yellow-bellied slider, *Trachemys scripta*, Florida cooter, *Pseudemys floridana*, and Florida softshell, *Apalone ferox*, to evaluate the degree of omnivory, trophic position, and competitive interactions of these turtles, and to describe the trophic structure and sources of primary production in the food web of a northern Florida lake.

First, I examined whether the abundance of *T. scripta*, *P. floridana*, and *A. ferox* in 17 lakes in Leon Co., Florida showed some consistent pattern of correlation with environmental factors based on their trophic position. The abundance of *T. scripta* was greater in Tallahassee Red Hills lakes, whereas abundances of *P. floridana* and *A. ferox* between physiographic regions were nearly identical. *Trachemys scripta* exhibited greater abundances than that of *P. floridana* in eutrophic lakes, but was much less abundant than *P. floridana* in oligotrophic lakes. *Pseudemys floridana* occurred in equal abundances in lakes across the primary productivity gradient but never attained the highest densities of *T. scripta*. A principal components analysis indicated major positive covariation among percent area covered by macrophytes (PAC), total phosphorus, chironomid abundance, snail abundance, and macroinvertebrate abundance and negative covariation of periphyton productivity and percent area covered by macrophytes. The first three axes accounted for 81% of the variance. PC 1 was primarily a lake productivity axis and showed positive covariation between percent surface area covered by macrophytes (PAC), total phosphorus, chironomid abundance, and snail abundance and accounted for 38% of the variation. I found that lakes in northern Florida range from low-nutrient, sand-bottom lakes to moderately eutrophic, muck-bottom lakes with abundant macrophytes, but one of the best predictors of turtle abundances was periphyton. Abundances of all three focal turtle species were strongly correlated with a mud/muck substrate and both top-down (no alligator predation) and bottom-up (high periphyton productivity) factors. On a finer scale, abundances of the individual species were correlated with additional factors that may be related to trophic position: *T. scripta*,

– high phosphorus and high chironomid abundance; *P. floridana*, – low macrophyte cover and high chironomid abundance; and *A. ferox*, – high macroinvertebrate abundance, high snail abundance, and high phosphorus.

Chapter 2 evaluated the levels of omnivory and competitive interactions between two abundant sympatric emydid turtles, *Trachemys scripta* and *Pseudemys floridana*, that coexist across a productivity gradient in lakes in northern Florida. First, a foraging experiment indicated that both species were omnivorous in the juvenile stage, but *P. floridana* was more herbivorous and *T. scripta* consumed more insects and carrion. This low level of resource overlap was consistent with studies of gut contents and stable isotope analyses. Second, in a 13-month cage experiment in a natural pond under low resource conditions, the generalist *T. scripta* grew more slowly with conspecifics than with *P. floridana*, and the specialist *P. floridana* grew at the same rate with both *T. scripta* and conspecifics. *Trachemys scripta* with *P. floridana* exhibited the highest growth rate (3.5 mm/yr), slightly faster than *P. floridana* with conspecifics (2.3 mm/yr). *Trachemys scripta* was apparently unable to process macroalgae as well as *P. floridana* and the low abundance of invertebrate prey in the pond was apparently limiting. Gut specializations in *P. floridana* that allow for more efficient digestion and assimilation of plant nutrients could be the mechanism causing its better performance than that of *T. scripta*, a more generalist omnivore, when only low-quality, basal resources are available. Where intraspecific competition in one species is stronger than interspecific effects, this may influence the distribution of trophic generalists across a productivity gradient. A possible mechanism for competition among conspecifics may be aggressive interactions in habitats with limited resources.

In Chapter 3, I used stable isotope analyses ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) to examine the trophic structure and sources of primary production in the food web of Lake Jackson in Leon Co., Florida. Filamentous macroalgae was the foundation of the food web despite a much greater biomass of macrophytes. Macroalgae was the primary energy source for 34 of 42 animal taxa sampled. Eutrophication that causes changes in the amount and ratio of nitrogen and phosphorus could cause severe changes to the food web if inedible blue-green algae (cyanobacteria) displace filamentous macroalgae.

Estimated trophic positions revealed that the turtle assemblage consisted of two foraging patterns: herbivorous (*P. floridana*) and omnivorous (*T. scripta*, *Sternotherus odoratus*, *A. ferox*, *Chelydra serpentina*, and *Kinosternon subrubrum*). The trophic positions of the omnivorous

species ranged from 3.3 to 4.0. Trophic positions of the three focal species, *P. floridana*, *T. scripta*, and *A. ferox*, were significantly different from each other. Trophic position of adult *Apalone ferox* (TP = 3.8) was significantly greater than that of *T. scripta* (TP = 3.3). Gut contents analysis indicated that adult *A. ferox* consumed primarily insects, snails, fish, and macroalgae, whereas adult *T. scripta* consumed mostly insects (odonate naiads), macrophytes, and macroalgae. Trophic position increased with size in *A. ferox* reflecting an ontogenetic diet shift from mostly insects by juveniles to large predaceous insects, snails, and fish by large adults. Trophic position of juvenile *T. scripta* was 3.5, one position greater than that of juvenile *P. floridana* (TP = 2.4). This difference in trophic position continued in adult *T. scripta* (TP = 3.3) and *P. floridana* (TP = 2.3), with no clear dietary shift towards herbivory in adult *T. scripta*. Gut contents showed that juvenile and adult *P. floridana* consumed primarily macroalgae.

Food webs are complex in Florida lakes and there are many direct and indirect interactions among fish, reptiles, and amphibians. At Lake Jackson, there were few specialists (TP \geq 4.0) and few strict primary consumers. Predation on consumers with lower trophic positions lowered the average trophic position of top predators (e.g., alligator), whereas eating predatory insects that occupy a similar or greater trophic position elevated the trophic position of some turtles and frogs. Omnivory was prevalent (90% of consumers), and the food web was one trophic position shorter than those in fish-dominated, north temperate lake webs that have few turtles, less species diversity, and lower productivity.

INTRODUCTION

A fundamental goal of ecology is to determine the underlying processes that regulate community composition and explain observed patterns of distribution and abundance. The complexity of interactions among producers, primary consumers, and predators is best resolved by analyzing the structure of food webs (Paine 1980, Polis 1991). Trophic specializations such as omnivory could be important factors that regulate food web dynamics (e.g., food web stability), interspecific interactions, and patterns of abundance. In complex communities, the levels of omnivory, herbivory, and specialization among consumers affect food web dynamics, interspecific interactions, and trophic structure (Morin and Lawler 1996, Polis and Strong 1996, Blüthgen et al. 2003). Theoretical and empirical work has demonstrated that omnivory tends to stabilize food webs (Diehl 1993, Fagan 1997, Holt and Polis 1997, McCann and Hastings 1997, Holyoak and Sachdev 1998, McCann et al. 1998). In addition, recent studies of food webs in a variety of aquatic and terrestrial systems have revealed that omnivory is often more common than dietary specialization (Winemiller 1990, Hall and Raffaelli 1991, Martinez 1991, Polis 1991).

In lentic habitats, food webs have been studied primarily in deep (20 to >100 m), stratified, oligotrophic lakes of north temperate regions in Europe and North America (Carpenter et al. 1987, Persson et al. 1992, Lampert and Sommer 1997, Vander Zanden et al. 1999). Lakes in the Southeastern United States differ substantially from northern lakes in a variety of physical characteristics (Canfield 1981). For example, natural lakes in the southeastern U. S. Coastal Plain and peninsular Florida are usually relatively shallow (1-3 m deep) with little or no stratification, have greater average annual water temperatures than northern lakes, and may occasionally dry during periods of drought (Brenner et al. 1991). For many such lakes, the entire lake area is essentially littoral habitat with virtually no pelagic zone. With the exception of lakes suffering anthropogenic eutrophication (e.g., Lake Mendota, Wisconsin), north temperate lakes typically have relatively low species diversity, low primary productivity, low macrophyte biomass, and a high degree of species-specific dietary specialization among consumers (Tonn et al. 1990, Lampert and Sommer 1997, Vander Zanden et al. 1999). In contrast, food webs in

many southeastern lakes have high species diversity and high primary and secondary productivity. Fish often dominate northern lakes in North America and Europe; species richness of fish may vary from 0-21 species in small lakes (< 100 ha) to 6-28 species in large lakes (> 100 ha) (Eddy and Underhill 1974, Tonn et al. 1990, Vander Zanden et al. 1999), but in the southeastern United States, this dominance is shared with reptiles, amphibians, and macroinvertebrates. For example, large lakes in northern Florida commonly have 22 species of fish, 11 species of amphibians, and 15 species of reptiles, including 8 species of turtles, 6 species of snakes, and the American alligator (Dobbins and Rousseau 1982, Whitney et al. 2004).

The structure of food webs in southeastern U. S. lakes may be more complex and dynamic than north temperate lakes and may be more similar to food webs in tropical river floodplains because of high species diversity and temporal variability in water levels (Winemiller 1990, 1996). Thus, food web studies in southeastern lakes can address the question of whether greater complexity, species richness, compartmentalization, connectance, and omnivory are likely to increase the probability of stability in large complex food webs. Although trophic interactions have been examined by stable isotope analysis in a shallow, hypereutrophic lake in Florida, these studies only examined fish communities (Gu et al. 1996, Gu et al. 1997). No previous studies have examined either the trophic structure of food webs or the levels of omnivory and specialization in the whole food web of a natural southeastern lake.

In particular, turtles are abundant in southeastern lakes, but their potentially critical role in lake food webs has never been studied. In some southeastern lakes, the biomass and density of turtles can equal or exceed that of other vertebrates, and the annual productivity of turtles (per unit area) is exceeded only by some fishes (Iverson 1982, Congdon et al. 1986). Some aquatic turtles grow to relatively large sizes, attain high densities, have few significant predators as adults, and include a variety of trophic niches (Ernst et al. 1994). For example a predominant species, the omnivorous yellow-bellied slider, *Trachemys scripta*, reaches high densities in optimal habitats; 88 to 353 turtles/ha in South Carolina ponds, 77 to 333 turtles/ha in Mississippi farm ponds, and 115-361 turtles/ha in Florida ponds (Auth 1975, Congdon et al. 1986, Parker 1990, Aresco unpubl. data). Hence, as with large terrestrial herbivores, turtle populations within a defined niche of abiotic factors may be regulated by primary production (“bottom-up”) rather than predation (“top-down”) (Bury 1979, McNaughton et al. 1989, Polis and Strong 1996). Because turtles are long-lived organisms that vary widely in foraging behavior and trophic

position, they may be especially important in regulating community dynamics in some aquatic systems (Congdon and Gibbons 1996). Thus, understanding the factors that regulate turtle abundance may provide new insights into the relative importance of top-down vs. bottom-up influences on the structure and composition of complex freshwater communities.

Omnivory is an important feature of the life histories of some common aquatic and semi-aquatic turtles, and omnivory could be driving the structure of food webs in southeastern U. S. lakes. Turtles in several families (e.g., Emydidae, Kinosternidae, Chelydridae) feed on both plants and animals and can exhibit ontogenetic diet shifts (Lagler 1943, Mahmoud 1968, Clark and Gibbons 1969, Moll 1976, Vogt 1981, Vogt and Guzman 1988). The level of omnivory varies within and among species, often depending on resource availability, energy requirements, and foraging efficiency. In lakes with a diverse assemblage of omnivorous freshwater turtles, a large proportion of the predator-prey interactions in the food web will include turtles. Thus, evaluating the trophic relationships among turtles and other consumers is a prerequisite to understanding the properties of southeastern lake food webs and the importance of omnivory in structuring food webs.

Several previous studies of the diversity and abundance of freshwater turtles across environmental gradients have demonstrated that most species are habitat generalists with wide habitat distributions, but with patterns of abundance associated with gradients in water velocity, turbidity, river channel morphology, substrate-type, hydroperiod, and productivity (Bodie et al 2000, Anderson et al. 2002). Reliable estimates of the abundance of turtles are more difficult to determine, and, thus, few studies have examined the environmental characteristics associated with turtle abundance across habitat gradients (Congdon and Gibbons 1996, DonnerWright et al. 1999, Marchand and Litvaitis 2004). Ecologically similar turtle species or guilds often coexist across environmental gradients of productivity or predation. Primary productivity gradients may be especially important to turtle abundance and community composition. In lentic habitats, variation in the abundance of turtle species may depend on the level of open water nutrients such as phosphorus, and whether the resulting primary productivity is manifested in standing crop of macrophytes, macroalgae, or phytoplankton. For example, in Florida, some lakes may have low open water nutrients and low standing crop of macrophytes, but high periphyton productivity. Across such gradients, an interaction of the effects of predation and resource levels or variation

in abiotic factors must regulate the abundance and distribution of individual species (Steiner 2003, Wolf and Batzli 2004).

Competitive interactions between *trophic* generalists and specialists can be particularly interesting, especially when a generalist shares a particular food resource with a specialist (Chase and Belovsky 1994, Chase 1996, Beckerman 2000). Where the shared resources are abundant or other food items are available to the generalist, competition is expected to be negligible (Weins 1989). However, under conditions in which the shared resource becomes scarce (either spatially or temporally), competition with a specialist can limit the performance (e.g., growth and/or survival) of a generalist, especially if the specialist possesses unique functional or morphological features (Sanderson 1991, Ralston and Wainwright 1997).

Varying levels of omnivory among coexisting species are an overlooked aspect of studies of food web dynamics and niche relationships. Asymmetric competition has been demonstrated most often where one species is negatively affected by the interaction whereas the other species is not affected (Lawton and Hassell 1981, Morin and Johnson 1988, Inouye 1999). Such asymmetric interspecific competition can occur by exploitation competition where use of limited resources by one species is optimized via morphological or physiological specializations or interference competition where a subordinate species (e.g., smaller body size) is prevented from utilizing a preferred habitat or resource (Török and Tóth 1999, Bardsley and Beebee 2001, Sorenson et al 2004, Young 2004). Alternatively, competition can occur where intraspecific effects in one species are stronger than interspecific effects. Interference competition may be the primary mechanism of intraspecific competition. In environments with fluctuating resource levels and high species densities, intraspecific competition can play an important role in regulating distribution, especially in trophic generalists across a productivity gradient (Belovsky and Slade 1995).

There are no previous experimental studies that have examined competition for food resources between a diet generalist and specialist (Abrams 1980, Connell 1983, Underwood 1986). Under low resource conditions the outcome of competition between a generalist omnivore and the specialized herbivore is not clear. A generalist omnivore that can easily switch between herbivory, carnivory, and scavenging, depending on the quality and quantity of resources, may have higher growth and survival rates than a competitor due to its plastic foraging strategy. Alternatively, a more specialized herbivore may outcompete a generalist omnivore if

only low-quality, basal resources are available and its unique specializations allow for more efficient assimilation of nutrients needed for growth and survival. These predictions set up the potential for asymmetric competition when they are forced to divide the niche under low resource conditions, and the outcome may depend on the type of limiting resource or density of hetero- or conspecifics. I propose that intraspecific effects can override interspecific effects, reducing interspecific competition in cases in which one species can make more efficient use of a limiting resource. Intraspecific (density-dependent regulation) and interspecific competition can interact with key environmental factors to affect turtle abundance and the composition of turtle communities (Bury 1979). However, aside from anecdotal observations and correlative studies, the relative importance of competition in structuring turtle communities is unknown (Bury 1979, Congdon and Gibbons 1996, Bodie et al. 2000).

The Coastal Plain of the southeastern United States provides an excellent area to study turtle assemblages. Specifically, freshwater turtle species richness in the Gulf Coastal Plain of northern Florida is among the highest in the world (Iverson and Etchberger 1989). A maximum of seven sympatric turtle species co-occur in some lake habitats (Ernst et al 1994, Aresco unpubl. data). The most abundant large freshwater turtles in lentic habitats of northern Florida are a generalist omnivore, the yellow-bellied slider (*Trachemys scripta scripta*), a specialist algivore, the Florida cooter (*Pseudemys floridana*), and a morphologically distinct trionychid species, the Florida softshell (*Apalone ferox*). Each species differs significantly in their trophic position in the food web. All three of these species have broad distributions throughout the southeastern United States and share a wide habitat distribution (i.e., occupy all available areas across a productivity gradient) but vary substantially in abundance within the gradient. Coexistence and variation in abundance may be due to species-specific differences in resource requirements or use (i.e., diet generalist vs. specialist).

My overall research objective was to evaluate whether omnivory regulates patterns of abundance, the outcome of interspecific interactions, and trophic structure in a lake food web. In order to address these questions my specific research objectives were to (1) determine whether the abundances of *T. scripta*, *P. floridana*, and *A. ferox* show some consistent pattern of correlation with environmental factors based on their trophic position, (2) quantify differences in the degree of omnivory between hatchling *T. scripta* and *P. floridana*, (3) assess whether an omnivorous turtle, *T. scripta*, outcompetes a specialist, *P. floridana*, when forced to share the

niche under low resource conditions, (4) determine the trophic relationships, relative omnivory, and ontogenetic shifts in diet and trophic position among the 5 most common turtle species, and (5) describe trophic structure, energy pathways, and sources of primary production in the entire lake food web in one major lake using stable isotope analyses ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$).

CHAPTER 1

ENVIRONMENTAL CORRELATES OF THE ABUNDANCES OF THREE SPECIES OF TURTLES IN LAKES IN NORTHERN FLORIDA

INTRODUCTION

The abiotic and biotic factors influencing landscape-level patterns of diversity and species richness in freshwater communities have been well studied (Gorman and Carr 1978, Jackson and Harvey 1989, Winemiller 1990, Leitman et al. 1991, Keast 1996, Winemiller 1996, Lampert and Sommer 1997, Wilkinson and Edds 2001). Specifically, how physical and chemical factors such as water velocity, wetland size, alkalinity, and dissolved oxygen, and biotic factors such as primary and secondary productivity affect freshwater fish abundance and community structure are relatively well known (Power et al. 1988, Bachmann et al. 1996, Winemiller 1996, Wilkinson and Edds 2001, Petry 2003, Bhat 2004). In some freshwater habitats the biomass and density of turtles may equal or exceed that of other vertebrates, and the annual productivity of turtles (per area) is exceeded only by some fishes (Iverson 1982, Congdon et al. 1986). Many aquatic turtle species grow to relatively large sizes, attain high densities, and have few significant predators as adults. Hence, as with large terrestrial herbivores, turtle populations within a defined niche of abiotic factors may be regulated by primary production (bottom-up) rather than predation (top-down) (Bury 1979, McNaughton et al. 1989, Polis and Strong 1996). Because turtles are long-lived organisms that vary widely in foraging behavior and trophic position, they may be especially important in regulating community dynamics in some aquatic systems (Congdon and Gibbons 1996, Aresco, see Chapter 3). Thus, understanding the factors that regulate turtle abundance may provide new insights into the

relative importance of top-down vs. bottom-up influences on the structure and composition of complex freshwater communities.

Reliable estimates of the abundance of turtles are difficult to determine, and, thus, few studies have examined the environmental characteristics associated with turtle abundance across habitat gradients (Congdon and Gibbons 1996, DonnerWright et al. 1999, Marchand and Litvaitis 2004). A few recent studies have examined the diversity of freshwater turtles across environmental gradients and demonstrated that most species are habitat generalists with wide habitat distributions (DonnerWright et al. 1999, Bodie et al 2000, Anderson et al. 2002). However, patterns of abundance of turtle species within broad gradients may be associated with fine-scale variation in water velocity, turbidity, substrate type, hydroperiod, and productivity (Marchand and Litvaitis 2004). Ecologically similar turtle species or guilds often coexist across environmental gradients of productivity or predation. Primary productivity gradients may be especially important to turtle abundance and community composition. In lentic habitats, variation in the abundance of turtle species may depend on the level of open water nutrients such as phosphorus, and whether the resulting primary productivity is manifested in standing crop of macrophytes, macroalgae, or phytoplankton. For example, in Florida, some lakes may have low open water nutrients and low standing crop of macrophytes, but high periphyton productivity. Across such gradients an interaction of the effects of predation and resource levels or variation in abiotic factors must regulate the abundance and distribution of individual species (La Peyre et al. 2001, Latta and Faaborg 2002, Steiner 2003, Wolf and Batzli 2004).

Most studies of turtle communities have focused on the resource niche of turtles by evaluating microhabitat segregation, feeding strategies, and dietary preferences (Mahmoud 1968, Bury 1979, Vogt 1981, Teran et al. 1995, Bodie and Semlitsch 2000). Observational studies show that sympatric turtle species partition available food resources and/or the microhabitat in which they feed. For example, Williams and Christiansen (1981) found that the diets of *Apalone muticus* and *A. spiniferus* overlapped widely, but that the two species partitioned the habitat in which they fed. Vogt (1981) studied the dietary overlap of three sympatric species of *Graptemys* and found that *G. geographica* was a mollusk specialist; *Graptemys pseudogeographica* and *G. ouachitensis* were omnivorous, but *G. ouachitensis* was a surface-feeding specialist. Both Vogt and Guzman (1988) and Moll (1990) studied food partitioning in a neotropical freshwater turtle community. They found a wide degree of overlap between species, but observed that dietary

similarity decreased as population density increased. Clearly, a realistic approach to understanding the assembly of freshwater turtle communities requires quantifying how the abundance of individual species covaries with biotic (e.g., diet and food resources, predator density, vegetation structure) and abiotic (e.g., substrate, lake area) niche dimensions.

The Coastal Plain of the southeastern United States provides an excellent area to study turtle assemblages. Specifically, freshwater turtle species richness in the Gulf Coastal Plain of northern Florida is among the highest in the world (Iverson and Etchberger 1989). A maximum of seven sympatric turtle species co-occur in some lake habitats (Ernst et al. 1994, Aresco unpubl. data). This study examines the core of a turtle assemblage in lakes in northern Florida that includes two abundant emydid species, a specialist algivore, *P. floridana*, a generalist omnivore, *T. scripta*, and a morphologically distinct trionychid species, *A. ferox*. Each species differs significantly in their trophic position in the food web (Aresco see Chapter 3). The species in this assemblage may share a wide habitat distribution (i.e., occupy all available areas across a productivity gradient) but vary substantially in abundance within the gradient. Coexistence and variation in abundance may be due to species-specific differences in resource requirements or use (i.e., diet generalist vs. specialist). Therefore, the objectives of this study were to determine whether these species show some consistent pattern of correlation with environmental factors based their trophic position in the food web. Specifically, I conducted an intensive field survey to determine the covariation between abundance of the three focal species, *T. scripta*, *P. floridana*, and *A. ferox*, and a set of environmental variables in 17 lakes in 2 physiographic regions of Leon Co., Florida.

METHODS

Study System

The most abundant large freshwater turtles in lentic habitats of northern Florida lakes are the yellow-bellied slider (*Trachemys scripta scripta*), the Florida cooter (*Pseudemys floridana*), and the Florida softshell (*Apalone ferox*) (Carr 1952). All three of these species have broad distributions throughout the southeastern United States. *Apalone ferox* occurs on the lower Coastal Plain from southern South Carolina to Mobile, Alabama and throughout peninsular

Florida. *Trachemys s. scripta* occurs from southeastern Virginia to northern peninsular Florida and westward through the Florida panhandle and southern Alabama. *Pseudemys floridana* occurs from southeastern Virginia, southward through most of peninsular Florida, and westward through extreme southern Alabama to Mobile Bay (Ernst et al., 1994). Thus, *Trachemys s. scripta* and *P. floridana* coexist in lakes and ponds of the Coastal Plain from southeastern Virginia to north-central Florida, while all three species co-occur throughout the range of *A. ferox*, excluding the extreme southern portion of the Florida peninsula (Ernst et al., 1994). Both *T. scripta* and *P. floridana* can attain high densities in optimal habitats; densities of *T. scripta* range from 88 to 353 turtles/ha in South Carolina ponds, 77 to 333 turtles/ha in Mississippi farm ponds, and 115-361 turtles/ha in Florida ponds (Auth 1975, Congdon et al. 1986, Parker 1990, Aresco unpubl. data). *Trachemys scripta*, *P. floridana*, and *A. ferox* may occasionally occur in slow-moving rivers and river floodplains, but such habitats are considered to be peripheral and were not included in this study. *Pseudemys floridana* attains a larger maximum size (females 28-32 cm, 2.5-3.5 kg) than *T. scripta* (females 20-26 cm length, 1.5-2.8 kg) (Aresco 2004).

Study Lakes

The study was conducted at 17 lakes in Leon County in northwestern Florida, ranging in size 0.6 to 2330 ha, with average depths of 1 to 2 m (Fig. 1.1, Table 1.1). These lakes are typical of lakes found elsewhere in the lower Coastal Plain of the southeastern United States. The five lakes that are within the Munson Sandhills (MSH) physiographic region and the Norfleet/Spring Hill Ridge lake region have a substrate dominated by deeply weathered beach and dune sand. The lakes in this region are clear and acidic (pH <5.5). All of the lakes in the Munson Sandhills region are located in the Apalachicola National Forest and the surrounding upland habitats consist of mature, second-growth longleaf pine (*Pinus palustris*) with a groundcover dominated by wiregrass (*Aristida stricta*). The twelve lakes that are within the Tallahassee Red Hills (TRH) physiographic region and the Tifton/Tallahassee lake region have substrates of phosphatic sand, silty sand, and clay with underlying karst formations (Table 1.1). Lakes and ponds in this region are slightly acidic to neutral (pH 6.0-7.0) (Brenner et al. 1990). Chapman Pond, McCord Pond, and Waverly Pond are within City of Tallahassee parks in suburban areas and are surrounded by primarily by residential neighborhoods (Fig. 1.1). These ponds receive urban stormwater runoff from lawns and streets containing fertilizers, pesticides, and vehicle fluids. The upland habitats

surrounding Lake Tom John, Coolview Pond, Megginnis Arm, Lake Jackson, and Little Lake Jackson are a mosaic of residential homes, roads, and undeveloped mixed pine/hardwood habitats or agricultural land. These lakes also receive high nutrient stormwater runoff from developed areas within their watersheds (Livingston 1997). Upland habitats around Gannett Pond, Lake Iamonia, Lake Piney Z, and Orchard Pond are primarily undeveloped mixed pine/hardwood forest or agricultural land. Lake Jackson and Lake Iamonia are sinkhole lakes. During drought conditions, a lowering of the water table causes leakage into the groundwater through the sinkholes and most of the lake bottom dries, an event that has occurred 9 times during the last 100 years, drying on average every 12 years. These lakes last dried in 1999-2000 and refilled in 2001. Although some species of freshwater turtles are still frequently harvested for their meat in some areas of Florida (e.g., *A. ferox*) (Enge 1993), I observed only occasional harvest of *A. ferox* in Lake Jackson, Megginnis Arm, and Little Lake Jackson.

Turtle Abundance

Turtle abundance was quantified using a standardized trapping method for one sampling interval at each lake in either 2002 or 2003. Turtles were trapped with single-entrance, double-throated hoop nets (3.5-m length, 1-m diameter hoops, 5-cm mesh) attached to a 30.5-m lead net. Two traps were set at least 200 m apart at each lake during the months of May-September. The large mesh size precluded capture of small turtle species (e.g., common musk turtle [*Sternotherus odoratus*] and the eastern mud turtle [*Kinosternon subrubrum*]) and small individuals of larger species. To reduce the possibility of trapping bias towards species that may prefer bait (e.g., *T. scripta*) traps were not baited. The lead net functioned as a submerged drift fence that intercepted turtles and directed them into the trap. Traps were set in water <1 m deep and checked 1-2 times daily. The common snapping turtle, *Chelydra serpentina*, is typically found in low relative abundance in north Florida lakes and in this study was trapped at only 2 of 17 lakes (12%) (mean CPUE = 0.048 turtles/day). Thus, this species was not included in the subsequent analyses of environmental correlates.

Traps were set for one 4-day period at each locality (96 trap hours x 2 traps = 192 trap hours = 8 trap days per lake) to obtain a standardized abundance for each species. Raw capture data were pooled for the two traps at each lake and converted to catch per unit effort (CPUE = number of individuals of each species caught/trap days). For each turtle collected, I recorded

species and sex and measured carapace length (CL), plastron length (PL), and mass (g). Captured turtles were individually marked by notching the marginal scutes with a triangular file and released at the location of capture.

In order to assess the possibility of trapping bias among species, I compared the relative abundance estimate for each species calculated from the 5-day trap sampling to the known absolute abundances of each species at three lakes (Waverly Pond, Chapman Pond, and McCord Pond) where I had collected all individuals of all turtle species during a complete drawdown and sediment removal operation (Aresco and Gunzburger 2004). For each species, I compared the relative abundance of turtles trapped to actual abundance at each pond using Spearman rank correlation analysis.

To determine whether turtle abundance varied between the two physiographic regions, I compared estimates of total abundance (CPUE) of each species between physiographic regions (TRH vs. MSH) using a Kruskal-Wallis one-way ANOVA.

Environmental Correlates

The biotic and abiotic environmental correlates chosen for measurement at each lake were considered *a priori* to be those most likely to be important to the abundance of turtles (Table 1.2). Eighteen variables were chosen to include abiotic factors, resources (bottom-up), and predator (top-down) characteristics in 6 general categories: (1) maximum surface area of each lake (2) primary substrate type, (3) physiographic region, (4) lake primary productivity, (5) macrofauna, (6) turtle predator (alligator) presence (Table 1.2).

General Lake Characteristics

Maximum surface area of each lake was determined using the GIS program ArcMap and 1999 digital ortho quarter quads (DOQQ) available from the Florida Department of Environmental Protection. I classified the substrate of each lake as primarily sand, mud (fine silt), or muck (organic). To test whether abundance of turtles was associated with physiographic region *per se*, lakes were classified as either in the Munson Sandhills (MSH) or the Tallahassee Red Hills (TRH).

Primary Productivity

Lake primary productivity was measured in terms of (a) standing crop biomass of macrophytes (kg wet weight/m²), (b) percent lake surface area covered with macrophytes (c) periphyton productivity (g/m²/y), and (d - f) concentrations (µg/L) of chlorophyll *a*, nitrogen, and phosphorus. Macrophytes and macroalgae comprise a large proportion of the nutrient pool in Florida lakes and are not included in measurements of the chlorophyll *a* content of open water (Canfield et al. 1983). Periphyton is a type of green filamentous macroalgae that grows on the stems of macrophytes or as floating mats (e.g., *Spirogyra*, *Cladophora*, *Chara*, *Nitella*, *Hydrodictyon*, and *Pithophora*). Macrophytes and periphyton may be the more relevant measure of primary productivity in this study because some turtle species feed on macrophytes and macroalgae.

Standing crop biomass of macrophytes was quantified between May and August of 2003 and 2004. I established five transects at each lake that spanned 3 depth zones: shallow (0.1-0.5 m), medium depth (>0.5-1.0 m), and deep water (>1.0 m). A 0.25 m² quadrat was placed in each zone along each transect and all plants within the quadrat were harvested and separated into the following categories based on growth form: emergent, floating, and submerged. Plants from each category were placed in a mesh bag that was shaken vigorously to remove excess water and weighed with a Pesola hang-scale. Mean wet weight (kg wet weight/m²) of total macrophytes and for each category are reported for each lake. Percent surface area covered with macrophytes (PAC) was visually estimated at each lake and included species such as water lilies (*Nymphaea odorata*), maidencane grass (*Panicum hemitomon*), pickerelweed (*Pontedaria cordata*), and American lotus (*Nelumbo lutea*), water hyacinth (*Eichhornia crassipes*), and soft rush (*Juncus effusus*).

I determined periphyton productivity at each lake by establishing 2 periphyton samplers in the littoral zone from May to July 2004. I placed 2 wooden stakes at least 100 m apart, each with 4 glass microscope slides affixed with metal clips horizontally to the top of a 15-x-15-cm square of rigid, fine plastic mesh that was attached to the top of each stake. The samplers were positioned so that the slides remained 10-20 cm below the water surface. The slides were collected after 45 days at each lake. I allowed the slides to air dry at 32°C for 48 h, scraped the dried periphyton from each slide with a razor blade onto pre-weighed GF filter paper, weighed each sample to the nearest mg, and calculated mean periphyton productivity at each lake as grams/m²/y. I collected water samples at each lake throughout the study and sent them to the

University of Florida Department of Fisheries and Aquatic Sciences laboratory under the LAKEWATCH program to determine open water concentrations ($\mu\text{g/L}$) of chlorophyll *a*, nitrogen, and phosphorus.

Macrofauna Abundance

I sampled each lake once during May-September 2003 and determined the abundance of macrofauna using a 0.25 m² aluminum box sampler at 5 haphazard locations in the littoral zone of each lake where turtles typically forage (water depth 0.4 -1 m). I collected all macrofauna within the box sampler by performing 10 dipnet (1 mm mesh) sweeps within the box sampler. The net was swept vigorously through any macrophytes and the substrate within the box sampler to ensure collection of epiphytic and benthic macroinvertebrates. All macrofauna were identified to the lowest possible taxonomic level and counted. I summed the number of individuals in each of four categories of macrofauna: small fish, chironomids, snails and all other macroinvertebrates (insects, crawfish) collected in each of the 5 box samples at each site to yield an abundance value per 1.25 m² for each category. The presence or absence of amphipods was also recorded. Chironomids and amphipods were separated from the macroinvertebrate category as they are often used as indicators of water quality (Parrish 1975). Snails were separated as they represent a unique food source for turtles.

Predator Presence

I determined whether adult American alligators (*Alligator mississippiensis*), probably the only aquatic predator of adult turtles, were present at each lake. Turtles are the primary food source for alligators in some areas, and alligators may reduce the abundance of some turtle species (Delany and Abercrombie 1986, Delany et al. 1999). I determined the presence or absence of alligators by surveying each lake on at least 5 nights between May and July 2003. For each survey I stood on the shoreline and used a spotlight that produces detectable red eye reflection at approximately 200 m (Woodward and Marion 1978). An estimation of alligator density at each lake was not possible due to thick aquatic vegetation at some lakes.

Analysis of Turtle Abundance and Environmental Correlates

In order to determine the environmental correlates of turtle abundance, I examined whether sites that were similar in abundance of turtles were similar in environmental characteristics using Mantel analyses. I constructed matrices of distances between sites based on log transformed turtle abundance data ($\ln(x + 1)$) (3 individual species matrices and a turtle community matrix with all species) and 18 environmental variables. All variables were tested for normality. For skewed data I arcsine transformed percentages (i.e., % cover), square-root transformed counts, and natural log transformed [$\ln(x + 1)$] lake area, water data, and plant biomass data prior to analysis so that they would better meet the normality assumptions. Each matrix was constructed by calculating Euclidean distances between all pairwise combinations of lakes (Legendre and Legendre 1998). I performed Mantel analyses using the R program to determine whether there was a significant correlation between the off-diagonal elements of the distance matrices based on the individual species abundance and total turtle abundance of the sites and the matrix of environmental characteristics (Mantel 1967, Legendre and Legendre 1998, Wilkinson and Edds 2001). The Mantel analysis is a nonparametric procedure that allows for analysis of both continuous and categorical data (including presence/absence data). The Mantel analysis is a randomization procedure that calculates the probability that 2 distance matrices are more similar than expected by chance alone (Jackson and Harvey 1989). This statistical method rearranges the rows of the first matrix randomly and tests if the actual correlation is >95% of the correlations created by 1,000 random permutations of the first matrix.

Each of the 18 environmental variables were tested for each species separately and then sequentially eliminated from that matrix if the variable was not significant, such that the final matrix represents only the set of variables with nonrandom correlations (r) with the turtle abundance matrix. I combined the individual variables that emerged as significant and tested those in combination, so that when the final set of significant individual variables were combined there was still a significant correlation. If the combined test was significant, the analysis was considered complete. If the combined test was not significant, I looked for the two most highly correlated variables, eliminated the variable with the lower variance, and then repeated the procedure. The procedure was repeated until the data was reduced to a suite of variables that was significant. This procedure was repeated for each species separately to identify the suites important for each species and then for overall turtle abundance to identify the suite of variables most highly related to turtle abundance. A significant correlation (Mantel r) between the

abundance matrix and the environmental matrix demonstrates that lakes similar in abundance of turtles are similar in environmental characteristics and identifies the suite of environmental variables that are important for each species separately and combined.

I used ANOVA and post hoc tests using a Bonferroni adjustment to determine whether turtle abundance (overall and for each species) differed among lakes with different substrates (mud, muck, or sand).

Analysis of Covariation of Environmental Variables among Lakes

Spearman rank correlations were used to examine the relationships among the 14 continuous environmental variables. The critical correlation coefficient was corrected for simultaneous tests ($r_s < 0.538$). All variables were tested for normality. For skewed data I arcsine transformed percentages (i.e., % cover), square-root transformed counts, and natural log transformed ($\ln(x + 1)$) lake area, water data, and plant biomass data prior to analysis so that they would better meet the normality assumptions. In order to examine the covariation of environmental variables among lakes, I performed a Principal Components Analysis (PCA) on a correlation matrix of a set of 6 environmental variables that were identified as important for each species separately in the Mantel tests. I then performed three separate discriminant function analyses (DFA) on three categorical variables, substrate type (mud, muck, and sand), alligator presence/absence, and physiographic region (TRH vs. MSH) with the 6 environmental variables. In order to identify the important environmental variables that discriminate among groups in each DFA, I used the DF scores combined with the original 6 variables and performed Pearson correlation analyses. Lastly, log likelihood ratio tests were used to determine whether alligator presence/absence was correlated with substrate type.

RESULTS

Turtle Abundance

The abundance of turtles varied among the lakes trapped. Numbers of turtles captured ranged 0 to 62 turtles per lake (CPUE = 0 - 7.75) (Table 1.3). Mean CPUE of all turtles was 1.77 (SE = 0.549). *Trachemys scripta* had the greatest overall abundance (mean CPUE = 1.16, SE = 0.37) and was trapped at 71% of lakes (median CPUE = 0.50, range 0 – 5.63) (Fig. 1.2). In

contrast, mean CPUE of *P. floridana* at all lakes was only 0.43 (SE = 0.13). This species was widely distributed; it was trapped at 76% of all lakes (median CPUE = 0.25, range 0 – 2.00) (Fig. 1.2). *Apalone ferox* was trapped at 53% of lakes with a mean CPUE = 0.18 (SE = 0.06) (median CPUE = 0.125, range 0 – 0.875) (Fig. 1.2). The presence of *A. ferox* was also confirmed by other methods (direct observation, dead on nearby roads, excavated during pond dredging, or captured at drift fences) at 7 lakes in which this species was not caught in the turtle traps, so this species was actually present at 95% of lakes in this study.

Overall turtle abundance was greater in lakes in the Tallahassee Red Hills (mean CPUE = 2.27, n = 12) than in the Munson Sandhills (mean CPUE = 0.576, n = 5), but this difference was not statistically significant (Kruskal-Wallis, $P = 0.072$, Mann-Whitney $U = 13.0$). Mean abundance of *T. scripta* was significantly greater in Tallahassee Red Hill lakes (Kruskal-Wallis, $P = 0.014$, Mann-Whitney $U = 7.0$) (Fig. 1.3). Mean abundance of *P. floridana* and *A. ferox* between physiographic regions was nearly identical (Fig. 1.3). Overall turtle abundance was greater in lakes with mud and muck substrates than in those with sand substrates ($F = 11.5$, $P = 0.001$). By species, ANOVA demonstrated that abundance of *T. scripta* was greater in lakes with mud and muck substrates than in those with sand substrates ($F = 13.9$, $P < 0.0001$) (Fig. 1.4). Abundance of *P. floridana* was greater in lakes with a mud substrate compared to those with a muck substrate (ANOVA, $F = 4.57$, $P = 0.030$). There were no differences in abundance of *P. floridana* among lakes with sand vs. muck or mud vs. sand substrates. Abundance of *A. ferox* did not vary significantly with type of substrate.

I found no evidence of a trapping bias, leading me to conclude that the estimates of CPUE are comparable across species and lakes. Spearman rank correlation demonstrated that rank order of relative abundance of turtles trapped in a 5-day sampling period reflected the actual abundance ($r_s = 0.83$, $P < 0.01$) (Table 1.5).

Covariation of Environmental Variables among Lakes

Spearman rank correlation analysis among 14 continuous variables demonstrated that the strongest correlations ($r_s > 0.538$) were between open water nutrients and chlorophyll *a* (Tables 1.1, 1.6, 1.7). However, periphyton productivity was not related to nutrients or chlorophyll *a* and was negatively correlated with each of the aquatic macrophyte categories (Fig. 1.5). There was a positive correlation between lake area and floating macrophyte biomass, but a negative

correlation between lake area and total phosphorus. The macrophyte categories of PAC and emergent plants were strongly positively correlated with open water nutrients and chlorophyll *a*, but submerged aquatic vegetation was negatively correlated with these same variables (Table 1.7). There were also interesting correlations among animal abundances and various measures of productivity. Chironomids were strongly correlated with open water nutrients, whereas presence of amphipods was negatively correlated with these variables. Snails were found in 6 lakes (mean = 5.8 individuals per 1.25 m², SE = 3.6, range 0 – 61), and their abundance was positively correlated with PAC and phosphorus, but negatively correlated with lake area. Abundance of littoral fish across lakes ranged from 0 to 135 individuals per 1.25 m² (mean = 36.8, SE = 9.4) and was correlated with emergent macrophytes and chlorophyll *a* (Tables 1.5 and 1.6). The abundance of macroinvertebrates varied widely across all lakes and ranged from 0 to 69 individuals per 1.25 m² (mean = 31.2, SE = 5.5) but showed no strong correlations with any environmental variable (Tables 1.6 and 1.7). The Spearman *r* between *T. scripta* and *P. floridana* ($r_s = 0.44$) was greater than that between *A. ferox* and *T. scripta* ($r_s = 0.27$) or *A. ferox* and *P. floridana* ($r_s = 0.21$).

PCA on the covariation among lakes for periphyton productivity, percent area covered by macrophytes (PAC), total phosphorus, chironomid abundance, snail abundance, and macroinvertebrate abundance demonstrated that 81% of the variance was explained on the first three axes, each of which had eigenvalues >1 (Table 1.7). PC 1 is a lake productivity axis and showed covariation between percent surface area covered by macrophytes (PAC), total phosphorus, chironomid abundance, and snail abundance and explained 38% of the variation. After that variation was accounted for, PC 2 indicated a strong negative relationship between periphyton productivity and percent area covered by macrophytes and that axis explained 25% of the variation (Fig. 1.5, Table 1.7). An interesting result of the PCA is that it demonstrates that there were two distinct lake productivity axes, periphyton does not covary in the same way that lakes covary with the other four variables. PC 3 explained 18% of the variation and is a secondary productivity axis with covariation of chironomid abundance and macroinvertebrate abundance.

Plots of PC 1 vs. PC 2 with abundance of each turtle species demonstrated that PC 1 may influence abundance patterns of *T. scripta*, but that these axes do not account for abundance patterns of *P. floridana* or *A. ferox* (Figs. 1.6-1.8).

Discriminant function analysis showed that the two physiographic regions differed in lake productivity (DF 1 canonical $r = 0.88$, eigenvalue = 3.41). Pearson correlations of DF 1 scores and the 6 primary lake variables used in PCA identified PAC ($r_s = 0.83$) and total phosphorus ($r_s = 0.89$) as the most important variables in discriminating TRH and MSH lakes (Table 1.8). The analysis classified 94% of the 17 lakes with their correct group based on physiographic region.

A second discriminant function analysis indicated that the presence/absence of alligators was associated with lake productivity variables (DF 1 canonical $r = 0.93$, eigenvalue = 6.48). Pearson correlations of DF 1 scores and the 6 primary lake variables used in PCA identified periphyton productivity as the most important variable in discriminating lakes with and without alligators ($r_s = -0.73$). Substrate was the main physical difference between lakes in the Tallahassee Red Hills and Munson Sandhills; all TRH lakes had mud or muck substrates and all MSH lakes had a sand substrate). A third discriminant function analysis indicated that type of substrate (sand, mud, or muck) was associated with several lake productivity variables (DF 1 canonical $r = 0.98$, eigenvalue = 23.06; DF 2 canonical $r = 0.83$, eigenvalue = 2.17) (Fig. 1.9). Pearson correlations of DF 1 scores and the 6 primary lake variables identified chironomid abundance ($r_s = -0.67$) as the variable most important in discriminating between lakes with a mud substrate and those with sand and muck substrates. Abundance of chironomids was greater in lakes with a mud substrate. Pearson correlations of DF 2 scores and the 6 primary lake variables identified PAC ($r_s = 0.82$) and total phosphorus ($r_s = 0.87$) as the variables most important in discriminating between lakes with a muck substrate and those with mud and sand substrates (Table 1.9). PAC and total phosphorus were greater in lakes with muck and mud substrates than those with sand bottoms (Table 1.9). Discriminant functions correctly classified 82% of the 17 lakes with their correct group based on substrate. There was a significant correlation between presence/absence of alligators and substrate type ($\chi^2 = 8.02$, $P = 0.018$); presence of alligators was positively correlated with muck and sand substrates.

Environmental Correlates of Turtle Abundance

Individual Mantel analyses by species revealed significant correlations between abundance of *T. scripta*, *P. floridana*, and *A. ferox* and a suite of environmental variables consisting of both biotic and abiotic factors (Table 1.10). Lakes with a higher abundance of *T.*

scripta had a mud/muck substrate, no alligators, high periphyton productivity, high abundance of chironomids, and high open water phosphorus (Mantel $r = 0.75$, $P = 0.001$) (Fig. 1.10). Similarly, a significant correlation existed between lakes with high abundance of *P. floridana* and those with a mud substrate, no alligators, high periphyton productivity, high abundance of chironomids, and low PAC (Mantel $r = 0.50$, $P = 0.020$) (Fig. 1.11). There was a strong association between abundance of *A. ferox* and a set of five environmental variables that included no alligators, high periphyton productivity, high macroinvertebrate abundance, high snail abundance, and high total open water phosphorus (Mantel $r = 0.48$, $P = 0.013$) (Fig. 1.12). There was no difference in the results of the Mantel analyses with or without physiographic region included as a variable for any of the three species. A comparison of the results of the Mantel analysis of turtle abundance and DFA for physiographic region demonstrated that, with the exception of phosphorus for *T. scripta* and PAC for *P. floridana*, turtles responded to different variables than the ones that separated physiographic regions.

A Mantel test based on distance matrices of total turtle abundance of all three species and environmental variables suggested that lakes similar in environmental characteristics have similar overall turtle abundance (Fig. 1.13). These results revealed a strong correlation between lakes with high turtle abundance and high periphyton productivity, mud/muck substrate, and no alligators (Mantel $r = 0.69$, $P = 0.001$).

DISCUSSION

I found that abundances of all three turtle species in this study are correlated with a similar suite of environmental variables. Overall turtle abundance was highest in lakes with high periphyton productivity, a mud/muck substrate, and no alligators. A strong positive association between turtle abundance and high primary productivity (macroalgae) and a negative association with the presence of alligators suggests that both bottom-up and top-down controls may be important limiting factors to turtle populations.

Primary productivity is often correlated with the abundance and biomass of higher trophic levels. Studies of bird and fish communities in Florida lakes indicate that primary productivity influences biomass and abundance (Hoyer and Canfield 1994, Bachmann et al. 1996). Specifically, eutrophic lakes with high open water phosphorus, nitrogen, and chlorophyll

a had greater biomass and abundance of birds and fish. Likewise, in this study, total open water phosphorus was a variable that partially accounted for the abundance of *T. scripta* and *A. ferox*. However, overall turtle abundance was most positively correlated with a different measure of primary productivity, one that is directly consumed by turtles: macroalgae in the form of periphyton. Macroalgae are an important food of *T. scripta* and *P. floridana* (Parmenter 1980, Lagueux et al. 1995, Bondavalli and Ulanowicz 1999, Aresco see Chapter 3). Algae are easily digestible compared to fibrous macrophytes and are high in protein (Boyd and Lawrence 1967). At Lake Jackson, macroalgae was present in the gut of 97% of adult *P. floridana* (Aresco see Chapter 3). Likewise, 29% of *A. ferox* and 37% of *T. scripta* had directly consumed macroalgae. *Pseudemys floridana* is specialized to digest macrophytes and macroalgae, because it has a longer relative gut length compared to *T. scripta*. Jackson (1996) reported that mean digestive tract length (stomach plus small intestine and colon corrected for plastron length) was 15% longer in *P. floridana* than in *T. scripta*. As with other herbivorous reptiles, both *T. scripta* and *P. floridana* rely on symbiotic gut microflora to digest plant cell walls, but the longer gut length in *P. floridana* and its larger body size must provide a greater volume of microflora and more efficient digestion of plant material than *T. scripta* (Bjorndal and Bolten 1990, Bjorndal 1991). In lakes where macroalgae comprise a high proportion of the diet of turtles, growth rates of turtles may be faster than in habitats with low algal productivity. Thus, algal productivity may directly affect fitness if faster growth rates result in earlier maturity and increased lifetime reproductive output.

In addition to direct consumption of macroalgae, a stable isotope analysis of the Lake Jackson food web demonstrated that macroalgae was the primary basal resource of the food web, despite the prevalence of macrophytes (Aresco see Chapter 3). Stable isotope analyses ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) revealed that macroalgae provided full or partial contribution to the growth of 75% of 41 animal taxa sampled at Lake Jackson (Aresco see Chapter 3). The importance of periphyton is further emphasized by the finding here that lakes typically classified as oligotrophic, based on low concentrations of open water nutrients, had high periphyton productivity. In fact, periphyton productivity was not related to nutrients or chlorophyll *a* and was negatively correlated with percent surface cover of macrophytes. This result suggests that in lakes with high periphyton productivity, open water phosphorus is assimilated primarily by periphyton rather than floating and emergent macrophytes. The negative correlation between periphyton productivity and

macrophyte PAC may be due to shading of the periphyton by the macrophytes. Although not measured in this study, water clarity and light penetration may be an important factor that interacts with resources (open water phosphorus and nitrogen) to influence periphyton biomass in large lakes (Carrick and Steinman 2001).

Predation by alligators on turtles may be significant in some habitats in the southeastern United States (Delany and Abercrombie 1986, Delany et al. 1999, Amanda Rice, University of Florida, personal communication). Florida red-bellied turtles (*P. nelsoni*), peninsula cooters (*P. floridana peninsularis*), *T. scripta*, striped mud turtles (*Kinosternon baurii*), *A. ferox*, and *S. odoratus* were present in the diet of alligators in studies in north-central Florida (Delany and Abercrombie 1986, Delany et al. 1999). Although only large alligators (>3 m) may be able to capture and crush large turtles, juvenile turtles are susceptible to alligators of all size classes. Freshwater turtle populations within the range of crocodylians may have lower juvenile and adult survivorship than turtle populations that are outside the range of crocodylians. Long-term demographic studies of turtles demonstrate that populations are most sensitive to mortality rates of adults; increases in annual mortality rates (<5%) of adults can lead to population declines (Brooks et al. 1991, Congdon et al. 1993, 1994). Therefore, the presence of a significant aquatic predator on adult turtles in the some parts of the southeastern United States probably adds a limiting factor to turtle populations that is not present in other regions (Gibbons et al. 1979). The strong negative association with turtle density and presence of alligators in this study may demonstrate such an effect. However, without an experimental analysis, which was not feasible in the scope of this research, the relative importance of macrophytes, macroalgae, and alligators cannot be sorted out.

A mud or muck (organic) substrate in lakes and ponds was an important factor that was positively correlated with turtle abundance in north Florida lakes. Similarly, Marchand and Litvaitis (2004) reported that more painted turtles (*Chrysemys picta*) were captured in ponds with a muck substrate than in ponds with an inorganic substrate. In the St. Croix River in Minnesota and Wisconsin, abundances of *Chelydra serpentina*, *Chrysemys picta*, and the false map turtle (*Graptemys geographica*) were associated with muck substrates (DonnerWright et al., 1999). Substrate may indirectly affect turtle populations in two ways. First, a mud or muck substrate provides optimal microhabitat for benthic invertebrates and may also be associated with greater macrophyte or algal productivity. The covariance of chironomid larval abundance and turtle

abundance with high levels of phosphorus and a mud/muck substrate in this study suggests such an association between secondary productivity of benthic invertebrates and turtle abundance. Second, substrate type may affect survival of turtles, especially of juveniles. During extremes in temperature, especially in shallow lakes, turtles may benefit from a soft, deep, mud/muck bottom into which they can bury into during aestivation or winter dormancy. In southeastern lakes, some turtles (e.g., *T. scripta*, *C. serpentina*) may be better able to avoid predation by alligators by burying into soft mud or muck substrates than in sandy substrates.

The overlap of 4 out of 5 environmental variables associated with the abundance of both *T. scripta* and *P. floridana*, and 3 environmental variables associated with abundance of these species and *A. ferox*, suggested wide niche overlap on a coarse-scale habitat gradient in lakes and ponds in northern Florida. The abundance of all three species was strongly correlated with both top-down (no alligator predation) and bottom-up (high periphyton productivity) factors. However, within the broad predator-productivity niche space, the mechanism of coexistence and habitat distribution is probably fine-scale niche separation through partitioning of food resources that may be related to trophic and morphological differentiation among these turtle species. Thus, the pattern of correlation of abundance with environmental factors may be based on trophic position of each species in the food web.

Stable isotope analysis demonstrated that the generalist omnivore, *T. scripta*, and the specialist algivore, *P. floridana*, differ significantly in their trophic position in the food web (Aresco see Chapter 3). *Trachemys scripta* is one trophic position greater than *P. floridana* and consumes primarily arthropods and macrophytes. The pattern of abundance between *T. scripta* and *P. floridana* clearly differed in north Florida lakes. Abundance of *P. floridana* was not related to high open water phosphorus, as was *T. scripta*, whereas *T. scripta* abundance was not related to PAC as was *P. floridana*. Although there were no specific trophic-related environmental variables related to the abundance pattern of *T. scripta*, axis 2 of the PCA indicated a strong positive correlation between macroinvertebrate abundance and PAC and a negative correlation of these variables with periphyton productivity. Thus, this axis could explain the difference in the abundance patterns of *T. scripta* and *P. floridana* across the productivity gradient.

Covariation between open water phosphorus and PAC and the strong negative relationship revealed in this study between standing crop of PAC and periphyton suggests a link

between trophic position of *P. floridana* and environmental variables. Greater macroalgal resources may be available in low PAC lakes and may explain why the specialist algivore *P. floridana* had greater abundance in lakes with low PAC. Trophic position of *Apalone ferox* is significantly greater than that of *T. scripta* and it consumes greater numbers of arthropods and snails (Dalrymple 1977, Aresco see Chapter 3). Covariation between high phosphorus levels and high snail abundance suggests that abundance patterns of *A. ferox* may also be related to trophic position. Thus, the results of this study suggest that patterns of abundance of sympatric freshwater turtle species can be strongly influenced by environmental variables that are correlated with their trophic position in the food web. Within the species-specific trophic niche, intraspecific competition could be more important than exploitative interspecific resource competition in regulating population density (Aresco see Chapter 2).

Table 1.1. Summary data of lake area, primary substrate, and primary productivity as measured by open water nutrients and chlorophyll *a*, periphyton, and macrophyte biomass and percent area covered by macrophytes (PAC) for 17 study lakes in Leon County, northwestern Florida. Environmental variables were measured at each lake between May and September 2003. The lakes are ordered by size.

Lake ^a	Lake area (ha)	Substrate	Phosphorus ($\mu\text{g/L}$)	Nitrogen ($\mu\text{g/L}$)	Chlorophyll <i>a</i> ($\mu\text{g/L}$)	Periphyton ($\text{g/m}^2/\text{y}$)	Macrophyte biomass (kg wet/m^2)	PAC
Coolview Pond (TRH)	0.6	mud	72	650	7	0.38	4.85	100
Chapman Pond (TRH)	1	mud	47	380	10	3.39	6.54	100
Waverly Pond (TRH)	1.5	mud	98	1,240	40	4.00	2.84	5
McCord Pond (TRH)	2	muck	33	830	33	4.64	6.49	98
Andrew Lake (MSH)	4	sand	5	330	2	1.05	2.10	5
Trout Pond (MSH)	5	sand	11	504	6	2.83	2.26	12
Lake Tom John (TRH)	6	mud	54	920	32	7.56	1.65	12
Megginnis Arm (TRH)	8	muck	62	390	11	2.23	10.7	70
Clear Lake (MSH)	11	sand	3	290	3	5.05	4.28	10
Lofton Ponds (MSH)	11	sand	5	430	3	1.13	1.59	10
Gannett Pond (TRH)	21	muck	52	880	68	0.09	10.8	100
Little Lake Jackson (TRH)	21	muck	24	535	12	0.28	17.1	40
Moore Lake (MSH)	27	sand	5	350	3	2.52	2.78	1
Lake Piney Z (TRH)	78	muck	5	480	7	1.16	3.82	90
Orchard Pond (TRH)	85	muck	10	400	6	0.99	7.97	65

Table 1.1: Continued.

Lake Jackson (TRH)	1,620	muck	23	780	9	0.80	5.88	80
Lake Iamonia (TRH)	2,330	muck	19	860	19	1.37	11.4	88

^aPhysiographic region: TRH = Tallahassee Red Hills and MSH = Munson Sandhills.

Table 1.2. Environmental variables (and abbreviations) measured at 17 lakes in Leon County, Florida between May and September 2003.

Variable Name	Abbreviation
(1) Lake area	AREA
(2) Substrate type	SUBSTRATE
(3) Physiographic region	REGION
(4) Primary Productivity	
(a) Standing crop biomass of macrophytes	
Mean emergent macrophyte biomass	EMERGENT
Mean floating macrophyte biomass	FLOATING
Mean submerged macrophyte biomass	SUBMERGED
Mean total macrophyte biomass	BIOMASS
(b) Percent lake surface area covered by macrophytes	PAC
(c) Mean periphyton productivity	PERIPHY
(d) Mean chlorophyll <i>a</i> concentration	CHLA
(e) Mean open water total nitrogen concentration	NITR
(f) Mean open water total phosphorus concentration	PHOS
(5) Macrofauna Abundance	
Total macroinvertebrate abundance	INVERT
Total small fish abundance	FISH
Total chironomid abundance	CHIRON
Total snail abundance	SNAIL
Presence or absence of amphipods	AMPHIPOD
(6) Predator	
Presence or absence of adult alligators	ALLIGATOR

Table 1.3. Catch per unit effort (CPUE) (no./ day) of turtles trapped at lakes and ponds in Leon County, Florida, 2002-2003. At each lake two unbaited hoop traps and 30-m lead nets were set at each site for a total of 192 trap hours per lake (8 trap days). Numbers in parentheses are actual numbers of turtles trapped.

Location ^a	All Turtles	<i>P. floridana</i>	<i>T. scripta</i>	<i>A. ferox</i>
Lake Tom John (TRH)	7.75 (62)	2.00 (16)	5.63 (45)	0.125 (1)
Coolview Pond (TRH)	4.00 (32)	0.50 (4)	3.25 (26)	0.250 (2)
Waverly Pond (TRH)	3.50 (28)	1.25 (10)	1.75 (14)	0.500 (4)
McCord Pond (TRH)	3.13 (25)	0	2.25 (18)	0.875 (7)
Chapman Pond (TRH)	3.13 (25)	0.250 (2)	2.50 (20)	0.375 (3)
Lake Jackson NW (TRH)	1.63 (13)	0.375 (3)	1.25 (10)	0
Megginnis Arm (TRH)	1.63 (13)	0.375 (3)	1.25 (10)	0
Moore Lake (MSH)	1.38 (11)	1.00 (8)	0	0.375 (3)
Lake Iamonia (TRH)	1.00 (8)	0.500 (4)	0.500 (4)	0
Lofton Ponds (MSH)	0.750 (6)	0.375 (3)	0.125 (1)	0.250 (2)
Little Lake Jackson (TRH)	0.750 (6)	0.125 (1)	0.625 (5)	0
Andrew Lake (MSH)	0.500 (4)	0.250 (2)	0.250 (2)	0
Lake Piney Z (TRH)	0.375 (3)	0	0.375 (3)	0
Gannett Pond (TRH)	0.250 (2)	0	0	0.250 (2)
Clear Lake (MSH)	0.250 (2)	0.125 (1)	0	0.125 (1)
Orchard Pond (TRH)	0.125 (1)	0.125 (1)	0	0
Trout Pond (MSH)	0	0	0	0

^aPhysiographic region: TRH = Tallahassee Red Hills lakes and MSH = Munson Sandhills lakes.

Table 1.4. Comparison of relative abundance of 3 turtle species captured in Leon County, Florida by trapping during a 5-day period with 2 unbaited hoop traps and 30-m lead nets (“Trapped”) vs. overall relative abundance determined by hand-capture, trapping, and mechanical excavation (“Actual” Full Count) at 3 ponds during complete drawdown and sediment removal (Waverly Pond, March 2004; Chapman Pond, September 2003; McCord Pond, October 1999 - March 2000).

Pond/Species	Relative Abundance	
	Sample Trapped	“Actual” Full Count
Waverly Pond		
<i>Trachemys scripta</i>	0.50	0.42
<i>Pseudemys floridana</i>	0.36	0.29
<i>Apalone ferox</i>	0.14	0.27
Chapman Pond		
<i>Trachemys scripta</i>	0.77	0.73
<i>Pseudemys floridana</i>	0.07	0.10
<i>Apalone ferox</i>	0.12	0.12
McCord Pond		
<i>Trachemys scripta</i>	0.56	0.63
<i>Pseudemys floridana</i>	0	0.09
<i>Apalone ferox</i>	0.22	0.08

Table 1.5. Summary data of secondary productivity as measured by abundance (no./1.25 m²) of littoral zone macroinvertebrates (excluding snails and chironomids), fish, snails, and chironomids for 17 study lakes in Leon County, northwestern Florida. The abundance of macrofauna was determined from May to September 2003 using a 0.25-m² aluminum box sampler at 5 haphazard locations in the littoral zone of each lake where turtles typically forage (water depth 0.4 -1 m).

Lake	Macroinvertebrates	Littoral fish	Snails	Chironomids
Coolview Pond	42	0	13	18
Chapman Pond	25	43	61	0
Waverly Pond	5	135	8	3
McCord Pond	0	16	15	1
Andrew Lake	52	18	0	0
Trout Pond	11	2	0	0
Lake Tom John	48	40	0	13
Megginnis Arm	16	124	0	0
Clear Lake	46	22	0	0
Lofton Ponds	24	9	0	0
Gannett Pond	62	64	0	0
Little Lake Jackson	8	18	0	0
Moore Lake	31	43	0	1
Lake Piney Z	69	11	0	0

Table 1.5: Continued.

Orchard Pond	13	21	1	0
Lake Jackson	13	33	1	2
Lake Iamonia	66	26	0	2

Table 1.6: Spearman rank correlations (r_s) among 14 continuous environmental variables measured at 17 lakes in Leon County, Florida. The critical correlation coefficient was corrected for simultaneous tests and significant correlations ($r_s > 0.538$) are indicated in bold.

	AREA	EMERGENT	FLOATING	SUBMERGED	BIOMASS	PAC	PERIPHY	CHLA
EMERGENT	0.34							
FLOATING	0.53	0.27						
SUBMERGED	0.16	-0.26	-0.01					
BIOMASS	0.32	-0.02	0.70	0.23				
PAC	-0.04	0.31	0.46	0.03	0.61			
PERIPHY	-0.35	-0.07	-0.28	-0.33	-0.40	-0.31		
CHLA	-0.08	0.78	0.13	-0.48	0.49	0.48	0.08	
NITR	-0.02	0.54	-0.12	-0.42	0.15	0.30	-0.04	0.82
PHOS	-0.47	0.46	-0.19	-0.28	0.28	0.54	0.10	0.80
INVERT	0.28	-0.20	0.06	0.02	-0.08	0.16	-0.13	-0.16
FISH	0.10	0.44	-0.02	-0.09	0.26	-0.10	0.22	0.44
CHIRON	-0.15	-0.01	-0.41	0.06	-0.14	0.04	0.19	0.34
SNAIL	-0.47	-0.03	0.04	0.07	0.18	0.44	0.09	0.25

Table 1.6: Continued.

	NITR	PHOS	INVERT	FISH	CHIRON	SNAIL
NITR						
PHOS	0.66					
INVERT	-0.13	-0.26				
FISH	0.14	0.22	0.01			
CHIRON	0.62	0.46	-0.04	0.12		
SNAIL	0.19	0.52	-0.47	0.02	0.36	

Table 1.7. Component loadings from principal components analysis performed on the correlation matrix among 6 environmental variables from 17 lakes. Percentages below axis number represent the proportion of the total variance associated with that axis. Eigenvalues are shown in parentheses.

Variables	Axis number		
	1	2	3
	38%	25%	18%
	(2.275)	(1.474)	(1.104)
PAC	0.70	0.62	-0.16
PHOS	0.89	0.02	0.10
PERIPHY	0.11	-0.86	0.22
CHIRON	0.47	-0.08	0.80
SNAIL	0.80	-0.15	-0.22
INVERT	-0.36	0.57	0.57

Table 1.8: Pearson correlations (r) of DF 1 scores (from a discriminant function analysis of physiographic region and 6 environmental variables) and the original 6 environmental variables. An asterisk indicates a significant correlation at $P < 0.05$.

	DF 1 Score
PAC	0.80*
PERIPHY	-0.18
PHOS	0.93*
INVERT	-0.15
CHIRON	0.37
SNAIL	0.41

Table 1.9: Pearson correlations (r) of DF 1 and DF 2 scores (from a discriminant function analysis of substrate type and 6 environmental variables) and the original 6 environmental variables. An asterisk indicates a significant correlation at $P < 0.05$.

	DF 1 Score	DF 2 Score
PAC	0.04	0.82*
PERIPHY	-0.47	-0.24
PHOS	-0.43	0.87*
INVERT	-0.04	-0.16
CHIRON	-0.67*	0.25
SNAIL	-0.61	0.30

Table 1.10. Results of Mantel tests on comparisons of distance matrices of abundances of three species of turtles and environmental variables at 17 lakes in Leon Co., Florida.

Turtle abundance matrix	Environmental matrix	Mantel r	P	Correlated environmental variables
<i>Trachemys scripta</i>	SUBSTRATE, PERIPHY, PHOS, CHIRON, ALLIGATOR	0.75	0.001	high periphyton production, no alligators, mud/muck substrate, high phosphorus, high chironomid abundance
<i>Pseudemys floridana</i>	SUBSTRATE, PERIPHY, PAC CHIRON, ALLIGATOR	0.50	0.020	high periphyton production, low macrophyte surface cover, no alligators, mud substrate, high chironomid abundance
<i>Apalone ferox</i>	INVERT, PERIPHY, PHOS, SNAIL, ALLIGATOR	0.48	0.013	high periphyton production, no alligators, high phosphorus, high snail abundance, high macroinvertebrate abundance

Table 1.11. Results of a Mantel test on distance matrices of total turtle abundance and environmental variables at 17 lakes in Leon Co., Florida.

Community matrix	Environmental matrix	Mantel r	P	Correlated environmental variables
All turtles	PERIPHY, SUBSTRATE, ALLIGATOR	0.69	0.001	high periphyton production, mud/muck substrate, no alligators

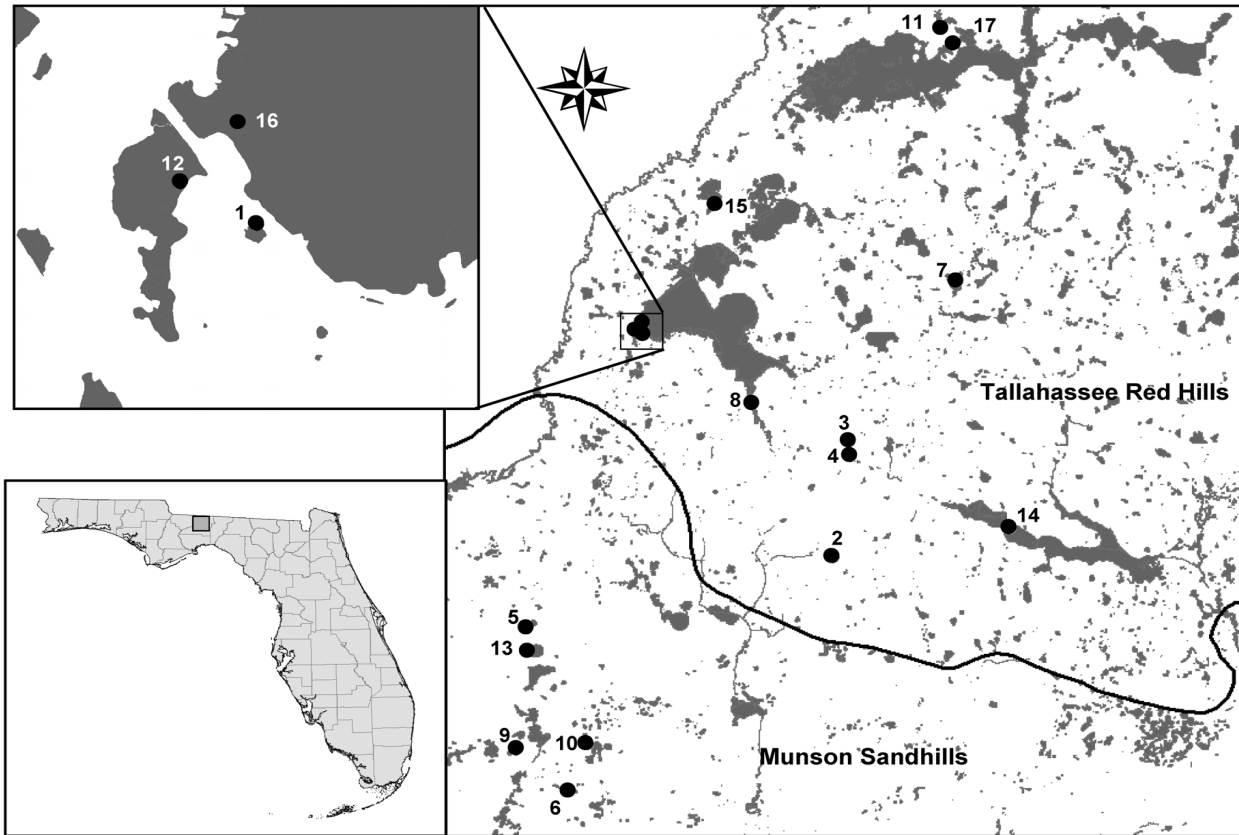


Figure 1.1. Location of 17 study lakes in Leon County, Florida. Dark line indicates separation of the Tallahassee Red Hills and Munson Sandhills physiographic regions. 1 = Coolview Pond, 2 = Chapman Pond, 3 = Waverly Pond, 4 = McCord Pond, 5 = Andrew Lake, 6 = Trout Pond, 7 = Lake Tom John, 8 = Megginis Arm, 9 = Clear Lake, 10 = Lofton Ponds, 11 = Gannett Pond, 12 = Little Lake Jackson, 13 = Moore Lake, 14 = Lake Piney Z, 15 = Orchard Pond, 16 = Lake Jackson, 17 = Lake Iamonia

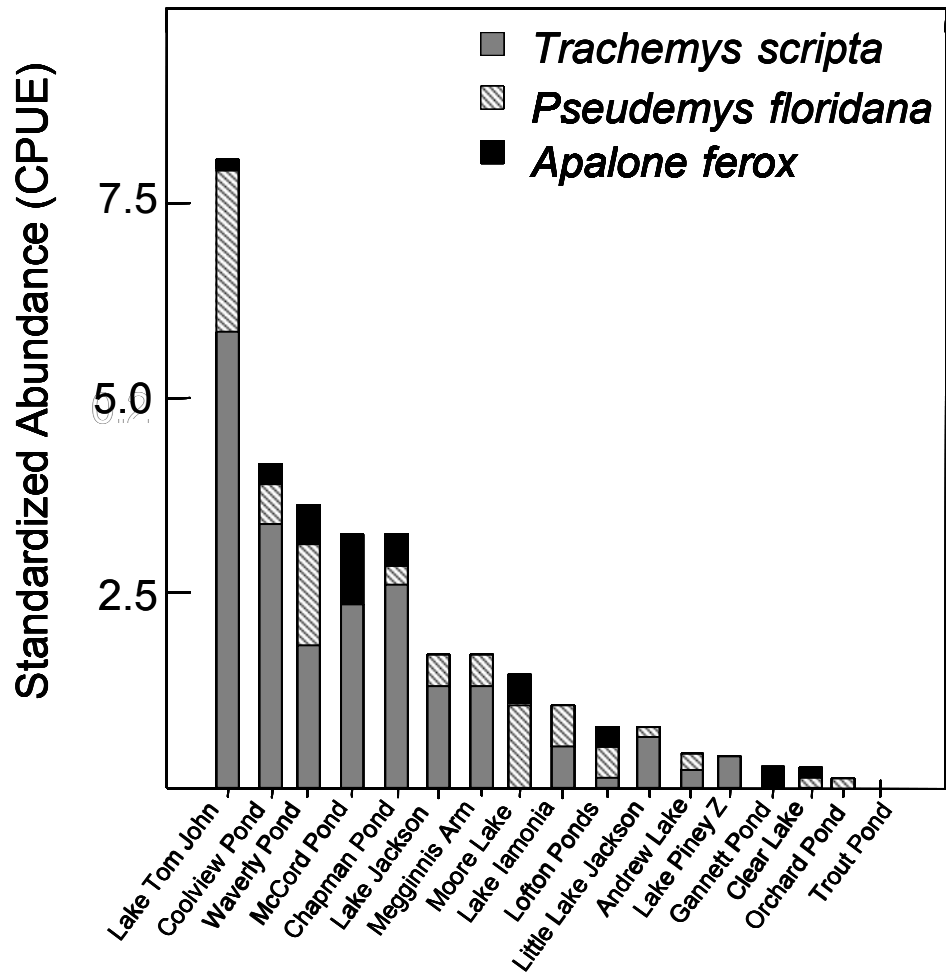


Figure 1.2. Comparison of abundance (standardized to catch per unit effort [CPUE]) (no./ day) of *Trachemys scripta*, *Pseudemys floridana*, and *Apalone ferox* trapped at 17 lakes and ponds in Leon County, Florida, 2002-2003. Two unbaited hoop traps and 30-m lead nets were set at each site for a total of 192 trap hours per lake (8 trap days).

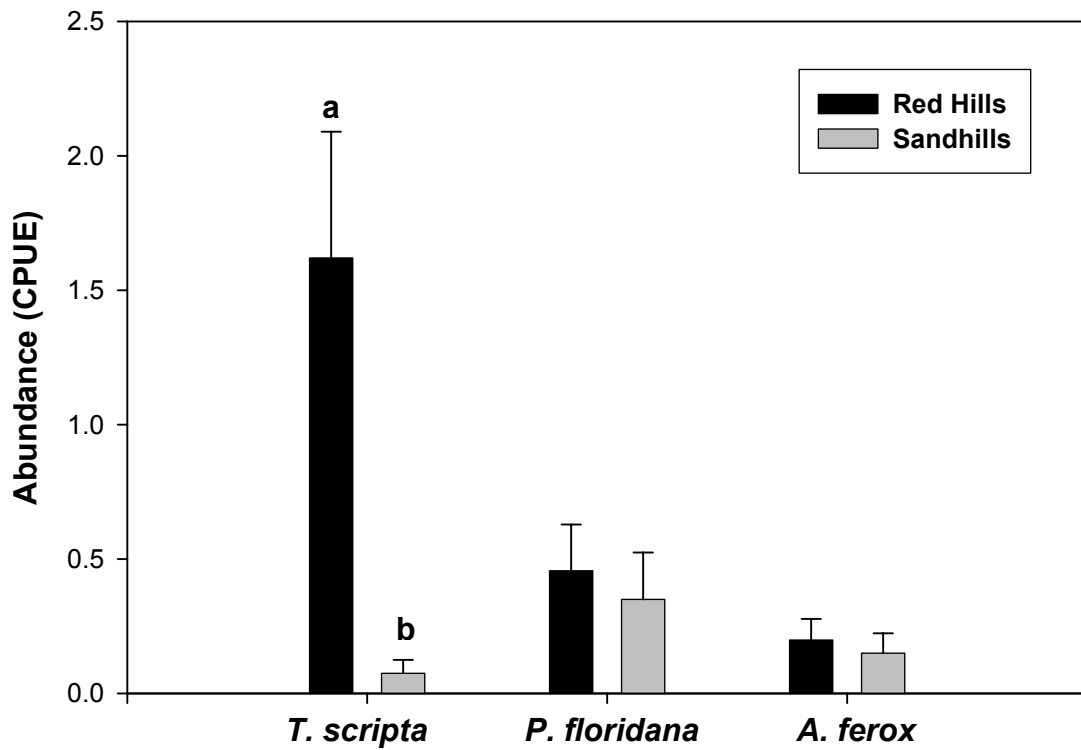


Figure 1.3. Mean catch per unit effort (CPUE) of *Trachemys scripta*, *Pseudemys floridana*, and *Apalone ferox* in the Tallahassee Red Hills lakes ($n = 12$) and the Munson Sandhills lakes ($n = 5$) trapped in Leon County, Florida, 2002-2003. Two unbaited hoop traps and 30-m lead nets were set at each site for a total of 192 trap hours per lake (8 trap days). Error bars = 1 standard error. Different letters denote a significant difference in abundance between regions.

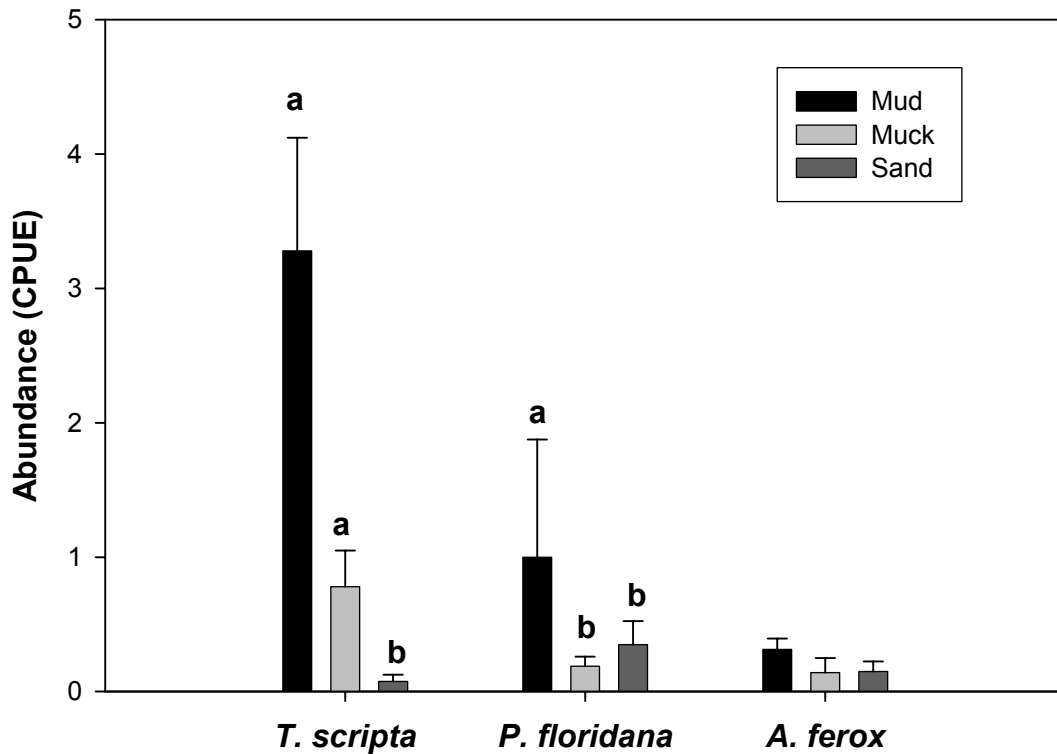


Figure 1.4. Mean catch per unit effort (CPUE) of *Trachemys scripta*, *Pseudemys floridana*, and *Apalone ferox* trapped in lakes with mud ($n = 4$), muck ($n = 8$), and sand substrates ($n = 5$) in Leon County, Florida, 2002-2003. Two unbaited hoop traps and 30-m lead nets were set at each site for a total of 192 trap hours per lake (8 trap days). Error bars = 1 standard error. Different letters denote a significant difference in abundance between substrates.

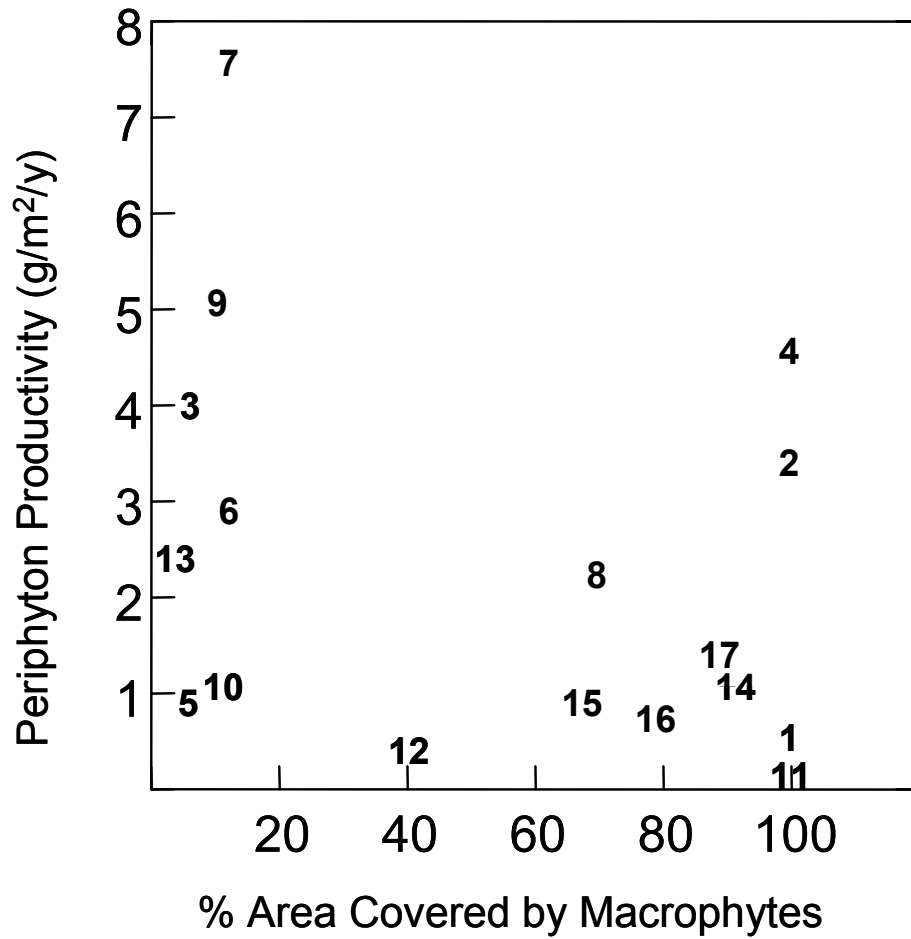


Figure 1.5. Plot of percent surface area covered by macrophytes (PAC) and periphyton productivity ($\text{g/m}^2/\text{y}$) at 17 lakes in Leon County in northern Florida. Numbers follow Fig. 1.1: 1 = Coolview Pond, 2 = Chapman Pond, 3 = Waverly Pond, 4 = McCord Pond, 5 = Andrew Lake 6 = Trout Pond, 7 = Lake Tom John, 8 = Megginis Arm, 9 = Clear Lake, 10 = Lofton Ponds, 11 = Gannett Pond, 12 = Little Lake Jackson, 13 = Moore Lake, 14 = Lake Piney Z, 15 = Orchard Pond, 16 = Lake Jackson, 17 = Lake Iamonia.

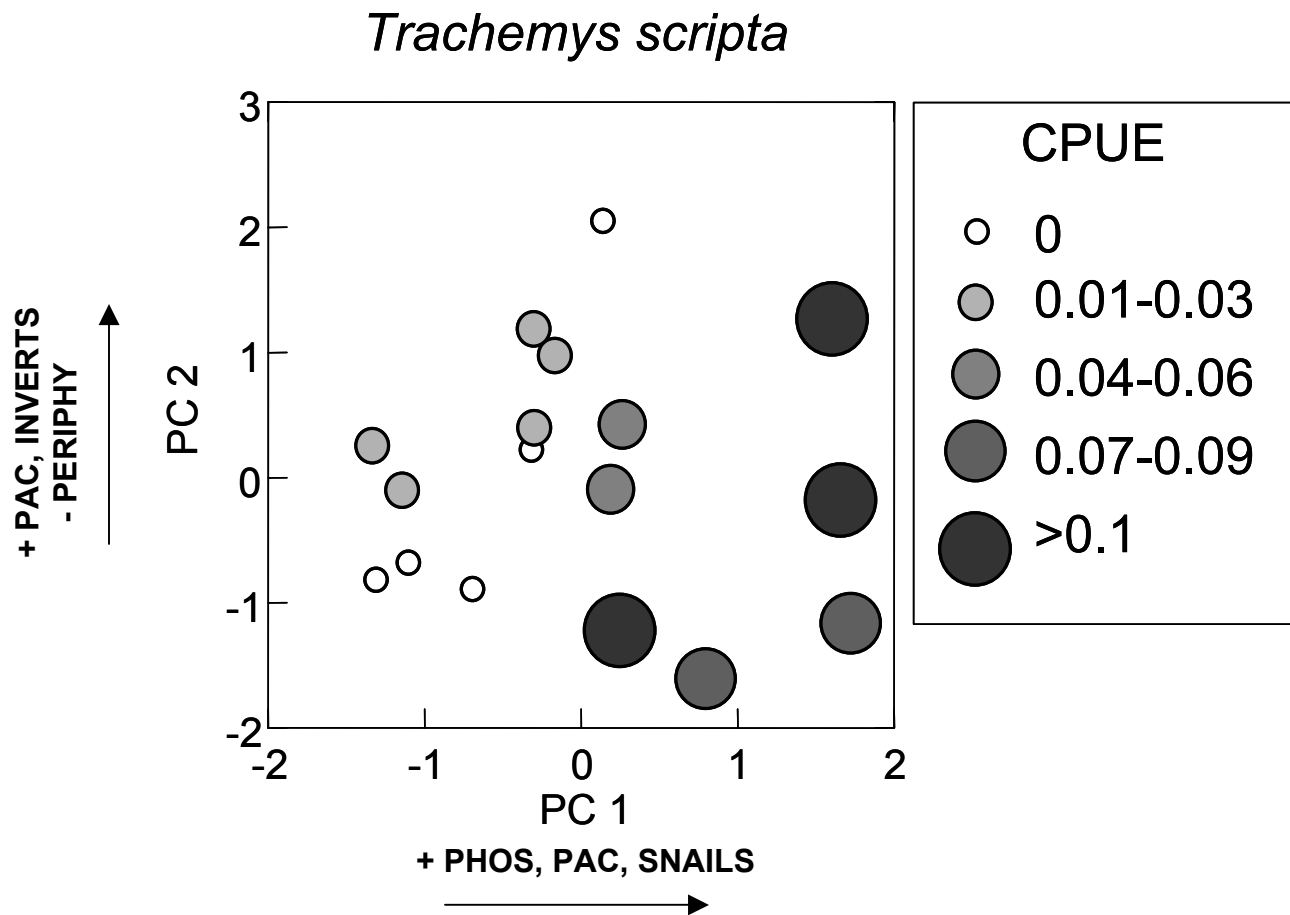


Figure 1.6. Plot of the first and second principal components axes of environmental variables of 17 lakes in Leon County, northern Florida. Sizes of the circles indicate the abundance of *Trachemys scripta* at each lake.

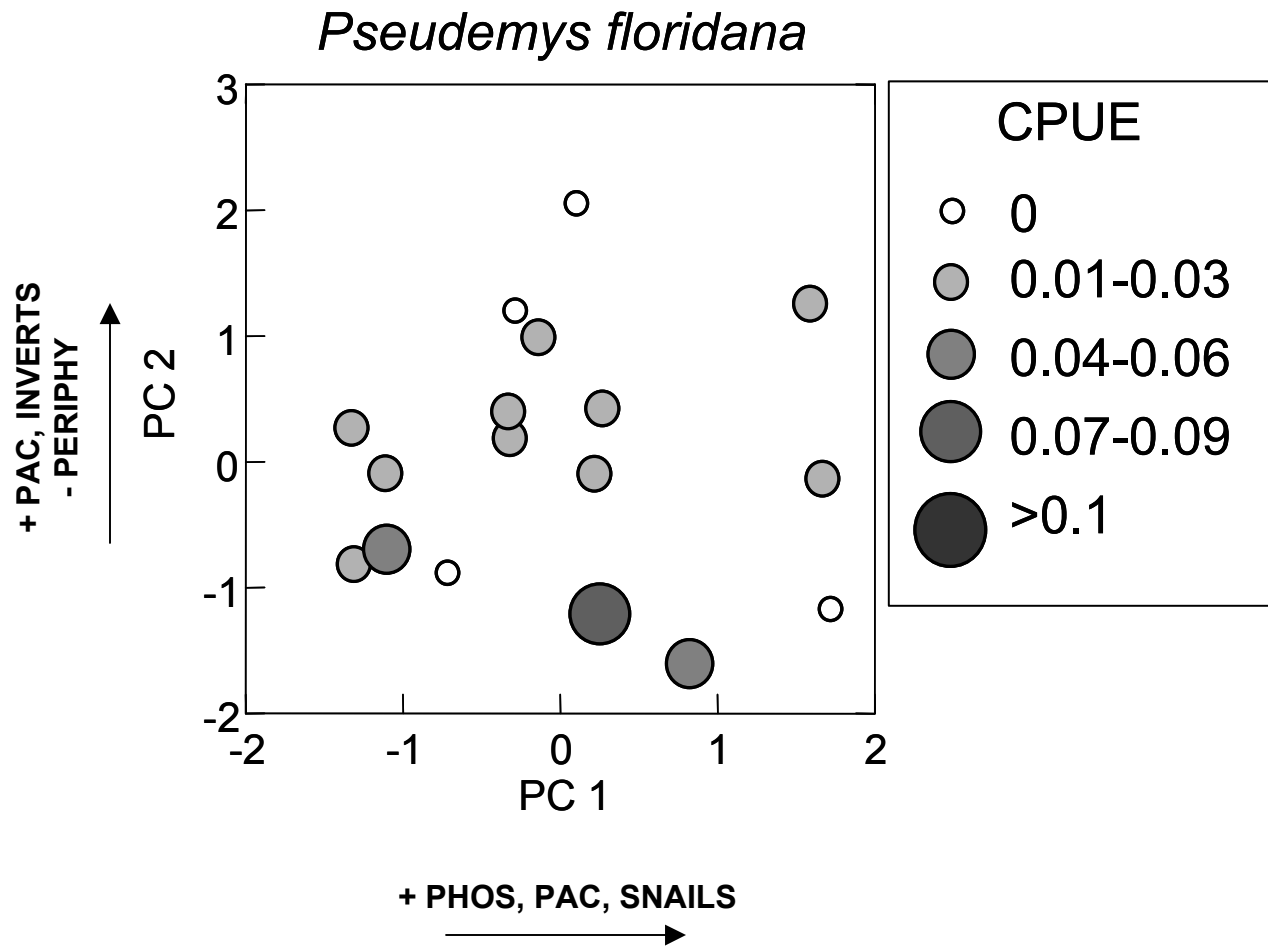


Figure 1.7. Plot of the first and second principal components axes of environmental variables of 17 lakes in Leon County, northern Florida. Sizes of the circles indicate the abundance of *Pseudemys floridana* at each lake.

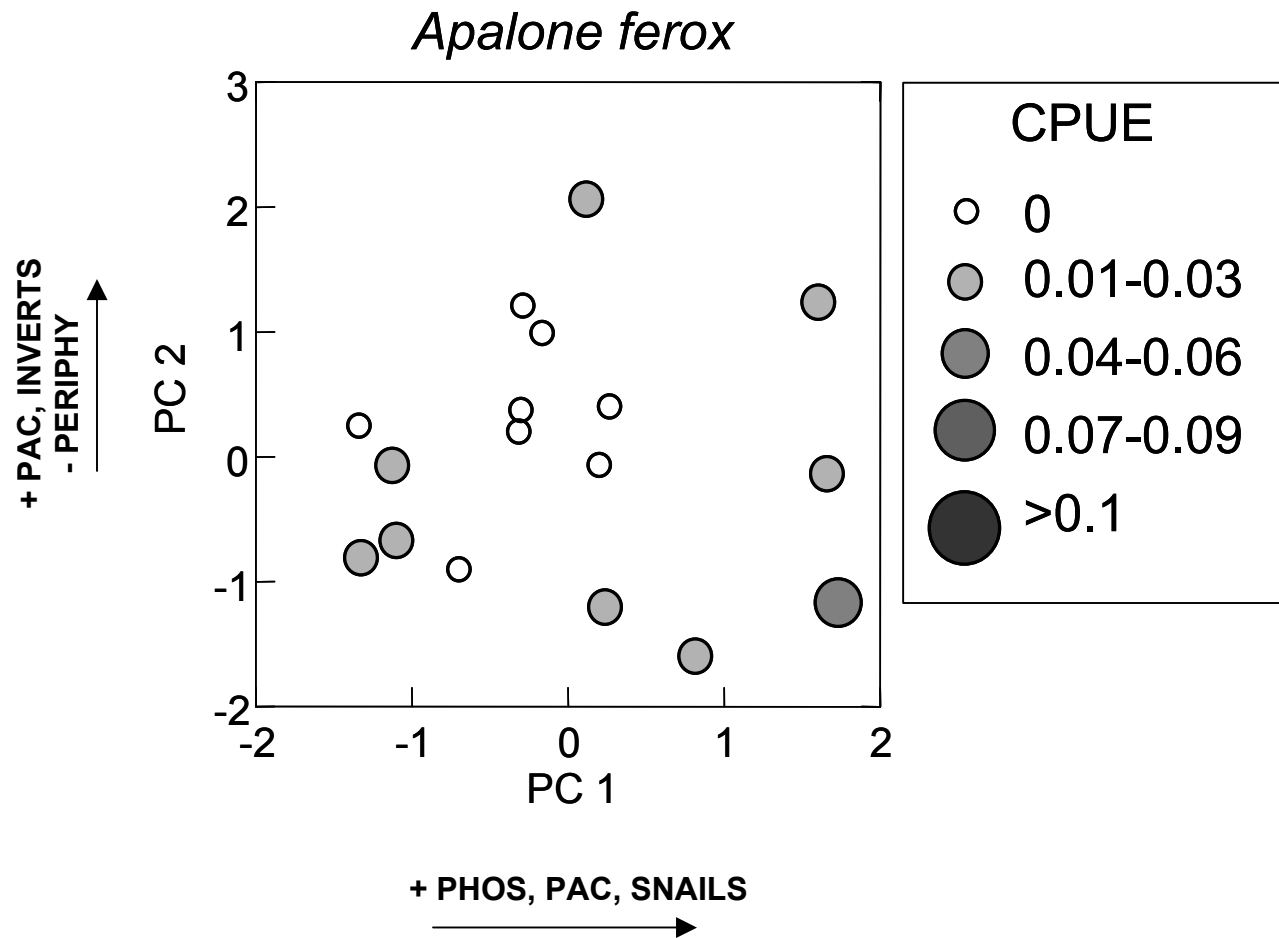


Figure 1.8. Plot of the first and second principal components axes of environmental variables of 17 lakes in Leon County, northern Florida. Sizes of the circles indicate the abundance of *Apalone ferox* at each lake.

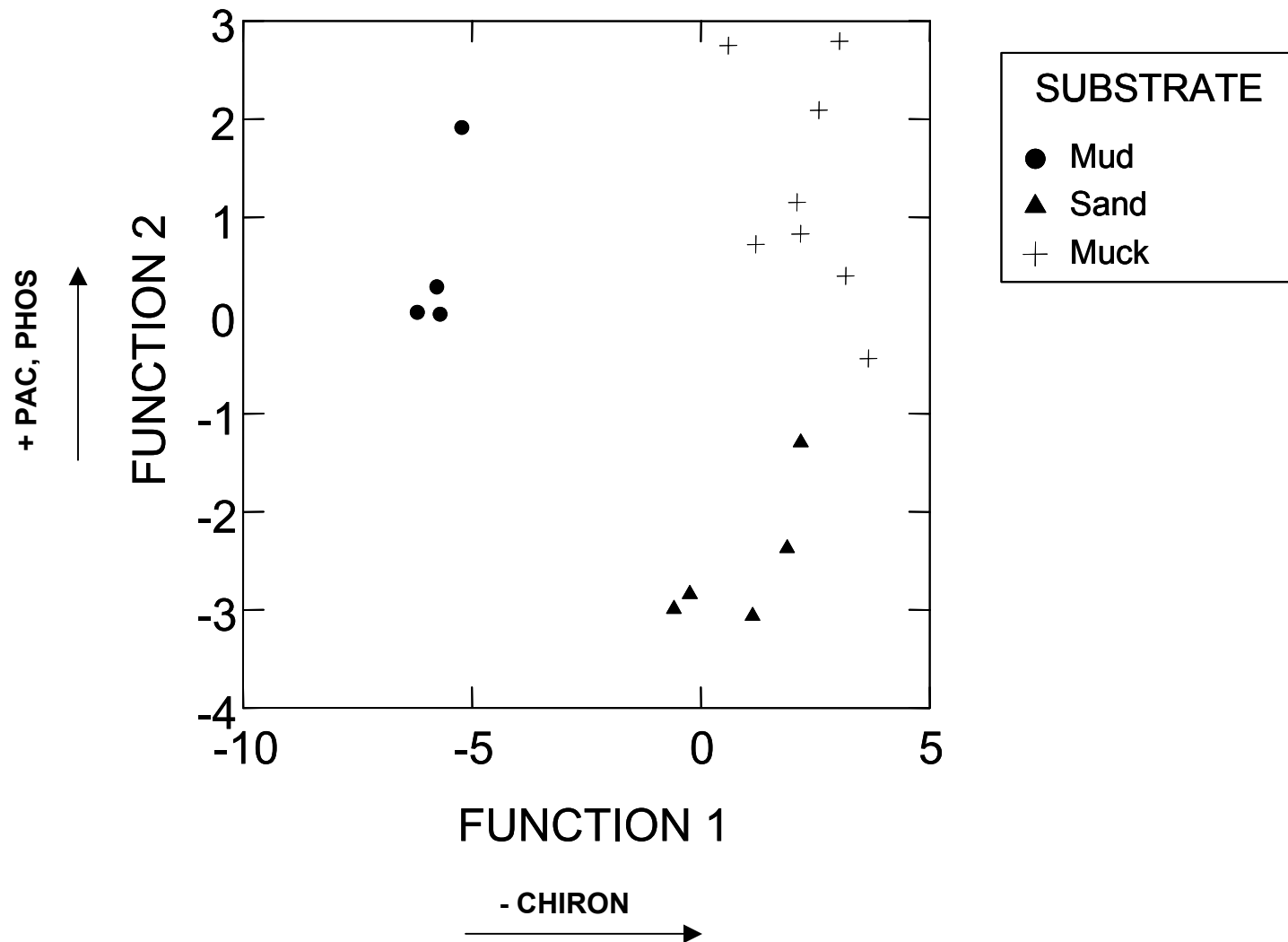


Figure 1.9. Plot of the discriminant functions of three substrate types (mud, sand, and muck) at 17 lakes in Leon County, northern Florida.

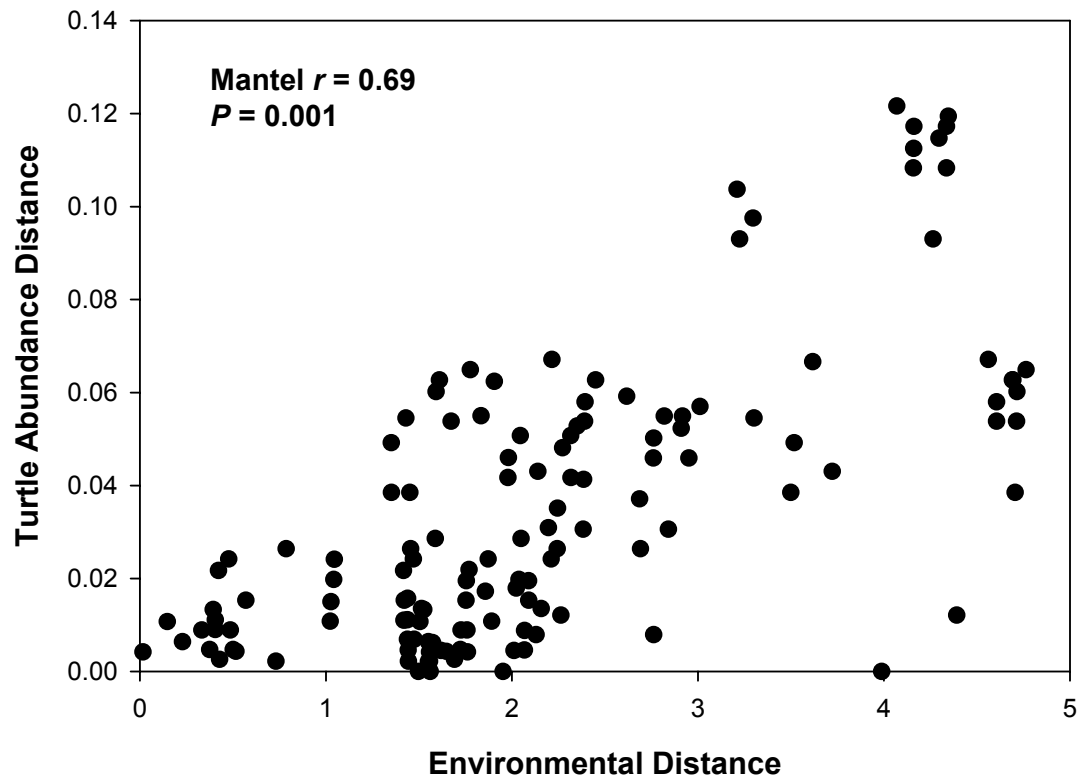


Figure 1.10. Plot of Euclidean distances between 3 environmental variables and abundances of all three species for all pairwise comparisons of 17 lakes in Leon County, northern Florida. A significant correlation (Mantel r) between the abundance matrix and the environmental matrix demonstrates that lakes similar in abundance of turtles are similar in environmental characteristics.

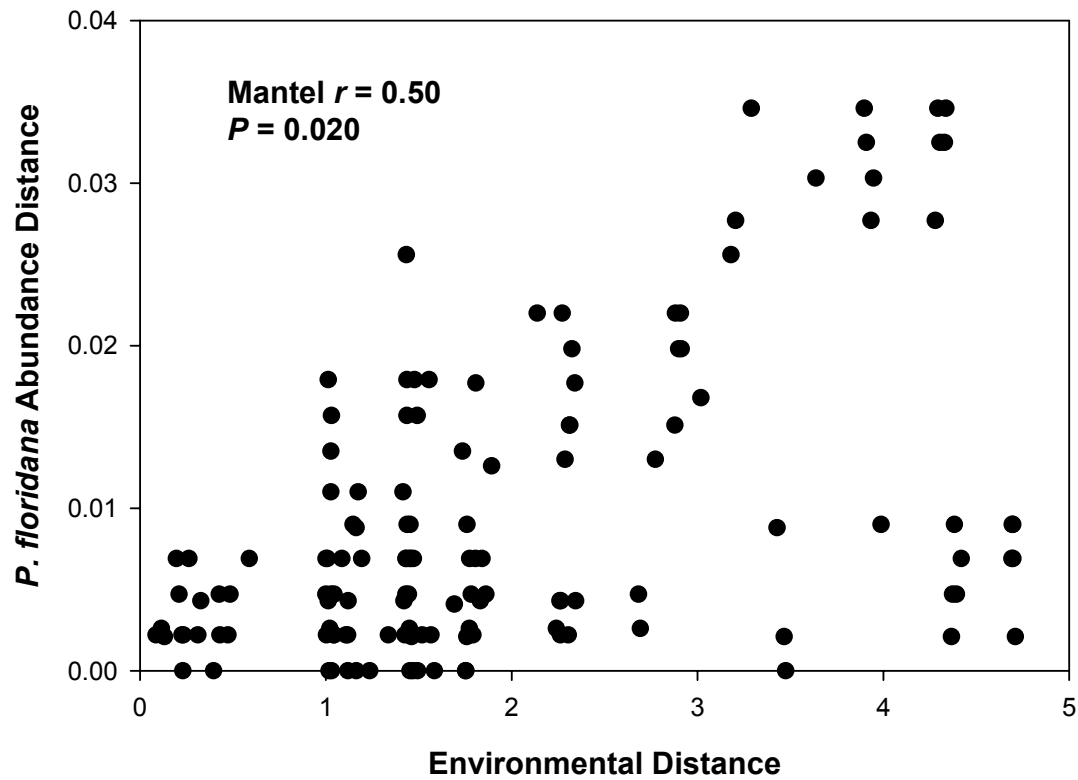


Figure 1.11. Plot of Euclidean distances between 5 environmental variables and abundance of *Pseudemys floridana* for all pairwise comparisons of 17 lakes in Leon County, northern Florida. A significant correlation (Mantel r) between the abundance matrix and the environmental matrix demonstrates that lakes similar in abundance of turtles are similar in environmental characteristics.

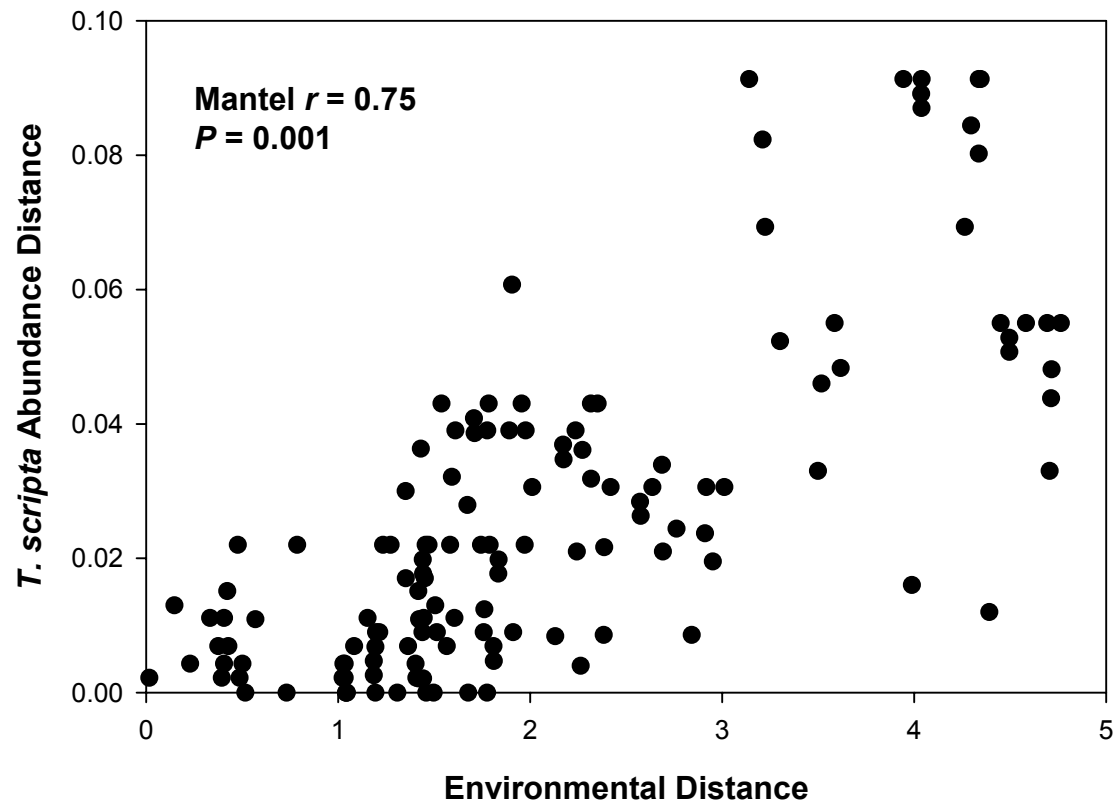


Figure 1.12. Plot of Euclidean distances between 5 environmental variables and abundance of *Trachemys scripta* for all pairwise comparisons of 17 lakes in Leon County, northern Florida. A significant correlation (Mantel r) between the abundance matrix and the environmental matrix demonstrates that lakes similar in abundance of turtles are similar in environmental characteristics.

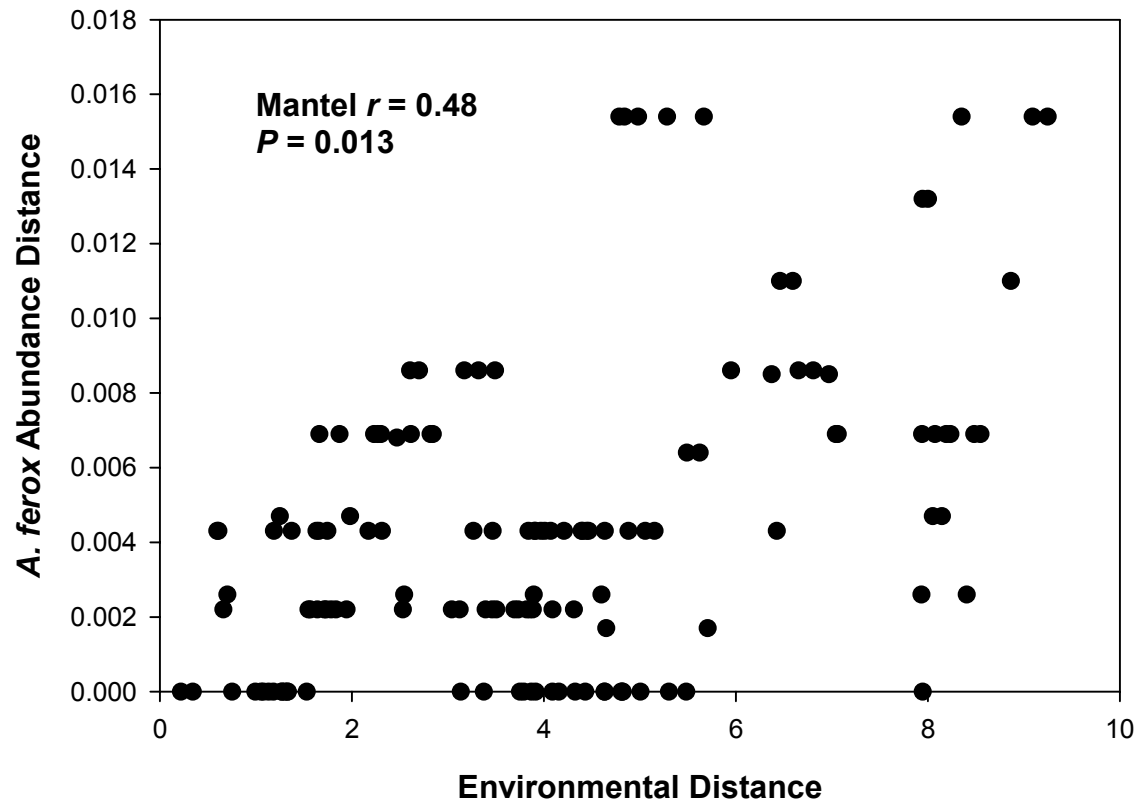


Figure 1.13. Plot of Euclidean distances between 5 environmental variables and abundance of *Apalone ferox* for all pairwise comparisons of 17 lakes in Leon County, northern Florida. A significant correlation (Mantel r) between the abundance matrix and the environmental matrix demonstrates that lakes similar in abundance of turtles are similar in environmental characteristics.

CHAPTER 2

OMNIVORY AND COMPETITION BETWEEN TWO FRESHWATER TURTLES

INTRODUCTION

The importance of interspecific competition in affecting the relative abundances of coexisting species may depend on the level of overlap of shared resources (Lawton and Strong 1981, Pacala and Roughgarden 1982, Connell 1983, Schoener 1983). Several studies have examined the influence of competition in regulating the distribution and abundance of coexisting habitat generalists and specialists (Brown 1989, Morris 1996). However, competitive interactions between diet generalists and specialists can be particularly interesting, especially when a generalist shares a particular food resource with a specialist (Chase and Belovsky 1994, Chase 1996, Beckerman 2000). Where the shared resources are abundant or other food items are available to the generalist, competition is expected to be negligible (Weins 1989). However, under conditions in which the shared resource becomes scarce (either spatially or temporally), competition with a specialist can limit the performance (e.g., growth and/or survival) of a generalist, especially if the specialist possesses unique functional or morphological features (Sanderson 1991, Ralston and Wainwright 1997).

Asymmetric competition has been demonstrated most often where one species is negatively affected by the interaction whereas the other species is not affected (Lawton and Hassell 1981, Morin and Johnson 1988, Parris and Semlitsch 1998, Inouye 1999). Such asymmetric interspecific competition can occur by exploitation competition in

which the use of limited resources by one species is optimized via morphological, or by physiological specializations or interference competition, in which a subordinate species (e.g., smaller body size) is prevented from utilizing a preferred habitat or resource (Connell 1980, Wiens 1989, Török and Tóth 1999, Bardsley and Beebee 2001, Sorenson et al 2004, Young 2004). An alternative form of competition can occur when intraspecific effects in one species are stronger than interspecific effects. Interference competition may be the primary mechanism of intraspecific competition. In environments with fluctuating resource levels and high species densities, intraspecific competition can play an important role in regulating distribution and abundance, especially with diet generalists across a productivity gradient (Belovsky and Slade 1995).

There are no previous experimental studies that have examined competition for food resources between a diet generalist and specialist (Abrams 1980, Connell 1983, Underwood 1986). Under low resource conditions the outcome of competition between a generalist omnivore and the specialized herbivore is not clear. A generalist omnivore that can easily switch between herbivory, carnivory, and scavenging, depending on the quality and quantity of resources, may have higher growth and survival rates than a competitor due to its plastic foraging strategy. Alternatively, a more specialized herbivore may outcompete a generalist omnivore if only low-quality, basal resources are available and its unique specializations allow for more efficient assimilation of nutrients needed for growth and survival. These predictions set up the potential for asymmetric competition when a specialist and a generalist are forced to divide the niche under low resource conditions. The outcome may depend on the type of limiting resource or density of hetero- or conspecifics. I propose that intraspecific effects can override interspecific effects, reducing interspecific asymmetric competition in cases in which one species can make more efficient use of a limiting resource.

Intraspecific (density-dependent regulation) and interspecific competition could interact with key environmental factors to affect turtle abundance and the composition of turtle communities (Bury 1979). However, aside from anecdotal observations and correlative studies, the relative importance of competition in structuring turtle communities is unknown (Bury 1979, Congdon and Gibbons 1996, Bodie et al. 2000). The two most abundant large freshwater turtles in lentic water habitats of northern

Florida are the yellow-bellied slider (*Trachemys scripta*) and the Florida cooter (*Pseudemys floridana*). These species are habitat generalists and coexist in virtually any lentic freshwater habitat, but their relative abundances vary widely across productivity gradients within these habitats (Cagle 1950, Mount 1975, Gibbons and Coker 1978, Ernst et al. 1994, Aresco see Chapter 1). *Trachemys scripta* exhibits greater abundances than *P. floridana* in eutrophic lakes, but is much less abundant than *P. floridana* in oligotrophic lakes (Aresco see Chapter 1, Table 1.3). *Pseudemys floridana* occurs in equal abundances in lakes across the primary productivity gradient and never attains the high densities of *T. scripta*. Thus, if competition occurs between these species, it is most likely operates in low productivity habitats. Interspecific competition may be especially important for juvenile turtles because growth during the juvenile stage affects survival probability and age at maturity, and such interactions may have long-term effects on population demography.

Omnivory may be an important factor that regulates food web dynamics and the intensity and importance of interspecific interactions (Pimm et al. 1985, Fagan 1997, Sandlin 2000). Although specialized digestive physiology is required to digest and assimilate both plant and animal tissues, omnivory is relatively common in both terrestrial and aquatic systems, especially among vertebrates (Winemiller 1990, Martinez 1991, Polis 1991).

Many aquatic omnivores exhibit ontogenetic diet shifts with size or habitat (Werner and Gilliam 1984, Diehl 1993, Polis and Strong 1996, Mittelbach et al. 1988). Diet shifts may occur gradually or rapidly and in the carnivorous to herbivorous direction or vice versa. *Trachemys scripta* is an opportunistic omnivore that feeds primarily on aquatic vegetation and invertebrates, but also scavenges on dead fish (Parmenter 1980, Parmenter and Avery 1990). In some habitats, *Trachemys scripta* exhibits an ontogenetic shift in diet from carnivory toward herbivory with an increase in body size (Clark and Gibbons 1969, Hart 1983). However, the degree of herbivory of *T. scripta* may vary with differences in the availability of plant and animal foods (Clark and Gibbons 1969, Hart 1983). In contrast, adults of *P. floridana* are reported to be entirely herbivorous, preferring filamentous algae (Allen 1938, Marchand 1942, Carr 1952, Thomas 1972, Aresco see Chapter 3). Both adult and juvenile *P. floridana* specialize on macroalgae

and do not demonstrate an ontogenetic diet shift from insects to plants as observed in other emydid turtle species (Aresco see Chapter 3). *Pseudemys floridana* has a longer gut relative to *T. scripta* and thus is more specialized to digest macrophytes and algae. Jackson (1996) reported that mean digestive tract length (stomach, small intestine, and colon) was 15% longer in *P. floridana* than in *T. scripta* of the same size. As with other herbivorous reptiles, both *T. scripta* and *P. floridana* rely on symbiotic gut microflora to digest plant cell walls, and the longer gut length in *P. floridana* and the generally larger body size provides a greater volume of microflora and more efficient digestion of plant material than *T. scripta* (Bjorndal and Bolten 1990, Bjorndal 1991).

In a high productivity lake food web in north Florida, there was a low level of resource overlap between these species as demonstrated by gut samples and stable isotope analysis (Aresco see Chapter 3). Trophic position (TP) of juvenile *T. scripta* was 3.5, greater than one position higher than that of *P. floridana* (TP = 2.3). This difference in trophic position continued in adult *T. scripta* (TP = 3.3) and *P. floridana* (TP = 2.3) (Aresco see Chapter 3). However, both species consumed macroalgae, and a decrease in lake productivity is correlated with *T. scripta* consuming greater amounts of macroalgae and an increase in similarity of its trophic niche with *P. floridana* (Aresco unpubl. data). Thus, variation in diet, coupled with the observed variation in abundance across a productivity gradient, sets up the potential for competition between these species under some conditions.

In this study, I first examined differences in the level of omnivory between hatchling *T. scripta* and *P. floridana* with a feeding experiment in the laboratory in order to evaluate the extent of shared plant and animal food resources. I then conducted a field experiment to test whether the effect of interspecific competition was greater than that of intraspecific competition between the omnivorous *T. scripta* and the specialist herbivore *P. floridana* when they were forced to share low resource conditions.

METHODS

Feeding ecology of *T. scripta* and *P. floridana*

Hatchling *T. scripta* and *P. floridana* were obtained in July 2001 from a reptile dealer who collected eggs from natural nests in northern Florida. Turtles were housed in 55-L plastic containers filled with well water to 10 cm. Because hatchling *T. scripta* and *P. floridana* forage in shallow water (<20 cm) of the littoral zone at Lake Jackson, Leon Co., Florida, and I surveyed this area for potential plant and animal foods. Duckweed (*Spirodela polyrhiza*) and filamentous and epiphytic algae (e.g., *Spirogyra*, *Cladophora*, *Chara*, *Nitella*) were the dominant sources of aquatic vegetation available as food for hatchling turtles. The most common invertebrate prey were hemipterans (*Belostoma lutarium*), odonate naiads (Libellulidae and Aeshnidae), coleopterans (*Dytiscus* sp., *Hydrophilus* sp), and grass shrimp (*Palaemonetes paludosis*). The least killifish (*Heterandria formosa*), mosquitofish (*Gambusia affinis*), and golden topminnow (*Fundulus chrysotus*) were the most abundant small vertebrates. Of these potential food sources, for this experiment I selected duckweed, *B. lutarium*, libellulid odonates, *P. paludosis*, and *H. formosa* (pre-killed to allow estimates of scavenging).

The laboratory experiment began in August 2001 when all hatchlings had fully absorbed their yolk sacs and all yolk scars were completely healed. Turtles were not fed between hatching and the start of the experiment. The experiment consisted of 5 replicates of eight treatments: two turtle types (either 1 *T. scripta* or 1 *P. floridana*), with each of either four prey types: 3 small *B. lutarium*, 7 libellulid odonate naiads, 3 *P. paludosis*, or 5 dead *H. formosa*. The number of prey was based on consumption rates of hatchling turtles in feeding trials. All treatments also contained 2 g duckweed. Duckweed and live prey were added to 55-L plastic experimental containers 24 hours prior to the addition of a hatchling turtle, the dead *H. formosa* were added simultaneously with the hatchling turtle. Turtles were allowed to forage for 24 hours; then they were removed; all remaining duckweed was weighed and prey animals were counted.

First, I pooled the number of the *B. lutarium*, libellulid naiads, *P. paludosis*, and dead *H. formosa* consumed into a single category: animal prey. Data were natural log transformed to meet the assumptions of normality. I compared the amount of duckweed

and number of animal prey consumed between *T. scripta* and *P. floridana* with ANOVA (SYSTAT 9). Second, I examined differences in the numbers of each type of animal prey (dead *H. formosa*, *B. lutarium*, libellulid naiads, and *P. paludosis*) consumed by *T. scripta* and *P. floridana*. I used two-sample *t*-tests (SYSTAT 9) to determine differences between each species for each prey type.

Competition Between *T. scripta* and *P. floridana*

I performed a field experiment with *P. floridana* and *T. scripta* to test the predictions that asymmetric competition may occur when these species are forced to divide the niche under low resource conditions and that the outcome of the competitive interaction may depend on the type of the limiting resource. The substitutive experimental design maintained the same overall turtle density in each treatment, but one species was substituted for another in the mixed species treatment. This experimental design evaluates whether intraspecific competition is equal to interspecific competition but not the magnitude of intra- or interspecific competition.

I chose a substitutive experimental design because of limitations in the number of juvenile turtles available for proper replication of an additive or response surface competition experiment (Inouye 2001). This design tests whether one species exhibits slower growth or lower survival under intraspecific versus interspecific competition (= competitive equivalence) with *a priori* comparisons that analyze each species separately: *P. floridana* alone to *P. floridana* with *T. scripta* and *T. scripta*, alone to *T. scripta* with *P. floridana*. Because turtles in the mixed species treatment are in the same cages, they are not independent and cannot be directly compared to each other.

This long-term experiment was conducted from 11 July 2002 to 3 August 2003 at Gannett Pond, a 21-ha pond on the property of the Tall Timbers Research Station, near Lake Iamonia, Leon County, Florida (Fig. 2.1). Gannett Pond is shallow (1 to 2-m depth) lake with muck substrate and has a littoral zone dominated by emergent macrophytes (maidencane grass, *Panicum hemitomon*; arrowhead, *Sagittaria latifolia*; pickerelweed, *Pontedaria cordata*, frog's-bit (*Limnobium spongia*), and macroalgae (*Chara*). Its deeper-water zone is completely covered with water lilies (*Nymphaea odorata*, *Nelumbo lutea*). Submerged plants were primarily bladderworts (*Utricularia* sp). The experiment

was set up under low resource, drought conditions. Water levels had receded from the normal littoral zone and only water lilies, macroalgae (*Chara*), and *Utricularia* were present. Juvenile (1-2 years old) *P. floridana* and *T. scripta* were used in the experiment because their growth rates during this stage are measurable over the time period of this experiment (approximately 1 year). Growth rate is a key demographic variable that directly determines age at maturity in turtles (Dunham and Gibbons 1990). The experiment consisted of six replicates of three treatments (4 *P. floridana* [CC], 4 *T. scripta* [SS], or 2 *P. floridana* + 2 *T. scripta* [CS and SC]). Turtles in each cage were matched for size. Stocking densities of turtles were consistent with the high field densities of juveniles produced after several good reproductive years (i.e., several cohorts in the juvenile size range) (Aresco unpubl. data). I constructed 18 1-m² enclosures using 1.3 cm mesh, galvanized metal hardware cloth. This mesh size allowed movement of small fish and invertebrates into the cages but prevented turtles from escaping. Cages were secured to the pond bottom in the littoral zone with wooden stakes at a depth of 30-40 cm. Cages within a block were located 1 m apart, and each block was located 5 m apart. Equal amounts of aquatic vegetation (e.g., *Utricularia* sp., *L. spongia*, *Chara* sp.) were initially added to each cage. Cages were stocked with turtles on 11 July 2002, and each turtle was individually marked with notches on the rear marginal scutes.

Water levels and cages were monitored weekly and cages had to be relocated in response to fluctuating water levels. Cages were relocated 6 times during July - September 2002, so that a cage depth could be maintained between 30 and 40 cm. I installed bottoms on the cages on 16 August using hardware cloth in order to facilitate recapturing the turtles and quickly moving cages. I moved all 18 cages to deeper water 11 times between 26 July 2002 and 24 February 2003. In early March 2003, heavy rain and flooding caused the pond level to rise 50 cm in 48 hours and almost completely covered the tops of cages in blocks 1-5 and completely covered cages in block 6. All except 3 turtles escaped from cages in block 6 and others escaped from cages in blocks 1-5. Therefore, block 6 was eliminated from the experiment and cages in other blocks that lost at least 3 turtles were also eliminated. Missing turtles in three cages were replaced to restore the proper cage density for the final 4 months of the experiment, but these turtles were not used in the analysis. Subsequent drying required moving cages again to deeper

water 3 times in April-May 2003. Heavy rains in early June required moving all cages to shallower water on 13 June 2003, where they remained until 2 August 2003. Thus, the final design consisted of the following replication of treatments: SS (n = 4), CC (n = 4), CS and SC (n = 5). The response variables for this experiment were growth rates of turtles over the course of the experiment and diet of turtles at the end of the experiment. Plastron length (PL) of each turtle was measured at the start of experiment on 11 July 2002 and at the end of the experiment on 2 August 2003 (387 days). Growth rates of turtles (final PL – initial PL) among 3 treatment levels (CC, SS, CS and SC) were compared using ANOVA and *a posteriori* contrast tests (CC-CS contrast: -1 +1 0 0 and SS-SC contrast: 0 0 +1 -1) in SYSTAT 9. Diet analysis was conducted from fecal samples collected from each turtle at the end of the experiment. Each fecal sample was examined with a dissecting scope for insect parts, algae, and other diet items. I determined the number of insects in each sample by matching wings, thorax, and head parts. Mean number of insects per turtle among treatments was compared with ANOVA. Data were square root transformed to meet the assumptions of normality. I also scored whether or not each fecal sample contained macroalgae and compared the number of turtles with and without algae among treatments using a Pearson chi-square.

RESULTS

Degree of Omnivory of *T. scripta* and *P. floridana*

The foraging experiment confirmed that both species of turtles are omnivorous in the juvenile stage, but that *T. scripta* is more carnivorous than *P. floridana*. When offered a choice between duckweed and animal prey, naive hatchling *P. floridana* ate significantly more duckweed than did *T. scripta* (ANOVA, $F = 4.11$, $P = 0.050$), and hatchling *T. scripta* ate 2 times more animal prey than did *P. floridana* (ANOVA, $F = 5.95$, $P = 0.019$) (Fig. 2.2).

Although both species were omnivorous, there were striking differences in the numbers of the type of prey consumed between *P. floridana* and *T. scripta*. Two-sample *t*-tests indicated that *T. scripta* consumed a significantly greater number of *B. lutarium* ($t = -2.496$, $P = 0.037$), libellulids ($t = -3.40$, $P = 0.047$), and dead *H. formosa* ($t = -1.294$, P

= 0.046) than did *P. floridana* (Fig. 2.3). However, few *P. paludosis* were consumed by either species, with no difference in mean number eaten.

Competition Between *T. scripta* and *P. floridana*

Differences in growth rates among the 3 treatments in the field experiment were marginally significant ($P = 0.11$, $F = 2.37$, $df = 3, 14$) (Table 2.1). More importantly, *a posteriori* contrast tests indicated that growth rates of *T. scripta* in combination with *P. floridana* were significantly greater than growth of *T. scripta* under intraspecific competition ($P = 0.028$, $F = 5.98$, $df = 1, 14$) (Fig. 2.4). However, there was no difference in growth between *P. floridana* in the presence of *T. scripta* and *P. floridana* alone (Fig. 2.4). Therefore, in terms of their effects, *Pseudemys floridana* views one *T. scripta* as equal to one *P. floridana*, but *T. scripta* views one *P. floridana* as less than one *T. scripta*.

The overall ANOVA of the number of insects eaten by turtles determined from fecal contents demonstrated a significant treatment effect ($P = 0.013$, $F = 4.95$, $df = 3, 16$) (Table 2.1). *A posteriori* contrasts tested the hypothesis that turtles in treatments with greater growth rates consumed more insects. *Trachemys scripta* with conspecifics ate fewer insects per turtle than with *P. floridana*, although this contrast was not statistically significant ($P = 0.11$, $F = 2.83$, $df = 1, 16$) (Fig. 2.5). This pattern follows the trend of *T. scripta* having lower growth rates with conspecifics than heterospecifics. Seventy-four percent of turtles at the end of the experiment had consumed some macroalgae, but there were no differences in the number of turtles among treatments with and without algae in their gut contents (Table 2.1).

DISCUSSION

Degree of Omnivory

The foraging experiment indicated that, although both *P. floridana* and *T. scripta* are omnivorous in the juvenile stage, there are striking differences in the amount of plants and animals consumed and the degree of omnivory. Because naïve, recently-hatched turtles were tested individually, the experiment demonstrates inherent differences in the

dietary preferences of these species under these conditions. A diet consisting of plants and insects may be adaptive in some turtles, as mixed diets have been demonstrated to be important to their nutritional requirements and growth (Bjorndal 1991).

In a diet study conducted at Lake Jackson, Leon Co., Florida, *T. scripta* ate significantly more insects and scavenged more on dead fish than did *P. floridana* (Aresco see Chapter 3). The low level of resource overlap between these species in the foraging experiment was also consistent with an analysis of trophic position (TP) of turtles using stable isotopes (Aresco see Chapter 3). At Lake Jackson, TP of juvenile *T. scripta* was 3.5, one position greater than that of *P. floridana* (TP = 2.3). This difference in TP continued in adult *T. scripta* (TP = 3.3) and *P. floridana* (TP = 2.3), with no evidence of the dietary shift towards herbivory in adult *T. scripta* that has been reported elsewhere (Clark and Gibbons 1969, Parmenter and Avery, 1990). At Lake Jackson, gut contents indicated that the difference in TP was due primarily to greater consumption of predatory arthropods by juvenile and adult *T. scripta* (Aresco see Chapter 3). Parmenter (1980) suggested that in habitats with sufficient fish carrion, an ontogenetic shift in diet of *T. scripta* should be reduced or not occur at all, as adults can maintain an optimal benefit:cost ratio of energy expenditure by feeding on dead fish rather than plants. At Lake Jackson, frequent water level and water temperature fluctuations provide the conditions for fish carrion to be available to scavengers. During full and partial drydowns of this sinkhole lake, thousands of dead fish become available to scavengers. Some turtles (e.g., *T. scripta* and *S. odoratus*) foraged extensively on this food source. In contrast, *P. floridana* migrated from drying pools much earlier in the drying cycle than *T. scripta* and did not scavenge on carrion (Aresco unpubl. data). Hence, the trophic position of turtles such as *T. scripta* are elevated by scavenging on predatory fish or by feeding on predatory arthropods that occupy a similar or greater trophic position. In habitats without scavenging opportunities or lower abundance of insects, it is more energetically efficient for adult *T. scripta* to eat plants or macroalgae than to search for insect prey (Parmenter and Avery 1990). Thus, the trophic position of *T. scripta* is lower in such habitats and more similar to that of the herbivorous *P. floridana*.

Competitive Interactions of *T. scripta* and *P. floridana*

The outcome of competition between coexisting turtle species may be determined by competitive exclusion through aggressive interactions or exploitation competition through greater foraging efficiency on fast-moving (high protein) prey or greater digestive efficiency of plants and algae (Webb 1962, Lardie 1965, Auth 1975, Bjorndal and Bolten 1990, Jackson 1996). When forced to divide the niche under low resource conditions, as in this study, *P. floridana* grew the same with both *T. scripta* and with conspecifics. However, *T. scripta* grew more slowly with conspecifics than with *P. floridana*. This experimental result suggested intraspecific competition in one species - the intraspecific effect of *T. scripta* on conspecifics was stronger than any interspecific effect.

Trachemys scripta and *P. floridana* are habitat generalists that occur across a range of lentic habitats that vary in quantity and quality of food. *Trachemys scripta* exhibits greater abundances than *P. floridana* in eutrophic lakes, but is much less abundant than *P. floridana* in oligotrophic lakes (Aresco see Chapter 1). Although *T. scripta* can switch between herbivory, carnivory, and scavenging, depending on the quality and quantity of available resources, *P. floridana*, an herbivore with specializations that allow for more efficient assimilation of nutrients, can perform better than a generalist omnivore if only low-quality, basal resources are available (Bjorndal and Bolten 1990). Thus, the outcome of competition in this study depended on the type of the limiting resource for each species (Osenberg 1989, Osenberg and Mittelbach 1996). For *T. scripta*, low abundance of invertebrate prey was apparently limiting, resulting in an intraspecific effect on growth. In contrast, *P. floridana* ate the only consistently available food source, macroalgae, and grew equally well with both *T. scripta* and conspecifics. Thus, the low abundance of *T. scripta* in oligotrophic lakes where periphyton is the primary basal resource may be caused in part by intraspecific competition rather than competition with *P. floridana* (Aresco see Chapter 1). A possible mechanism for intraspecific competition in *T. scripta* for limited resources is aggressive interactions among conspecifics (Cahn 1937, Lardie 1983, Kramer 1986).

Previous research has demonstrated a strong positive association between turtle abundance and high primary productivity in terms of macroalgae (Aresco see Chapter 1). At Lake Jackson, Florida, macroalgae (e.g., *Spirogyra*, *Nitella*, *Chara*) were a primary

food *P. floridana*, whereas *T. scripta* consumed insects, macrophytes, and macroalgae. In contrast, in low productivity lakes, *T. scripta* consumes greater amounts of macroalgae and its trophic niche is more similar to that of *P. floridana* (i.e., lower trophic position) (Aresco unpubl. data). In other studies, macroalgae (e.g., *Cladophora* sp.) were a large portion of the diet of *Pseudemys* spp. and *T. scripta* (Parmenter 1980, Lagueux et al. 1995). Resource edibility and digestibility can have an important influence on trophic interactions (Leibold 1989). Algae are more digestible than fibrous macrophytes and are higher in protein (Boyd and Lawrence 1967). In low productivity lakes where macroalgae comprise a high proportion of the diet of turtles, differential growth rates between turtle species may affect abundance. Because turtles attain sexual maturity at a minimum size rather than a specific age, variation in growth rates can result in a differential age at maturity among populations, which can have fitness consequences (Dunham and Gibbons 1990). Thus, algal productivity may directly affect fitness if faster growth rates result in earlier maturity and increased lifetime reproductive output. The results of this study suggest that in oligotrophic lakes, intraspecific effects can override interspecific effects, reducing interspecific competition where one species can make more efficient use of macroalgae, a potentially limiting resource.

Omnivory with an ontogenetic diet shift is a relatively common feeding pattern in freshwater systems and is often correlated with wide flexibility in habitat requirements (Polis et al. 1989, Lodge et al. 1994, Diehl 1995, Polis and Strong 1996). Omnivory may be an adaptive strategy in complex aquatic systems if omnivores can meet their energy needs more consistently and efficiently than competitors despite temporal and spatial resource variability (Holyoak and Sachdev 1998). A generalist omnivore may have an advantage over a specialist in high productivity environments, but inefficient conversion rates and intraspecific competition may limit density in low resource environments (Diehl and Feißel 2000). In contrast, a trophic specialist that is also a habitat generalist may be equally abundant and competitively superior in both high and low productivity environments if it can maintain equal growth rates compared to a trophic generalist. Evidence from this study suggests that to maintain sufficient growth rates across a productivity gradient, an optimal foraging strategy may be low levels of omnivory and high specialization on minimum basal resources (Persson et al. 1996). The trade-off

could be that population density of a specialist equals but never exceeds that of species with high levels of omnivory. Long-term manipulative field experiments could test this hypothesis and would help to clarify the outcome of competition between trophic generalist and specialists across a productivity gradient

Table 2.1. Summary statistics among 4 treatments in a 13-month field experiment designed to test equivalence of interspecific and intraspecific competition between juveniles of *Trachemys scripta* and *Pseudemys floridana*. The experiment was conducted from 11 July 2002 to 3 August 2003 at Gannett Pond, a 21-ha lake, Leon County, Florida. Data reported are mean growth rate (mm/yr), mean number of insects in gut contents at final sampling, and mean percent of turtles with algae in gut contents at final sampling. Sample size indicates the number of replicates of each treatment and SD is indicated in parentheses.

Treatment	Growth rate (mm/yr)	No. insects in gut	% with algae in gut
<i>P. floridana</i> ($n = 4$)	2.3 (2.6)	0.23 (0.33)	0.71 (0.27)
<i>T. scripta</i> ($n = 4$)	0.98 (0.30)	2.4 (1.4)	0.63 (0.48)
<i>P. floridana</i> (with <i>T. scripta</i>) ($n = 5$)	1.5 (1.7)	1.1 (0.45)	0.88 (0.25)
<i>T. scripta</i> (with <i>P. floridana</i>) ($n = 5$)	3.5 (1.9)	4.3 (4.8)	0.75 (0.50)

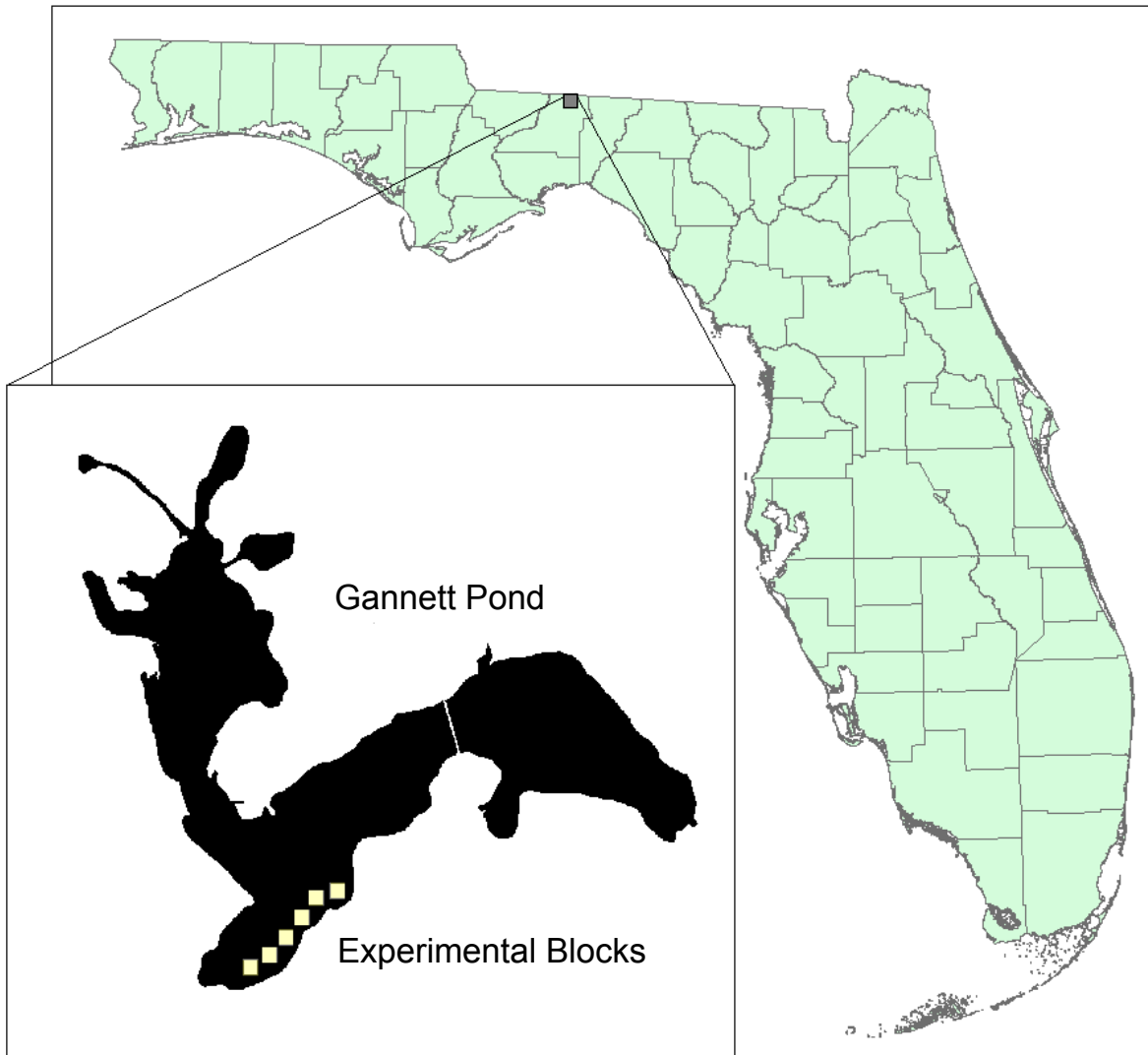


Figure 2.1. Location of Gannett Pond on Tall Timbers Research Station in northern Leon County, Florida where a 13-month field experiment was conducted to evaluate competitive interactions among juvenile *Trachemys scripta* and *Pseudemys floridana*. The location of 6 experimental blocks (3 cage treatments per block) is shown in the southwestern part of the pond.

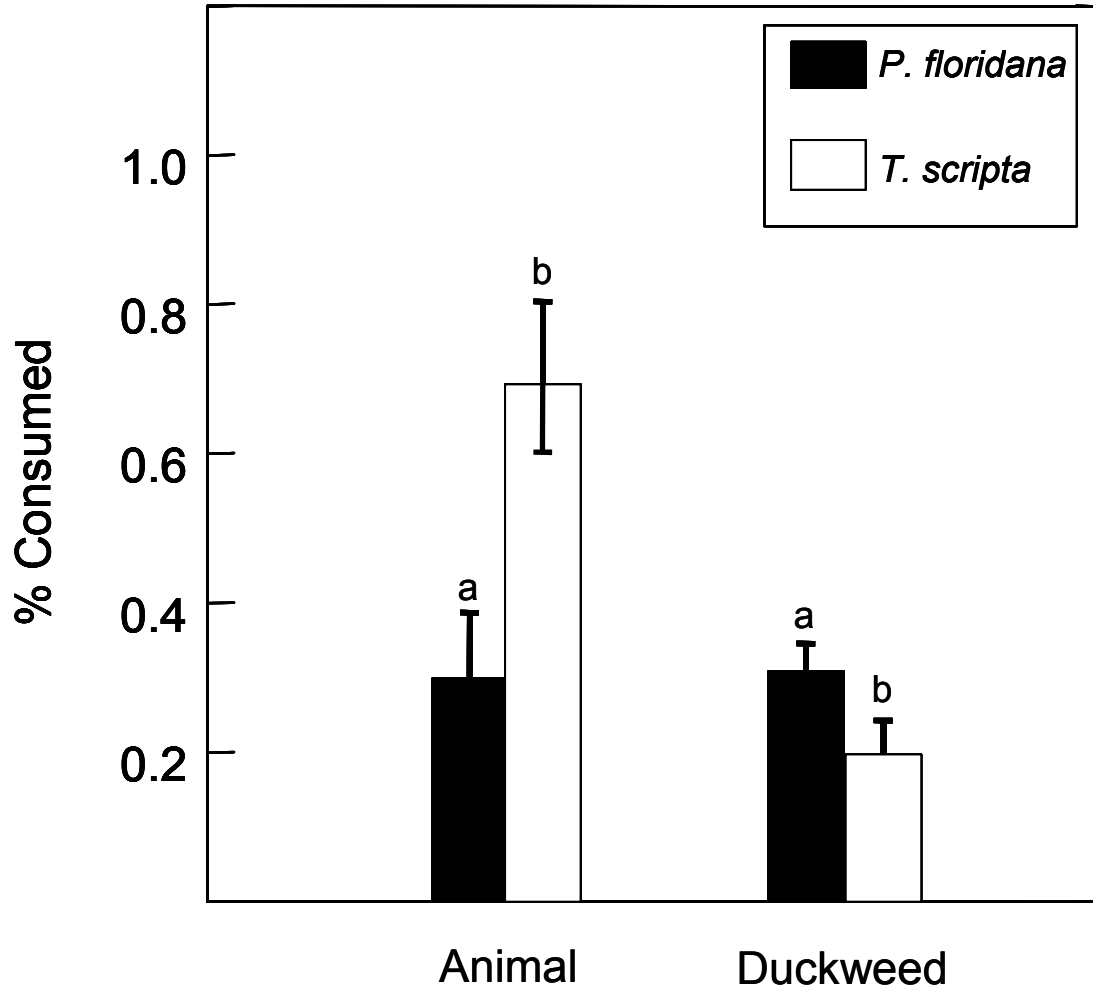


Figure 2.2. Comparison of percent animal prey (*Belostoma lutarium*, libellulid odonate naiads, grass shrimp and fish carrion of *Heterandria formosa*), and duckweed eaten by hatchling *Trachemys scripta* and *Pseudemys floridana* in a laboratory experiment. The experiment was conducted in the laboratory in August 2001 in 55-L experimental containers (glass aquaria). Turtles were hatched from eggs collected in northern Florida and were not fed between hatching and the start of the experiment. Error bars equal ± 1 SD.

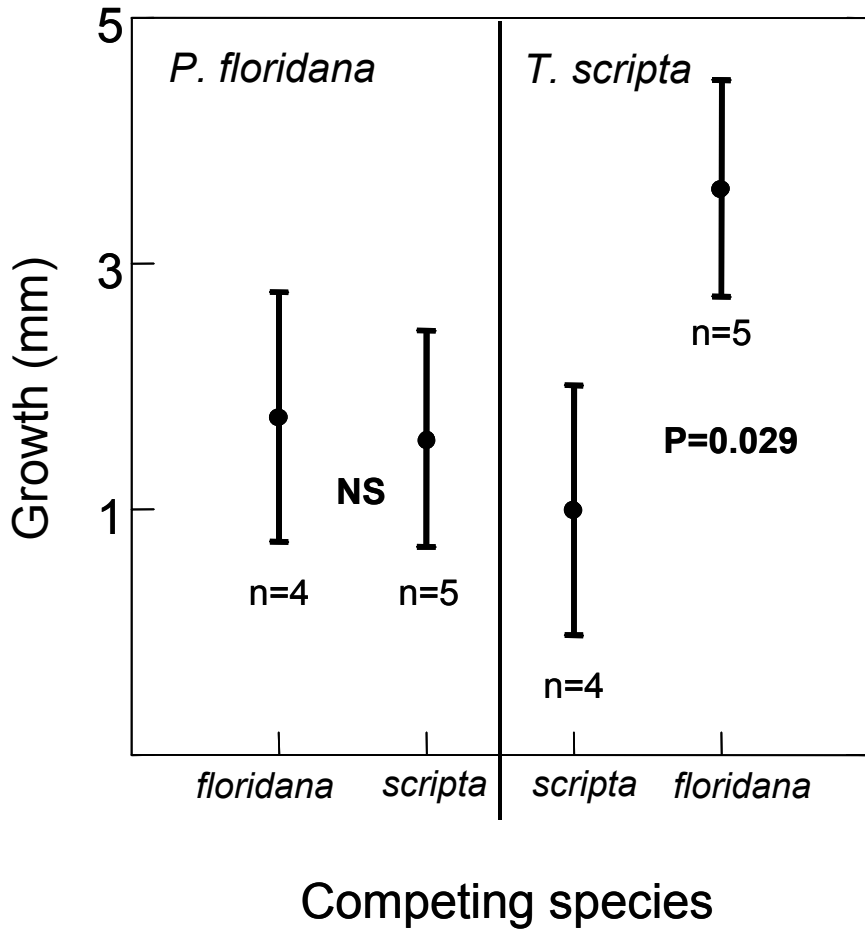


Figure 2.3. Differences in growth of *Trachemys scripta* and *Pseudemys floridana* among 4 treatments in a 13-month field experiment conducted from 11 July 2002 to 3 August 2003 at Gannett Pond, a 21-ha lake on Tall Timbers Research Station located near Lake Iamonia, Leon County, Florida. Mean growth (in plastron length) of *Trachemys scripta* in combination with *Pseudemys floridana* was significantly greater than growth of *Trachemys scripta* under intraspecific competition ($P = 0.029$, $F = 5.98$, $df 1, 14$).

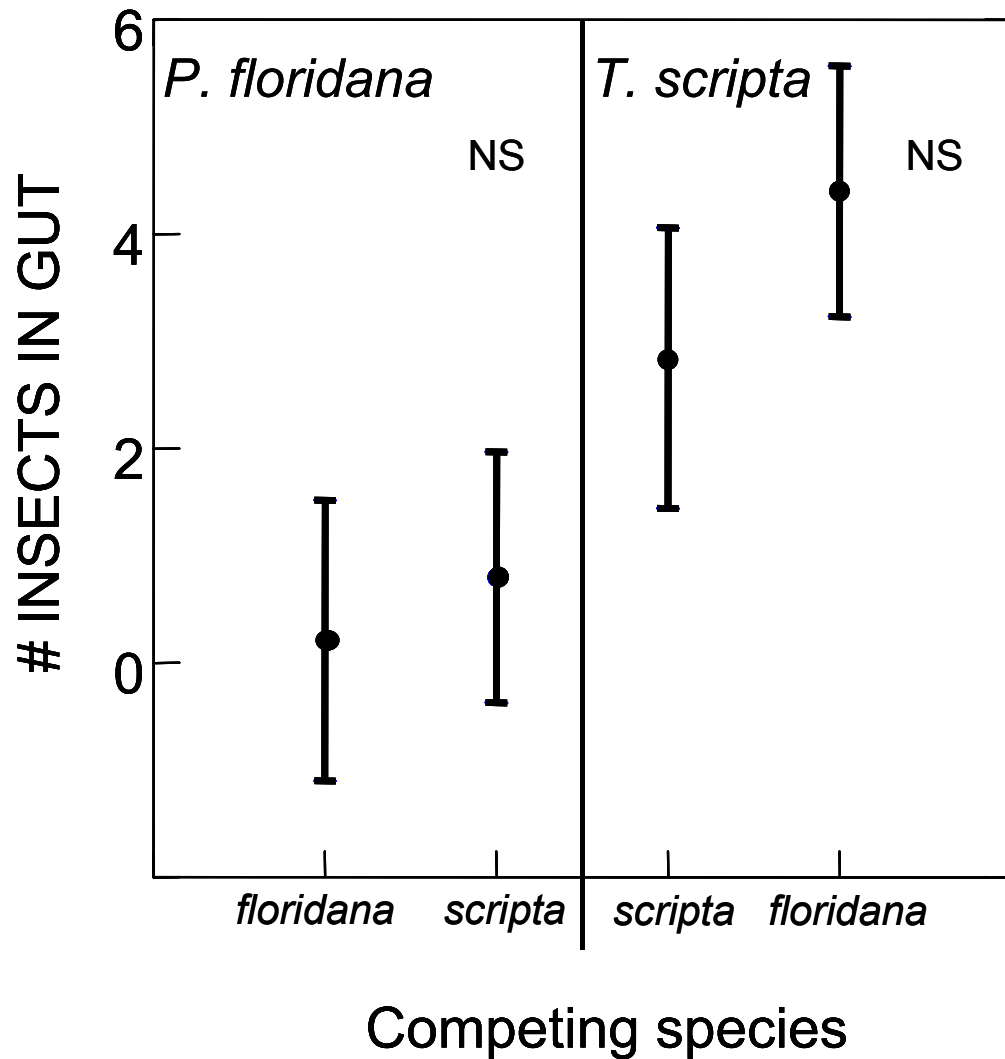


Figure 2.4. Differences in the number of insects found in fecal samples of *Trachemys scripta* and *Pseudemys floridana* among 4 treatments at the end of the field experiment ($P = 0.11$). The 13-month field experiment was conducted from 11 July 2002 to 3 August 2003 at Gannett Pond, a 21-ha lake on Tall Timbers Research Station located near Lake Iamonia, Leon County, Florida.

CHAPTER 3

TROPHIC STRUCTURE AND SOURCES OF PRIMARY PRODUCTION IN A NORTHERN FLORIDA LAKE

INTRODUCTION

The complexity of interactions among producers, primary consumers, and predators is best resolved by analyzing the structure of food webs (Paine 1980, Polis 1991). In complex communities, the levels of omnivory, herbivory, and specialization among consumers affect food web dynamics, interspecific interactions, and trophic structure (Morin and Lawler 1996, Polis and Strong 1996, Blüthgen et al. 2003). Theoretical and empirical work has demonstrated that omnivory tends to stabilize food webs (Diehl 1993, Fagan 1997, Holt and Polis 1997, McCann and Hastings 1997, Holyoak and Sachdev 1998, McCann et al. 1998). In addition, recent studies of food webs in a variety of aquatic and terrestrial systems have revealed that omnivory is often more common than dietary specialization (Sprules and Bowerman 1988, Winemiller 1990, Hall and Raffaelli 1991, Martinez 1991, Polis 1991).

In lentic habitats, food webs have been studied primarily in deep (20 to >100 m), stratified, oligotrophic lakes of north temperate regions in Europe and North America (Carlson 1977, Carpenter et al. 1987, Mills et al. 1987, Sprules and Bowerman 1988, Persson et al. 1992, Lampert and Sommer 1997, Vander Zanden et al. 1999). Lakes in the southeastern United States differ substantially from northern lakes in a variety of physical characteristics (Canfield 1981). For example, natural lakes in the southeastern U. S. Coastal Plain and peninsular Florida are usually relatively shallow (1-3 m deep) with little or no stratification, have greater average annual water temperatures than northern lakes, and may occasionally dry during periods of drought (Brenner et al. 1991).

For many such lakes, the entire lake area is essentially littoral habitat with virtually no pelagic zone. With the exception of lakes suffering anthropogenic eutrophication (e.g., Lake Mendota, Wisconsin), north temperate lakes typically have relatively low species diversity, low primary productivity, low macrophyte biomass, and a high degree of species-specific dietary specialization among consumers (Tonn et al. 1990, Lampert and Sommer 1997, Vander Zanden et al. 1999). In contrast, food webs in many southeastern lakes have high species diversity and high primary and secondary productivity. Fish often dominate northern lakes in North America and Europe; species richness of fish may vary from 0-21 species in small lakes (< 100 ha) to 6-28 species in large lakes (> 100 ha) (Eddy and Underhill 1974, Tonn et al. 1990, Vander Zanden et al. 1999), but in the southeastern United States, this dominance is shared with reptiles, amphibians, and macroinvertebrates. For example, large lakes in northern Florida commonly have 22 species of fish, 11 species of amphibians, and 15 species of reptiles, including 8 species of turtles, 6 species of snakes, and the American alligator (Dobbins and Rousseau 1982, Whitney et al. 2004).

The structure of food webs in southeastern U. S. lakes may be more complex and dynamic than north temperate lakes and may be more similar to food webs in tropical river floodplains because of high species diversity and temporal variability in water levels (Winemiller 1990, 1996). Thus, food web studies in southeastern lakes can address the question of whether greater complexity, species richness, compartmentalization, connectance, and omnivory are likely to increase the probability of stability in large complex food webs. Although trophic interactions have been examined by stable isotope analysis in a shallow, hypereutrophic lake in Florida, these studies only examined fish communities (Gu et al. 1996, Gu et al. 1997). No previous studies have examined either the trophic structure of food webs or the levels of omnivory and specialization in the whole food web of a natural southeastern lake.

In particular, turtles are abundant in southeastern lakes, but their role in lake food webs has never been studied. In some southeastern lakes, the biomass and density of turtles can equal or exceed that of other vertebrates, and the annual productivity of turtles (per unit area) is exceeded only by some fishes (Iverson 1982, Congdon et al. 1986). Some aquatic turtles grow to relatively large sizes, attain high densities, have few

significant predators as adults, and include a variety of trophic niches (Ernst et al. 1994). For example a predominant species, the omnivorous yellow-bellied slider, *Trachemys scripta*, reaches high densities in optimal habitats; 88 to 353 turtles/ha in South Carolina ponds, 77 to 333 turtles/ha in Mississippi farm ponds, and 115-361 turtles/ha in Florida ponds (Auth 1975, Congdon et al. 1986, Parker 1990, Aresco unpubl. data). Omnivory is an important feature of the life histories of some common aquatic and semi-aquatic turtles, and omnivory could be driving the structure of food webs in southeastern lakes. Turtles in several families (e.g., Emydidae, Kinosternidae, Chelydridae) feed on both plants and animals and can exhibit ontogenetic diet shifts (Lagler 1943, Mahmoud 1968, Clark and Gibbons 1969, Moll 1976, Vogt 1981, Vogt and Guzman 1988). The level of omnivory varies within and among species, often depending on resource availability, energy requirements, and foraging efficiency. In lakes with a diverse assemblage of omnivorous freshwater turtles, a large proportion of the predator-prey interactions in the food web will include turtles. Thus, evaluating the trophic relationships among turtles and other consumers is a prerequisite to understanding the properties of southeastern lake food webs and the importance of omnivory in structuring food webs.

There are two basic approaches to analyzing trophic relationships: the food chain versus the food web. Food chains have discrete trophic levels, no omnivory, and are clearly oversimplifications (Hairston and Hairston 1993, Polis and Strong 1996). In contrast, food webs use trophic position as a continuous variable that can account for omnivory and complexity. Trophic position is conventionally expressed as a noninteger value reflecting the energy-weighted mean number of trophic transfers between basal resources and a consumer (Vander Zanden and Rasmussen 1999, Post 2002). Evaluating the trophic position of all organisms in a complex food web is made difficult by its requirement of collecting diet data and by the fact that stomach contents data in may not represent long-term diet. Alternatively, stable isotopes of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ can be used to indicate the average diet and actual energy links. They reflect assimilation of energy sources integrated over long time-scales (e.g., >1 year in some vertebrates) (Vander Zanden and Rasmussen 1999). The heavy nitrogen isotope (^{15}N) of a consumer is enriched relative to its food by 2-4 ‰ (DeNiro and Epstein 1981, Minagawa and Wada 1984, Post 2002). Consumers that feed on the same prey have similar $\delta^{13}\text{C}$ values and

reflect the $\delta^{13}\text{C}$ of their prey (DeNiro and Epstein 1978). Thus, stable isotope analysis that combines both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ provides a method of estimating both trophic position in a food web and sources of primary production.

In this study, I examine the trophic structure, energy pathways, and sources of primary production in the food web of a large shallow lake in northern Florida using stable isotope analysis. I also estimate the trophic relationships, relative omnivory, and ontogenetic shifts in diet and trophic position in a turtle assemblage in order to calculate the role of turtles in organizing lake food webs.

Study Site

I collected tissues from primary producers, invertebrates, and vertebrates at Lake Jackson, a 1620 ha lake 11 km north of Tallahassee, Leon County, Florida, USA (Fig. 3.1). Within Lake Jackson, samples were collected at three sites: Little Lake Jackson, northwestern Lake Jackson, and Porter Sink (Fig. 3.1). Lake Jackson is located within the Tallahassee Red Hills physiographic region and the Tifton/Tallahassee lake region, an area dominated by phosphatic sand, silty sand, and clay plus underlying karst limestone formations and has a neutral pH of 7.0. Lake Jackson is a shallow closed basin with widely fluctuating water levels. Under normal conditions, average depth is approximately 1 - 2 m throughout except for the area surrounding two sinkholes. Water level is controlled naturally by a balance between rainfall and outflow through the sinkholes. During drought conditions, a lowering of the water table causes leakage into the groundwater through the sinkholes and most of the lake bottom dries, an event that has occurred 9 times during the last 100 years. The last drydown occurred in 1999-2000 and 70% of the lake bottom dried (Little Lake Jackson and Megginnis Arm became isolated from the main lake but did not dry completely). In the last three decades, human development in the lake basin and associated stormwater runoff has caused eutrophication in some portions of the lake (e.g., Megginnis Arm) (Livingston 1988, 1997). The invasive aquatic plant *Hydrilla verticillata* was introduced into Lake Jackson in the 1980's and remains problematic in the southern portions of the lake. Megginnis Arm receives more polluted stormwater runoff than other areas of the lake and, thus, has higher concentrations of open water phosphorus (62 $\mu\text{g/L}$, 2001-2004 average) than Little

Lake Jackson (23 $\mu\text{g/L}$) and northwestern Lake Jackson (23 $\mu\text{g/L}$) (Aresco unpubl. data). Therefore, Megginnis Arm was not included in this study because components of the food web may differ due to eutrophication.

METHODS

Isotope samples were collected in diverse ways. Tissue samples from turtles, snakes, frogs, and alligators were obtained from either muscle of road-killed individuals on a highway bisecting Lake Jackson or by claw clips taken from live individuals (Aresco 2005). Salamanders were collected during a sediment removal operation (Aresco and Gunzburger, 2004). Fish were collected by dipnet in the shallow, littoral zone May – August 2002-2003 and large numbers were obtained when Porter Sink drained in December 2002 and February 2003. Invertebrates were collected by dipnet in 2002 and 2003. Leaf tissue of dominant floating, submerged, and emergent macrophytes was collected during February 2002-August 2003. Particulate organic matter (POM), a mix of phytoplankton, diatoms, macroalgal fragments and detritus, may represent a distinct basal resource in the shallow littoral zone, and samples were collected during May-August 2003. Stable isotope values of zooplankton and macroalgae may vary temporally, so samples were collected over time to determine variation and average values. Open water zooplankton was collected at northwestern Lake Jackson using a 250- μm zooplankton tow net pulled from a boat. I collected 10 aggregate zooplankton samples during August 2002 – November 2003. Macroalgae (periphyton and filamentous algae) was collected between November 2001 and June 2004 ($n = 29$) at northwestern Lake Jackson and between October 2001 and August 2003 ($n = 17$) at Little Lake Jackson (Fig. 3.1). Algal samples were collected from mats in the littoral zone, from stems of maidencane grass and water lilies, and from shells of live turtles (green algae, *Basycladia* sp.). All samples were freeze-dried, ground to a fine powder with a mortar and pestle, and packed into 4-x-6-mm tin capsules for analysis by a mass spectrometer at the University of California Davis Stable Isotope Facility.

Because no previous studies had examined stable isotope values of turtles, preliminary data were necessary in order to explore whether more than one tissue type could be used interchangeably in the analysis (e.g., claw vs. muscle), to verify that $\delta^{13}\text{C}$

of turtle tissue reflects $\delta^{13}\text{C}$ of food sources, and to determine trophic fractionation of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ and the effect of a diet change on stable isotope values (i.e., lag time in turnover). First, I compared claw vs. muscle tissue in road-killed *T. scripta* ($n = 17$) and *P. floridana* ($n = 11$) and demonstrated with ANOVA that these two different tissues did not differ in stable isotope values for either species ($\delta^{13}\text{C}$: *T. scripta*, $P = 0.66$; *P. floridana*, $P = 0.78$; $\delta^{15}\text{N}$: *T. scripta*, $P = 0.13$; *P. floridana*, $P = 0.45$) (Fig. 3.2). Second, I fed 7 juvenile *T. scripta* only Wardleys™ TEN Reptile sticks for 1 year and compared $\delta^{13}\text{C}$ values of turtle claw tissue and food. This trial indicated that $\delta^{13}\text{C}$ of food (-17.18‰ , $\text{SE} = 0.10$) and turtles (-17.41‰ , $\text{SE} = 0.12$) were almost identical (Fig. 3.3). Third, I used the laboratory experiment to determine that fractionation of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ between turtles and commercial food pellets was 0.23 and 2.3, respectively.

Turtles may present additional complications for interpreting stable isotope analyses because they often have significant ontogenetic variation in diet. To better understand the effect of a diet change and tissue turnover rate on stable isotope values, I compared stable isotope values among 3 sets of juvenile *T. scripta*: wild only diet (2 yr olds) ($n = 18$), wild (2 yr olds) fed a captive diet for 6 months ($n = 3$), and captive only diet (commercial turtle food) ($n = 7$). This experiment demonstrated that $\delta^{15}\text{N}$ values of wild turtles fed commercial turtle food converged to $\delta^{15}\text{N}$ values of captive turtles in only 6 months (Fig. 3.3), whereas the lag time for complete turnover of tissue as reflected by $\delta^{13}\text{C}$ values was slower. After 6 months, $\delta^{13}\text{C}$ values of wild turtles fed commercial turtle food (-21.56‰ , $\text{SE} = 0.24$) were intermediate between wild-only turtles (-25.91‰ , $\text{SE} = 0.54$) and captive-only turtles (17.41‰ , $\text{SE} = 0.12$) (Fig. 3.4). Thus, this preliminary experiment suggested that for turtles, a diet switch requires 6 months to be detected by a change in the $\delta^{15}\text{N}$ isotope and 12 months to be detected by a change in the $\delta^{13}\text{C}$ isotope. Although juvenile turtles grow faster than adults, there is no evidence of variation in tissue turnover rates (e.g., claw, muscle) between juveniles and adults.

Because $\delta^{13}\text{C}$ of consumers that feed on the same prey have similar isotope values and reflect the $\delta^{13}\text{C}$ of their prey, it is possible to use stable isotope values to determine the sources of primary production in the food web. In freshwater systems, food webs may be based on macroalgae, macrophytes, detritus (terrestrial or aquatic), particulate

organic matter (POM) (a mix of littoral detritus, macroalgae, and phytoplankton), phytoplankton, or some combination of each of these sources. In order to determine which source(s) is the most important basal resource, I calculated the percent of consumers in the food web that overlapped with each category of primary producers. Overlapping 95% confidence intervals among different species indicated that they directly or indirectly used the same source of primary production in the food web. Stable isotope values of several species of macrophytes (C3 plants) were averaged to one value. Maidencane grass, a C4 plant, was analyzed separately. I was not able to collect pure open water phytoplankton for analysis at Lake Jackson, so I used isotope values of a unionid clam (paper pondshell [*Utterbackia imbecillis*]) that feeds exclusively on open water phytoplankton as a surrogate (Vander Zanden and Rasmussen 1999). Because juvenile *P. floridana* were collected only at Little Lake Jackson, I used the site-specific $\delta^{13}\text{C}$ values for primary producers at Little Lake Jackson for comparison. I compared the 95% confidence intervals of $\delta^{13}\text{C}$ of each species (and stage classes for some species) to that of each primary producer to determine the basal source of primary production. If 95% confidence intervals of a consumer are within that of a producer (and adjusted for trophic fractionation of $\delta^{13}\text{C}$), then this indicates the source of primary production for that food web link. If 95% confidence intervals of a consumer are within that of 2 specific producers with overlapping confidence intervals, then the method is informative in identifying those sources of primary production. Where the 95% confidence interval of a consumer overlaps with that of 3 or more primary producers, the method is not informative and suggests multiple sources of primary production through that energy link.

The $\delta^{15}\text{N}$ isotope was used to quantify within population variation in trophic position. Because of variation in $\delta^{15}\text{N}$ of basal resources among lakes within a system, consumer $\delta^{15}\text{N}$ values alone cannot be used to determine trophic position (Vander Zanden and Rasmussen 1999, Post 2002). Trophic position of reptiles, amphibians, and fish was estimated using the following technique that corrects for variation in $\delta^{15}\text{N}$ values of primary producers (trophic level 1) among different lakes or different habitats within a lake (e.g., pelagic vs. littoral zone) (Vander Zanden and Rasmussen 1999). Baseline $\delta^{15}\text{N}$ values were calculated using a primary producer (macroalgae), a primary consumer

(unionid mussel), or POM (Table 3.1). The trophic position of turtles, snakes, alligators, and frogs was estimated relative to the baseline $\delta^{15}\text{N}$ value with the equation $\text{TP} = ((\delta^{15}\text{N} - \delta^{15}\text{N}_{\text{baseline}}) / 2.3) + 1$, where TP is trophic position and 2.3‰ is the mean enrichment of $\delta^{15}\text{N}$ between trophic levels as determined in the laboratory experiment. The trophic positions of fish, sirens, and amphiumas were estimated relative to the baseline $\delta^{15}\text{N}$ value with the equation $\text{TP} = ((\delta^{15}\text{N} - \delta^{15}\text{N}_{\text{baseline}}) / 3.4) + 1$, where 3.4‰ is the mean enrichment of $\delta^{15}\text{N}$ between trophic levels as determined in previous studies of fish that have the same range of longevity and tissue turnover rates as Lake Jackson fish (DeNiro and Epstein 1981, Minagawa and Wada 1984, Hesslein et al. 1993, Vander Zanden et al. 1999, Post 2002). I used ANOVA and Bonferroni pairwise comparisons to determine differences in trophic position among adult *P. floridana*, *T. scripta*, *S. odoratus*, *A. ferox*, and *C. serpentina*.

Gut contents data only provide snapshots of the long-term diet of an organism and do not reveal which items that are consumed are actually assimilated into tissue. In contrast, stable isotopes values only reflect diet items that were actually digested and assimilated, not those that were either undigested or digested but assimilated at lower rates (Gannes et al. 1997). For example, a species may ingest a large volume of plant material but may not have the digestive physiology to digest and assimilate plant tissue. Therefore, in order to fully elucidate food web structure and interpret stable isotope data, it is important to understand how the results of stable isotopes and gut contents analysis compare with each other. In this study, I determined how trophic positions inferred from stable isotope analysis compared to gut contents in turtles ($n = 173$ individuals), alligators ($n = 7$), and fish ($n = 83$) at Lake Jackson. Turtles captured at northwestern Lake Jackson and Little Lake Jackson were held individually in water-filled, plastic containers for 24 hours to allow collection of fecal samples. Stomach contents were collected from road-killed turtles and alligators. Diet samples from both juvenile and adult *A. ferox*, *T. scripta*, and *P. floridana* were collected to compare the ontogenetic diet shift in these species to the ontogenetic shift in trophic position as determined from stable isotope analysis. I classified juvenile *A. ferox* as those individuals <120 mm plastron length and juvenile *T. scripta* and *P. floridana* as those individuals <100 mm plastron length. Fish were collected at Porter Sink, Lake Jackson by dip-net on 20 December 2002 and 14

February 2003 as water flowed into a sinkhole. Gut samples were stored in 95% ethanol and examined under a dissecting microscope. Diet items were classified into broad categories (e.g., insects, gastropods, crustaceans, fish, macroalgae, macrophytes) and percent occurrence of diet items was calculated.

RESULTS

Sources of Primary Production and Trophic Structure

Primary producers had $\delta^{13}\text{C}$ values that indicated three distinct signatures of basal resources in the food web, with non-overlapping 95% confidence intervals: phytoplankton, C3 macrophytes and C4 grass, and POM and macroalgae (Table 3.2, Fig. 3.4). Macroalgae and POM had the most enriched values of $\delta^{13}\text{C}$; phytoplankton was the least enriched; macrophytes and maidencane grass were intermediate between these other sources.

Stable isotope values of selected primary consumers in deeper water had a distinct difference in $\delta^{13}\text{C}$ signatures than those in the shallow littoral zone (Fig. 3.5). In deeper water, zooplankton and unionid clams have mean $\delta^{13}\text{C}$ values $<-30\text{‰}$, indicating that they feed on phytoplankton. In the shallow littoral zone, primary consumers such as chironomids, amphipods, snails, and tadpoles have mean $\delta^{13}\text{C}$ values ranging from -20.0 to -30.8, indicating either a macrophyte or macroalgae/POM based web (Fig. 3.5).

A comparison of the confidence intervals of $\delta^{13}\text{C}$ values of primary producers and 42 animal taxa indicates that macroalgae, either by itself or in combination with POM or other sources, is the most important source of primary production in the food web (Table 3.3). Forty-five percent of animal taxa had $\delta^{13}\text{C}$ signature values of primarily macroalgae-only, POM-only, macroalgae+POM, and macroalgae+macrophyte. The most prevalent macroalga found in Lake Jackson are musk grass (*Chara* spp.), stonewort (*Nitella* spp.), *Spirogyra* spp., *Pithophora* spp., and *Hydrodictyon* spp. In contrast, although Lake Jackson is dominated by emergent and submerged macrophytes, only 14% of animal taxa had $\delta^{13}\text{C}$ signature values of primarily C3 macrophyte-only, C4 maidencane-only, or macrophyte+maidencane (Table 3.3). Some wider-ranging consumers (36% of animal taxa sampled) like the

bowfin (*Amia calva*), cottonmouth (*Agkistrodon piscivorus*), Florida green watersnake (*Nerodia floridana*), and bluegill (*Lepomis macrochirus*) had $\delta^{13}\text{C}$ values that reflected multiple sources of primary production (including some macroalgae) (Table 3.2). They forage in both deep and shallow water or on prey with different $\delta^{13}\text{C}$ signature values. Overall, macroalgae provided full or partial contribution to the growth of 34 of 42 animal taxa (81%).

Carbon isotope ratios of adult *T. scripta*, *P. floridana*, *A. ferox*, and *S. odoratus* fell within the narrow range of -22 to -26 ppt (Table 3.2, Fig. 3.6). These carbon ratios indicated that these turtles feed in a macroalgal-based portion of the food web, either directly on macroalgae or on prey that feed on macroalgae. Juvenile *T. scripta* had $\delta^{13}\text{C}$ values that demonstrated they feed in a POM-based part of the food web (-22 to -27 ppt). Juvenile *P. floridana* had $\delta^{13}\text{C}$ values that reflected a combination of macroalgal and macrophyte feeding links (based on site-specific $\delta^{13}\text{C}$ values for Little Lake Jackson) (Fig. 3.6). Juvenile *A. ferox* had $\delta^{13}\text{C}$ values that indicated macrophytes were the important basal resource for its feeding links, reflecting $\delta^{13}\text{C}$ values of odonate naiads that are a primary dietary source (Table 3.2).

Despite the dominance of C3 macrophytes in the shallow littoral zone of Lake Jackson, two abundant, herbivorous, aquatic invertebrates (amphipods and hydrophilid beetles) and littoral fish (least killifish and mosquitofish) had signatures indicating a significant contribution of macroalgae in the form of periphyton and POM (Table 3.2). Diet data from these fish species indicate that least killifish feed primarily on macroalgae and POM and mosquitofish feed on zooplankton (Table 3.4). Several littoral zone predators, the fishing spider (*Dolomedes*), banded watersnake (*Nerodia fasciata*), greater siren (*Siren lacertina*), two-toed amphiuma (*Amphiuma means*), juvenile alligator (*Alligator mississippiensis*), southern leopard frog (*Rana sphenoccephala*), and pig frog (*Rana grylio*), all had $\delta^{13}\text{C}$ signatures consistent with those of macroalgae and/or POM, whereas signatures of other species indicated a mixture of macroalgae and several other sources (POM, macrophytes, and phytoplankton) (Table 3.2, Fig. 3.7).

Most fish species in the deeper-water zone had stable isotope values that reflected multiple sources of primary production, indicating that they forage in multiple subwebs (e.g., deep and shallow zones) or on prey with different $\delta^{13}\text{C}$ signature values (Table 3.2). Lake chubsucker (*Erimyzon sucetta*), black crappie (*Pomoxis nigromaculatus*), and golden shiner (*Notemigonus crysoleucas*) had $\delta^{13}\text{C}$ signature values consistent with direct or indirect energy links from macrophytes (macrophyte detritus) or maidencane grass.

Trophic Relationships of Turtles and Other Herpetofauna

A trophic position model of the Lake Jackson food web based on stable isotopes demonstrated 2 major divisions in the trophic structure of turtles – herbivores (*P. floridana*) versus omnivores (*T. scripta*, *S. odoratus*, *A. ferox*, *K. subrubrum*, and *C. serpentina*) (Fig. 3.8) (ANOVA, $F = 29.9$, $P < 0.0001$). Pairwise comparisons indicated that mean TP of adult *P. floridana* was significantly less than that of adult *T. scripta*, *A. ferox*, *S. odoratus*, and *C. serpentina*) and mean TP of *A. ferox* was significantly greater than that of *P. floridana* and *T. scripta* (Table 3.5). *Kinosternon subrubrum* ($n = 1$) was the only turtle species with a TP of 4.0 or greater. Adult *A. ferox* ($n = 21$) had a mean TP of 3.8, indicating that it is one of the top predators in the food web. For *P. floridana*, adults had a TP of 2.3 and juveniles had a TP of 2.4, only slightly above the theoretical TP of a strict herbivore (2.0) (Table 3.5, Fig. 3.8). There was no relationship between size of *P. floridana* and TP ($r^2 = 0.006$, $P = 0.61$, $n = 45$) (Fig. 3.9), indicating that there was no ontogenetic shift in TP. Trophic positions of adult and juvenile *T. scripta* were 3.0 and 3.5, respectively (Table 3.5). Similar to *P. floridana*, there was no detectable ontogenetic shift in TP of *T. scripta* ($r^2 = 0.05$, $P = 0.11$, $n = 51$) (Fig. 3.10). In contrast, there was a significant positive relationship between size and TP in *A. ferox* ($r^2 = 0.47$, $P < 0.0001$, $n = 35$) (Fig. 3.11). There was little overlap between TP of *P. floridana* and that of *T. scripta* and *A. ferox* (Fig. 3.12). TP of adult *T. scripta* overlapped more with that of juvenile *A. ferox* than adults (Fig. 3.12).

Gut contents of *A. ferox*, *T. scripta*, and *P. floridana* closely matched their respective TP inferred from stable isotopes (Table 3.6). Juvenile *A. ferox* ($n = 14$)

consumed almost exclusively insects (odonate naiads), whereas diet of adult *A. ferox* ($n = 36$) consisted of primarily of insects (e.g., *Lethocerus americanus*), snails, macroalgae, and fish (Table 3.6). In addition, 67% of adult *A. ferox* had eaten large quantities of water lily seeds (*Nymphaea odorata*) that filled the entire volume of the gut in several individuals. Two large adult *A. ferox* ate American coots (*Fulica americana*). There were striking differences in diet of *T. scripta* and *P. floridana* at Lake Jackson. The diet of juvenile *T. scripta* ($n = 18$) was mostly composed of insects (e.g., odonate naiads) and macrophytes (e.g., *Utricularia*). The diet of adult *T. scripta* ($n = 38$) was similar to that of juveniles, with macrophytes (e.g., *Utricularia*, *Pontedaria cordata*), insects, and macroalgae (*Chara*) consumed most frequently. Three adult *T. scripta* had fish scales in their guts. In contrast, both juvenile and adult *P. floridana* specialized on macroalgae (e.g., *Spirogyra*, *Chara*, *Nitella*) (Table 3.6). Only 7 of 21 (33%) juvenile *P. floridana* and 1 of 35 (3%) of adult *P. floridana* consumed insects. Juvenile *P. floridana* ate a relatively equal proportion of macrophytes (e.g., *Utricularia*) as did juvenile *T. scripta* but adult *P. floridana* consumed substantially fewer macrophytes than did adult *T. scripta* (Table 3.6). In gut contents of 6 *S. odoratus*, 4 individuals ate insects, 3 ate maidencane grass (*Panicum hemitomon*) seeds, and 1 scavenged on fish. The diet of 4 *C. serpentina* was dominated by macrophytes (e.g., *Utricularia*, American lotus [*Nelumbo lutea*], and duckweed [*Lemna minor*]) and predatory insects (*L. americana*). One individual also consumed macroalgae and seeds. Although gut contents suggested that *C. serpentina* is primarily herbivorous, trophic position based on stable isotopes was 3.5 and reflects a more carnivorous diet. This result indicates inefficient digestion and assimilation of plant material by *C. serpentina*.

The mud snake (*Farancia abacura*) had the greatest TP (TP = 4.6) among reptiles and amphibians in the lake food web, indicating that it specializes on other consumers (i.e., amphiuma) (Fig. 3.7). Similarly, the two-toed amphiuma with a mean TP of 4.0, is also considered one of the top predators in the littoral zone food web and feeds primarily on secondary consumers. In contrast, mean TP of the greater siren (*Siren lacertina*) was 3.1, a trophic position lower than that of the amphiuma because it directly consumes macroalgae. Aquatic and semi-aquatic frogs (pig frog, bullfrog [*Rana catesbeiana*]), and leopard frog had trophic positions of 3.2 to 3.5, indicating that they

feed on both primary and secondary consumers (Table 3.5). Trophic position of three semi-aquatic snakes (Florida green water snake, banded water snake, and cottonmouth [*Agkistrodon piscivorus*]) ranged from 3.2 to 3.8 (Table 3.5). Trophic position of juvenile alligators (TP = 2.7) was slightly lower than that of adult alligators (TP = 3.3). Gut contents of juvenile alligators ($n = 6$) consisted primarily of predatory insects (e.g., *Belostoma*, *L. americana*, *Dytiscus*, odonate naiads, adult odonates), along with crayfish, snails, and frogs (*Acris gryllus*, *Rana* sp.), whereas stomach contents of one adult alligator (1.8 m total length) contained an American coot and musk turtle (*S. odoratus*). Most alligators had detritus, woody debris, and macrophyte fragments in their guts.

Trophic Relationships of Fish

Florida gar, *Lepisosteus platyrhincus*, (TP = 4.1) and bowfin, *A. calva*, (TP = 3.7) were the top fish predators in the food web and fed primarily on fish (Figs. 3.13 and 14). Trophic position of largemouth bass (*Micropterus salmoides*) (TP = 3.5), black crappie (TP = 3.5), and warmouth (*Lepomis gulosus*) (TP = 3.3) were slightly lower, indicating that they feed on primary and secondary consumers. Gut contents of bass and crappie indicated that they fed on both fish and carnivorous and herbivorous invertebrates (shrimp and odonate naiads) (Table 3.4). Bluegill (*L. macrochirus*) had a TP of 3.1 and fed on diverse prey including zooplankton, small fish (least killifish and mosquitofish), grass shrimp, and odonate naiads. Spotted bullhead had the same trophic position as bluegill but fed exclusively on snails. Gut contents indicated that the golden shiner and mosquitofish fed mostly on zooplankton (Table 3.4). Differences in TP of the golden shiner (3.0) and mosquitofish (2.6), however, suggest that the mosquitofish is more herbivorous (algae or POM). Similarly, lake chubsucker had a TP of 2.6, indicating that it likely feeds on a combination of zooplankton and macrophyte detritus. Stable isotopes indicated a low trophic position of the golden topminnow (*F. chrysotus*) (TP = 2.3) and least killifish (TP = 2.4) and gut contents indicated that least killifish are primarily herbivores (algae/POM) in the shallow littoral zone (Table 3.4, Fig. 14).

DISCUSSION

Primary Productivity and Trophic Structure in the Lake Jackson Food Web

Lake Jackson is a highly productive lake. Much of the primary productivity was accounted for by macrophytes and standing crop ranged from 6,000 g/m² in the main lake to 17,000 g/m² in Little Lake Jackson (an arm of the main lake) (Aresco see Chapter 1). In contrast, macroalgae [filamentous algae (e.g., *Chara*) and periphyton] contributed much less to total standing crop, probably because of removal by grazers, and this resource may be limiting (Cattaneo and Mousseau 1995, Carrick and Steinman 2001). Productivity of epiphyton that grows on the stems and roots of macrophytes ranged from only 1 to 2 g/m²/y (dry mass) (Aresco see Chapter 1). At Lake Jackson, the ¹³C signatures of macroalgae differed from those of macrophytes, and the tissues of a consumer reflect the basal sources of organic carbon. An abundance of vascular plant detritus occurs on the lake bottom and has the same isotopic signature as living macrophytes from which it is derived. Despite the dominance of macrophyte production at Lake Jackson, macroalgae (filamentous mats, periphyton, and littoral POM [micro+macroalgae]) was proportionately a much greater source of primary production for consumers than macrophytes, macrophyte-based detritus, and open-water phytoplankton. Forty-five percent of animal taxa sampled had ¹³C signatures that indicated macroalgae-based sources, compared to only 14% for macrophytes (including maidencane grass). Further, 36% of animals sampled exhibited a wide range of ¹³C signatures that overlapped with multiple sources of primary production, including phytoplankton, macrophytes, POM, and macroalgae. Therefore, stable isotope analysis revealed that macroalgae provided full or partial contribution to the growth of 81% of 42 animal taxa sampled at Lake Jackson.

Macroalgae-based food webs in macrophyte or terrestrial litter dominated systems have been shown in some riverine, marsh, and lake habitats (Finlay 2001). For example, in the Orinoco River floodplain, the bulk of primary production was in dense macrophyte mats, but algal production (periphyton and phytoplankton) provided the main energy source for consumers (Hamilton et al. 1992). Likewise, in the oligotrophic Florida Everglades, periphyton mats (average standing crop 88 g /m²) are the base of the food

web in a system dominated by cattail, sawgrass, and spikerush (where standing crops can exceed 2800 g/m²) (Hofstetter 1976, Turner et al. 1999, Geddes and Trexler 2003). In contrast, phytoplankton was the base of the food web in most previous studies of lake systems (Kling et al. 1992, Persson et al 1992, Gu et al. 1997, Herwig et al 2004). However, Hecky and Hesslein (1995) demonstrated that in phytoplankton-dominated lakes, benthic macroalgae growing on rocks and logs accounted for the bulk of the energy in the food web. My results from a shallow north Florida lake were consistent with the conclusion that macroalgae represented a small fraction of the biomass of producers but were the primary energy source to consumers. This finding is likely to extend to other shallow, macrophyte-dominated lakes in Florida.

Most lake food web studies, and thus the source of most current lake food web theory, are based in north temperate regions where species richness and diversity is lower than in Florida lakes (Persson et al. 1992, Lampert and Sommer 1997, Vander Zanden et al. 1999, Vander Zanden and Rasmussen 1999). For example, while the species richness of fish in lakes in the Great Lakes region of Ontario and Quebec is similar to that in Florida lakes (Barnett and Schneider 1974, Tonn et al. 1990, Bachmann et al. 1996), there are typically <10 species of aquatic and semi-aquatic reptiles and amphibians in such habitats (e.g., *C. serpentina*, *Graptemys geographica*, *C. picta*, *Nerodia sipedon*, *R. catesbeiana*, *R. pipiens*) and these species are restricted to shallower littoral marshes of large, deep stratified northern lakes or in smaller lakes and ponds with emergent macrophytes (Lagler 1943, Ernst et al 1994, Courtois et al. 1995, Gibbons and Dorcas 2004). In contrast, lakes in the lower Coastal Plain of the southeastern United States generally have at least 26 species of reptiles and amphibians representing wide variation in trophic niches, many of which are omnivorous. These species often occur at high abundances and can represent a significant proportion of the total lake biomass (Iverson 1982, Congdon et al. 1986). Thus, food webs in southeastern lakes may have more omnivores than in other aquatic systems and the interaction of widespread omnivory with high primary productivity can produce unexpected results such as shorter food chains but with more subweb structure and greater connectivity.

Omnivory is common in natural food webs (Hall and Raffaelli 1991, Polis 1991, Diehl 1993) and combined with high species richness can increase feeding links and

connectivity in the food web (Winemiller 1990). Omnivory was prevalent in the Lake Jackson food web and most secondary consumers had a trophic position of less than 4.0. This result indicates that there were few specialists ($TP \geq 4.0$) that forage on particular groups except for the Florida gar, a strict piscivore, and the mud snake that specializes on aquatic salamanders (Mount 1975). Likewise, at the bottom of the food web, there were only 2 vertebrate species that were considered strict primary consumers – the Florida cooter and the least killifish – along with tadpoles. The trophic structure of the Lake Jackson food web is defined by omnivory and intraguild predation that functions to shorten food web length (Polis et al. 1989).

Several theoretical and empirical studies have found that increasing productivity adds trophic levels, increases interaction strengths, and increases stability (Oksanen et al. 1981, Schoener 1989, Polis and Strong 1991). In a stable isotope study of pelagic consumers in series of oligotrophic northern lakes, Vander Zanden et al. (1999) found that food chain length increased with the amount of productive space (productivity x area) and explained variation in chain length better than a single predictor of lake productivity. They also found that food chains leading to the top predator, lake trout (*Salvelinus namaycush*), varied by almost 2 trophic levels among lakes. The longest chain consisted of 5 trophic “levels” leading to lake trout, which had a TP of 4.6 (Vander Zanden et al. 1999, Vander Zanden et al. 2000).

Primary productivity may regulate the number of trophic levels in a food web in counterintuitive ways, especially in dynamic and variable environments (Pimm and Kitching 1987, Persson et al. 1992, Persson et al. 1996). The frequency of omnivory in a food web may increase along a gradient of primary productivity, but an increase in omnivory may reduce the number of trophic levels by expanding the web horizontally rather than vertically through immense numbers of trophic interactions (Fig. 3.15). In food webs with widespread omnivory, food web length may be limited to fewer than 4 trophic levels. The trophic structure of the fish assemblage at Lake Jackson consisted of several species that are functionally omnivorous predators including largemouth bass, bowfin, and black crappie, but with TPs of only 3.5 to 3.7. Similarly, many other predators in the Lake Jackson food web (e.g., alligator, Florida green water snake) had lower than expected TPs.

Predation on consumers that occupy lower positions in the food web can explain the reduction of the TP of top predators. For example, the Florida green water snake had a mean TP of 3.4, slightly lower than the TP of the banded watersnake (TP = 3.8). Although *Nerodia* eat primarily frogs and a variety of small fish (Gibbons and Dorcas 2004), the inclusion of tadpoles and herbivorous fish (e.g., least killifish) in their diet functions to decrease their actual TP to less than 4.0. Aquatic frogs (pig frog, bullfrog, and leopard frog) are functionally secondary consumers with a mean TP of 3.3 to 3.5. However, feeding on predatory insects with a similar trophic position elevates their own trophic position to above 3.0. The two-toed amphiuma had a mean TP of 4.0, indicating that it feeds exclusively on secondary consumers. In contrast, mean TP of the greater siren was 3.1 and is lower than the amphiuma because it directly consumes macroalgae and primary consumers (e.g., least killifish).

Alligators are perceived as the top predators in Florida lakes. However, alligators had lower than expected ^{15}N stable isotope values and TP relative to other functional predators in the Lake Jackson food web. Two adult alligators (1.8 and 2.1 m) had a mean TP of 3.3, and a sample of juvenile alligators (0.5 – 1.3 m) had a mean TP of only 2.7. In comparison, adult *T. scripta* had a mean ^{15}N of 6.55 and TP of 3.3. Alligators are opportunistic omnivores and feed on a variety of aquatic, semiaquatic, and terrestrial prey (Delany and Abercrombie 1986, Shoop and Ruckdeschel 1990, Delany et al. 1999, A. Rice, University of Florida, personal communication). One explanation for their relatively low TP could be that a significant portion of their energy is derived from primary consumers such as crayfish or snails. A more likely explanation is that part of their diet is from the terrestrial food web (i.e., birds, mammals, terrestrial-feeding amphibians, and dragonflies), which has a lower baseline ^{15}N value than the aquatic food web (Shoop and Ruckdeschel 1990). In our study, we found that the stomach contents of juvenile alligators contained crayfish, semi-terrestrial frogs (e.g., *Acris gryllus*), predatory aquatic insects, and adult dragonflies. Interestingly, a study that examined stable isotope values of fossil alligators found that ^{15}N values were also reported to be lower than expected compared to softshell turtles and other species found together in the fossil beds (Ostrom et al. 1993, Ostrom et al. 1994). Lastly, alligators frequently incidentally ingest

large amounts of detritus while foraging and if even some of this material is assimilated, that could explain their lower than expected TP in food webs.

Omnivory and Trophic Relationships of Turtles

Many turtles are classic omnivores because they can exhibit both lifetime omnivory and niche shifts from juveniles to adults (life history omnivory). For example, *T. scripta* is an opportunistic omnivore that feeds on a variety of aquatic vegetation, invertebrates, and carrion (Cagle 1950, Parmenter 1980, Parmenter and Avery 1990). In general, *T. scripta* exhibits an ontogenetic shift in diet from carnivory to herbivory with an increase in body size (Clark and Gibbons 1969, Hart 1983). The degree of herbivory of adult *T. scripta* may vary with spatial or temporal differences in the availability of plant and animal foods (Hart 1983, Parmenter 1980). For example, Moll (1977) found that adults are more carnivorous in habitats where aquatic plants are less abundant than insects. They may also change their diet seasonally from summer omnivory to winter herbivory, a shift that may be related to food availability (Parmenter 1980).

Both *P. floridana* and *T. scripta* are omnivorous in the juvenile stage, but there are striking differences in the proportion of the type of prey consumed and the degree of omnivory (Aresco see Chapter 2). In a foraging experiment, *T. scripta* ate significantly more insects and scavenged more on dead fish than did *P. floridana* (Aresco see Chapter 2). The analysis of TP of turtles using stable isotopes in this study was consistent with the low level of resource overlap between these species demonstrated by gut samples. At Lake Jackson, TP of juvenile *T. scripta* was 3.5, one position greater than that of juvenile *P. floridana* (TP = 2.4). This difference in TP continued in adult *T. scripta* (TP = 3.3) and *P. floridana* (TP = 2.3), with no evidence of a dietary shift towards herbivory in adult *T. scripta* that has been reported elsewhere (Clark and Gibbons 1969, Parmenter and Avery, 1990). At Lake Jackson, gut contents indicated that the difference in TP was due primarily to greater consumption of predatory insects by juvenile and adult *T. scripta*. Parmenter (1980) suggested that in habitats with sufficiently available fish carrion, an ontogenetic shift in diet of *T. scripta* should be reduced or not occur at all, as adults can maintain an optimal benefit:cost ratio of energy expenditure by feeding on dead fish rather than plants. In habitats without scavenging opportunities, it is more energetically

efficient for adult *T. scripta* to eat plants than to capture insect prey (Parmenter and Avery 1990). Thus, TP of adults may be lower in such habitats. At Lake Jackson, frequent water level and water temperature fluctuations provide the conditions for fish carrion to be available to scavengers. During full and partial drydowns of this sinkhole lake, thousands of dead fish become available to scavengers, and some turtles (e.g., *T. scripta* and *S. odoratus*) foraged exclusively on this food source. In contrast, *P. floridana* migrated from drying pools much earlier in the drying cycle than *T. scripta* and did not scavenge on carrion (Aresco unpubl. data). Stable isotope ratios of some turtle species represent long-term assimilation of diet sources, so tissue samples collected post-drydown at Lake Jackson (2001-2002) may reflect foraging on fish carrion during the drydown in 2000. Hence, trophic position of turtles such as *T. scripta* and *S. odoratus* may be elevated by scavenging on predatory fish or by feeding on predatory insects that occupy a similar or greater trophic position.

Based on trophic position, the turtle assemblage at Lake Jackson exhibited two foraging patterns: herbivorous (*P. floridana*) and omnivorous (*T. scripta*, *S. odoratus*, *A. ferox*, *C. serpentina*, *K. subrubrum*). In this study, *Pseudemys floridana* was a specialist on macroalgae in both the juvenile and adult stages. Other diet studies have showed that *P. floridana* prefers macroalgae and vascular aquatic plants, and may feed exclusively on the dominant aquatic plants in a given habitat, which may vary among lakes and seasonally within lakes (Allen 1938, Marchand 1942, Carr 1952, Thomas 1972). Among the omnivorous species, TP ranged from 3.3 to 4.0 and analysis of gut contents indicated that each species consumed some plant material or macroalgae. The extensive overlap of resource use by omnivorous turtles is unlike the pattern of specialization exhibited by fish communities in lakes and rivers (Winemiller 1990, Vander Zanden et al. 1999, Lewis et al. 2000). Such a foraging strategy among omnivorous turtles may increase niche breadth and reduce interspecific competition. Furthermore, a diet consisting of plants and animals may be adaptive in some turtles, as mixed diets have been demonstrated to be important to their nutritional requirements and growth (Bjorndal 1991).

At Lake Jackson, TP increased with size of *A. ferox*, in contrast to *T. scripta* and *P. floridana*. The change in TP indicated a shift in diet observed in this study from primarily macroinvertebrates in juvenile and subadult *A. ferox* to macroinvertebrates

(especially *Lethocerus americana*), fish, and other vertebrates (e.g., American coot [*Fulica americana*]) in large adults. Similarly, Dalrymple (1977) reported that juvenile *A. ferox* fed mostly on snails and insects, whereas large adults consumed primarily snails, insects, and fish. Predation on herbivorous macroinvertebrates (e.g., snails, crayfish) that feed lower in the trophic web and consumption of macrophyte seeds functions to lower the TP of *A. ferox* to less than 4.0. Likewise, trophic position of *C. serpentina* (TP = 3.5) was within the range of a generalist omnivore such as *T. scripta* rather than that of a top predator. *Chelydra serpentina* is known to feed on a wide variety of aquatic invertebrates, fish, amphibians, and plants (Lagler 1943, Punzo 1975). Aquatic plants are a major component of the diet of *C. serpentina* (Aresco et al. in press). In this study, gut contents of *C. serpentina* contained primarily aquatic plants but trophic position based on stable isotopes was 3.5 and indicated it was a higher-level consumer. Thus, the conflict between gut contents and stable isotopes in this case exemplifies why it is important to obtain both types of data in food web studies to understand the difference between consumption and assimilation.

Sternotherus odoratus functioned as both a predator and processor of organic material and its trophic position (TP = 3.6) was similar to that of other omnivorous turtles. *Sternotherus odoratus* forages primarily on the bottom and probes the substrate and aquatic plants for prey (Lagler 1943, Ernst et al. 1994). In central Florida, Bancroft et al. (1983) reported that *S. odoratus* ate vascular plants (*Nuphar*, *Vallisneria*, *Eichhornia*), filamentous algae, mollusks, and aquatic insects. At Lake Jackson, the diet of *S. odoratus* consisted of seeds and aquatic insects, but, as with *T. scripta*, scavenging on fish carrion was a major food source during certain periods, which could elevate its trophic position. Thus, the TP of *S. odoratus* revealed by stable isotope ratios indicated that it is a predator, but its function in the food web is also primarily that of a scavenger and seed consumer. Because omnivory tends to be stabilizing (McCann and Hastings 1997), the distinction between functional and trophic roles is important to understanding the role of omnivores in freshwater food webs (Parkyn et al. 2001). Trophic interactions that include facultative scavenging by turtles may represent important links in the food web that increase system stability (McCann et al. 1998, DeVault et al. 2003). However, although stable isotope analyses provide important estimates of trophic position and

energy links in a food web, estimates of abundance and biomass of consumers are required to determine interaction strengths and the interactions that are actually limiting populations (Wootton 1997).

Importance of turtles in lake food webs

Despite the abundance and potential importance of turtles in aquatic systems, these long-lived vertebrates have been overlooked in studies of food webs of freshwater communities. In some freshwater habitats, the biomass of turtles can equal or exceed that of fish (Iverson 1982, Congdon et al. 1986). Turtles are a major component of freshwater communities in the southeastern United States, and also in Central and South America, Southeast Asia, and Australia (Pritchard 1979, Ernst and Barbour 1989). The turtle assemblage at Lake Jackson is representative of turtle assemblages in other regions and consisted of a diversity of trophic niches including a strict herbivore (*P. floridana*) and a group of omnivores (*T. scripta*, *S. odoratus*, *A. ferox*, *C. serpentina*, *K. subrubrum*).

Among the omnivorous turtle species at Lake Jackson, trophic position ranged from 3.3 to 4.0 and, thus, these species function as intermediate consumers (with some herbivory) and top predators in the food web. The diet of omnivorous turtles may vary both ontogenetically and seasonally. Many omnivorous turtle species exhibit some form of life history omnivory, where a shift in diet during development is associated with ontogenetic changes in size, habitat, or nutritional requirements (Diehl 1993, Polis and Strong 1996). Such diet shifts may occur gradually or rapidly and in the carnivorous to herbivorous direction or vice versa (Clark and Gibbons 1969, Graham 1971, Moll 1976, Hart 1983, Parmenter and Avery 1990). In addition, turtles forage opportunistically on the dominant resources in a community and often demonstrate temporal and/or spatial diet shifts in response to fluctuations in resource levels (Mahmoud 1968, Parmenter 1980, Schubauer and Parmenter 1981, Ford and Moll 2004). Therefore, depending on interaction strengths, widespread omnivory by turtles could cause seasonally alternative stable states. For example, an omnivore may preferentially feed on an intermediate consumer during one time of year thereby suppressing prey density that enhances growth of basal resources (i.e., trophic cascades). However, a seasonal change in the abundance of the intermediate consumer may cause the omnivore to switch its diet to a basal

resource such as macroalgae, thus changing the dynamics of the food web. Thus, “trophic level switching” by omnivorous turtles is likely quite common and may also be caused by seasonal changes in energy requirements and/or metabolism rather than changes in prey abundance (Jackson et al. 2004).

Omnivory is generally defined broadly as feeding at more than one trophic level, however variation in the modes of omnivory and their effects on trophic interactions have been largely overlooked. Winemiller (1990) states that nearly all consumers could be considered omnivores following the general definition. In a theoretical model, Pimm and Lawton (1978) demonstrated that omnivores should rarely feed on organisms not occupying an adjacent trophic level. Similarly, a model by Yodzis (1984) predicted that omnivory should be rare, contending that specialized digestive physiology is required to feed on both plant and animal tissues. This implies a somewhat different mode of omnivory, namely an omnivore that is both a predator and herbivore. Contrary to the predictions of Yodzis (1984), omnivores that feed on both consumers and producers are somewhat common in terrestrial and aquatic systems, especially among turtles (Lagler 1943, Mahmoud and Klicka 1969, Parmenter and Avery 1990, Polis 1991). This mode of omnivory presents some unique problems for simple food web models as the increase in possible energy pathways can correspond to a suite of indirect effects. Omnivorous turtles exhibit foraging patterns that suggest that they can simultaneously depress both consumers and producers.

Omnivorous turtles may strongly influence the structure of aquatic food webs, especially in habitats where their biomass exceeds that of other consumers. Most simple food chain models position an omnivore as the top predator in the trophic structure. This model has inspired several empirical studies that consider trophic cascades, especially in aquatic habitats (Strong 1992, Diehl 1995). In nature, the effects of omnivores may diffuse the effects of consumption and productivity across the trophic spectrum and the effects of trophic cascades (top-down control) may be uncommon (Polis and Strong 1996). In lake communities with complex food webs, omnivorous turtles represent an entire class of omnivores that are both intermediate *and* top predators (e.g., *T. scripta*, *C. serpentina*, and *A. ferox*). No previous theoretical or empirical studies have examined this type of omnivory. In a food web with four trophic levels, these intermediate

omnivores may interact strongly with a top predator (e.g., American alligator) directly as prey and indirectly as competitors (Bondavalli and Ulanowicz 1999).

In complex lake food webs, omnivorous turtles feed at multiple trophic levels and many different organisms may be potential prey (Fig. 3.15). Prey species may differ in abundance, size, and energy value and the consumption rate of a particular prey may reflect tradeoffs. How omnivores determine what to consume has received little attention despite its potential importance to food web structure. Thus, a mechanistic model using optimal foraging theory could predict the direct and indirect effects of omnivory. The competitive and predatory interactions between three or more optimally foraging omnivores under variable resource levels may be difficult to determine, but would provide important insights into the importance of omnivory in food webs.

Table 3.1. Baseline $\delta^{15}\text{N}$ values to estimate trophic position of vertebrates at Lake Jackson (LJ = Lake Jackson, LLJ = Little Lake Jackson). Macroalgae was collected during November 2001 – June 2004 ($n = 29$) at northwestern Lake Jackson and during October 2001– August 2003 ($n = 17$) at Little Lake Jackson. Algae samples were collected from mats in the littoral zone, from stems of maidencane grass and water lilies (periphyton), and from shells of live turtles (green algae, *Basycladia* sp.). Unionid clams ($n = 3$) were collected from Porter Sink at Lake Jackson on 14 February 2003.

Taxa	Baseline Site	Baseline organism	Baseline $\delta^{15}\text{N}$ value
turtle (adult)	LJ and LLJ	macroalgae	1.33
turtle (juv)	LLJ	macroalgae	0.71
turtle (juv)	LJ	macroalgae	1.94
snake	LJ	macroalgae	1.94
snake	LLJ	macroalgae	0.71
alligator (adult)	LJ and LLJ	macroalgae	1.33
alligator (juv)	LLJ	macroalgae	0.71
alligator (juv)	LJ	macroalgae	1.94
frog	LJ	macroalgae	1.94
frog	LLJ	macroalgae	0.71
salamander	LJ	macroalgae	1.94
deep fish	LJ	unionid clam	4.51
small littoral fish	LJ	POM	2.32

Table 3.2. Mean (\pm SE) $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isotope values (‰) for primary producers, invertebrates, fish, reptiles, amphibians, birds, and mammals collected at Lake Jackson, Leon County, in northwestern Florida.

Taxon (<i>n</i>)	$\delta^{15}\text{N}$ (‰)	$\delta^{13}\text{C}$ (‰) ^a	Source ^b
<i>Primary producers</i>			
Maidencane grass (<i>n</i> = 7)	4.44 (0.83)	-27.81 (0.43) [-26.0 – -29.5]	
All macrophytes (<i>n</i> = 23)	2.96 (0.42)	-27.44 (0.54) [-26.3 – -28.6]	
Particulate organic matter (POM) (<i>n</i> = 6)	2.32 (1.08)	-24.43 (1.01) [-21.8 – -27.0]	
Macroalgae			
NWLJ (<i>n</i> = 32)	1.94 (0.41)	-24.53 (0.85) [-22.8 – -26.3]	
LLJ (<i>n</i> = 17)	0.71 (0.16)	-33.22 (0.74) [-31.7 – -34.8]	
Phytoplankton	1.10 (-)	-30.17 (-)	
<i>Herbivorous invertebrates</i>			
Bivalvia (Unionidae) (<i>n</i> = 3)	4.51 (0.12)	-30.40 (0.30) [-30.1 – -32.7]	phytoplankton
Zooplankton (<i>n</i> = 10)	5.80 (0.41)	-30.61 (0.41) [-29.7 – -31.5]	phytoplankton
Amphipoda (<i>n</i> = 1)	1.58 (-)	-26.05 (-)	
Coleoptera (Hydrophilidae) (<i>n</i> = 3)	5.64 (1.05)	-24.79 (0.03) [-24.5 – -25.1]	macroalgae, POM
Chironomid (<i>n</i> = 1)	4.40 (-)	-27.71 (-)	
Gastropoda (<i>Aminicola</i>) (<i>n</i> = 4)	4.46 (0.11)	-25.37 (1.70) [-20.0 – -30.8]	multiple sources

Table 3.2: Continued.

Shrimp (<i>Palaemonetes paludosis</i>) ($n = 3$)	4.72 (0.36)	-25.54 (0.57)	[-23.1 – -28.0]	multiple sources
Crayfish ($n = 5$)	3.16 (0.25)	-27.12 (0.73)	[-25.1 – -29.2]	grass
<i>Carnivorous invertebrates</i>				
Odonata (Libellulidae) ($n = 8$)	4.19 (0.16)	-27.88 (0.30)	[-27.2 – -28.6]	macrophyte, grass
Odonata (Aeshnidae) ($n = 3$)	5.72 (0.31)	-25.88 (0.88)	[-22.1 – -29.7]	multiple sources
Coleoptera (Dytiscidae) ($n = 2$)	4.21 (0.32)	-29.17 (0.01)	[-29.1 – -29.3]	grass
Hemiptera (Belostomatidae) ($n = 5$)	4.64 (0.21)	-26.12 (0.38)	[-25.1 – -27.2]	POM
Hemiptera (Naucoridae) ($n = 3$)	3.65 (0.24)	-25.86 (2.70)	[-14.3 – -37.2]	NA
Arachnida (<i>Dolomedes</i>) ($n = 3$)	7.72 (0.28)	-25.00 (0.34)	[-23.5 – -26.5]	macroalgae
<i>Fish</i>				
Florida gar ($n = 2$) (<i>Lepisosteus platyrhincus</i>)	11.48 (0.45)	-23.54 (0.56)	[-16.4 – -30.7]	NA
Bowfin ($n = 5$) (<i>Amia calva</i>)	10.43 (0.09)	-28.11 (0.87)	[-25.7 – -30.5]	multiple sources
Largemouth bass (<i>Micropterus salmoides</i>)				
Adult (14 – 49 cm) ($n = 17$)	9.68 (0.11)	-25.9 (0.31)	[-25.3 – -26.6]	POM
Juvenile (4 cm) ($n = 1$)	7.78 (-)	-24.46 (-)		
Black crappie (<i>Pomoxis nigromaculatus</i>)				

Table 3.2: Continued.

Adult (15.0 – 30 cm) ($n = 10$)	9.57 (0.24)	-27.00 (0.42)	[-26.1 – -27.9]	macrophyte, grass
Juvenile (3 cm) ($n = 1$)	6.30 (-)	-23.80 (-)		
Warmouth (15 – 17 cm) ($n = 5$) <i>(Lepomis gulosus)</i>	9.13 (0.32)	-25.53 (0.72)	[-23.5 – -27.5]	multiple sources
Bluegill <i>(Lepomis macrochirus)</i>				
Adult (7 – 18 cm) ($n = 19$)	8.26 (0.19)	-26.71 (0.46)	[-25.8 – -27.7]	multiple sources
Juvenile (1.5 – 6 cm) ($n = 8$)	7.00 (0.20)	-26.17 (0.58)	[-24.5 – -27.8]	multiple sources
Spotted bullhead ($n = 6$) <i>(Ameiurus serracanthus)</i>	8.19 (0.44)	-26.07 (1.00)	[-23.5 – -28.6]	multiple sources
Redear sunfish ($n = 7$) <i>(Lepomis microlophus)</i>	8.11 (0.54)	-26.16 (1.04)	[-23.6 – -28.7]	multiple sources
Golden shiner (11 – 19 cm) ($n = 11$) <i>(Notemigonus crysoleucas)</i>	8.01 (0.24)	-27.65 (0.35)	[-26.9 – -28.4]	macrophyte, grass
Coastal shiner ($n = 2$) <i>(Notropis petersoni)</i>	7.81 (0.45)	-25.22 (1.04)	[-12.1 – -38.4]	NA
Mosquitofish ($n = 13$) <i>(Gambusia affinis)</i>	7.72 (0.16)	-25.51 (0.55)	[-24.3 – -26.7]	macroalgae, POM
Least killifish ($n = 9$) <i>(Heterandria formosa)</i>	7.01 (0.08)	-24.96 (0.67)	[-23.4 – -26.5]	macroalgae, POM
Chain pickerel (juv 7 cm) ($n = 1$)	7.08 (-)	-22.10 (-)		

Table 3.2: Continued.

(Esox niger)

Golden topminnow (*n* = 5) 6.80 (0.31) -23.79 (1.24) [-20.3 – -27.3] multiple sources

(Fundulus chrysotus)

Lake chubsucker (*n* = 6) 6.72 (0.38) -27.71 (0.70) [-25.9 – -29.5] multiple source

(Erimyzon sucetta)

Turtles

Yellow-bellied slider (*Trachemys scripta*)

Juvenile (*n* = 18) 6.64 (0.32) -25.91 (0.54) [-24.8 – -27.0] POM

Adult (*n* = 39) 6.55 (0.17) -24.18 (0.28) [-22.4 – -25.9] macroalgae

Florida cooter (*Pseudemys floridana*)

Juvenile (*n* = 22) 3.84 (0.16) -29.68 (0.84) [-25.8 – -33.6] macroalgae, macrophyte^c

Adult (*n* = 27) 4.37 (0.20) -23.66 (0.43) [-22.8 – -24.5] macroalgae

Stinkpot (*n* = 16) 7.33 (0.39) -24.97 (0.42) [-24.1 – -25.9] macroalgae

(Sternotherus odoratus)

Eastern mud turtle (*n* = 1) 8.89 (-) -25.94 (-)

(Kinosternon subrubrum)

Florida softshell (*Apalone ferox*)

Juvenile (*n* = 14) 5.73 (0.12) -28.00 (0.28) [-27.0 – -28.6] macrophyte

Adult (*n* = 21) 7.74 (0.28) -23.15 (0.59) [-22.0 – -24.6] macroalgae, POM

Table 3.2: Continued.

Snapping turtle ($n = 3$) (<i>Chelydra serpentina</i>)	7.78 (0.27)	-24.79 (1.47)	[-18.5 – -31.1]	multiple sources
<i>Snakes</i>				
Florida green water snake ($n = 14$) (<i>Nerodia floridana</i>)	7.18 (0.17)	-26.88 (0.54)	[-25.7 – -28.1]	multiple sources
Banded water snake ($n = 7$) (<i>Nerodia fasciata</i>)	8.25 (0.77)	-25.42 (0.39)	[-24.5 – -26.4]	macroalgae, POM
Cottonmouth ($n = 3$) (<i>Agkistrodon piscivorus</i>)	7.27 (1.00)	-24.91 (0.78)	[-21.6 – -28.3]	multiple sources
Mud snake ($n = 1$) (<i>Farancia abacura</i>)	9.00 (-)	-26.34 (-)		
<i>Aquatic salamanders</i>				
Greater siren ($n = 13$) (<i>Siren lacertina</i>)	6.68 (0.21)	-26.45 (0.48)	[-25.4 – -27.5]	macroalgae
Two-toed amphiuma ($n = 4$) (<i>Amphiuma means</i>)	8.81 (0.26)	-26.33 (0.27)	[-25.5 – -27.2]	macroalgae

Frogs

Table 3.2: Continued.

Florida cricket frog ($n = 2$) (<i>Acris gryllus</i>)	2.96 (1.00)	-28.23 (1.54)	[-26.1 – -30.4]	terrestrial
Southern leopard frog (adult) ($n = 12$) (<i>Rana sphenoccephala</i>)	6.61 (0.33)	-23.02 (0.76)	[-21.3 – -24.7]	POM, terrestrial
Southern leopard frog (tadpole) ($n = 3$)	1.98 (0.07)	-24.81 (0.44)	[-22.9 – -26.7]	macroalgae
Southern toad ($n = 3$) (<i>Bufo terrestris</i>)	7.12 (0.44)	-24.25 (0.08)	[-23.9 – -24.6]	terrestrial
Bullfrog ($n = 5$) (<i>Rana catesbeiana</i>)	6.95 (0.17)	-25.92 (1.14)	[-22.8 – -29.1]	multiple sources
Pig frog ($n = 8$) (<i>Rana grylio</i>)	7.62 (0.27)	-25.03 (0.66)	[-23.5 – -26.6]	macroalgae
<i>American alligator (Alligator mississippiensis)</i>				
Juvenile (0.5 – 1.3 m) ($n = 21$)	5.29 (0.19)	-25.65 (0.22)	[-25.2 – -26.1]	macroalgae
Adult (1.8 – 2.1 m) ($n = 2$)	6.69 (0.75)	-25.58 (0.86)	[-14.6 – -36.8]	NA
<i>Birds</i>				
American anhinga ($n = 1$) (<i>Anhinga anhinga</i>)	5.51 (-)	-16.45 (-)		
<i>Mammals</i>				

Table 3.2: Continued.

Marsh rice rat ($n = 1$) (<i>Oryzomys palustris</i>)	5.84 (-)	-25.03 (-)
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^a95% confidence intervals of $\delta^{13}\text{C}$ values are shown in brackets.

^bSource = basal source of primary production for a consumer based on 95% C.I. within that of producer and adjusted for trophic fractionation of $\delta^{13}\text{C}$. Multiple sources = overlap with some combination of 3 or more sources, but uninformative for specific sources.

^cTurtles collected from Little Lake Jackson (LLJ) and reflect site-specific $\delta^{13}\text{C}$ values

NA = undetermined basal resource, low sample size, wide variation.

Table 3.3. Percentage of 42 animal taxa with 95% confidence intervals of mean $\delta^{13}\text{C}$ isotope values within confidence intervals of each category of basal resources in the Lake Jackson food web, Leon County, Florida.

Source	<i>n</i>	%
Phytoplankton	2	4.8
Macroalgae	9	21.4
Particulate organic matter (POM)	4	9.5
Macroalgae + POM	5	11.9
Macroalgae + macrophyte	1	2.4
Macrophyte	1	2.4
Maidencane grass	2	4.8
Macrophyte + maidencane	3	7.1
Multiple sources ^a	15	35.7

^aMultiple sources = overlap with some combination of two or more sources, but uninformative for specific sources.

Table 3.4. Frequency of occurrence of diet items in gut contents of fish ($n = 83$) collected at Porter Sink, Lake Jackson, Leon County, Florida on 20 December 2002 and 14 February 2003. All fish were collected by dip-net as water flowed into the sinkhole.

Species	Diet items
Least killifish (<i>Heterandria formosa</i>) ($n = 7$)	100% algae, 100% POM
Mosquitofish (<i>Gambusia affinis</i>) ($n = 7$)	100% zooplankton
Golden shiner (<i>Notemigonus crysoleucas</i>) ($n = 12$)	100% zooplankton, 8% plant material
Bluegill (<i>Lepomis macrochirus</i>)	
Adult ($n = 24$)	42% odonata, 38% zooplankton, 33% mosquitofish, 29% least killifish, 25% shrimp
Juvenile ($n = 1$)	100% zooplankton (ostracods)
Redear sunfish (<i>Lepomis microlophus</i>) ($n = 1$)	100% odonata (libellulid)
Warmouth (<i>Lepomis gulosus</i>) ($n = 1$)	shrimp, least killifish, odonata (libellulid)
Black crappie (<i>Pomoxis nigromaculatus</i>) ($n = 10$)	100% fish, 60% shrimp, 1% odonata (libellulid)
Spotted bullhead (<i>Ameiurus serracanthus</i>) ($n = 2$)	100% snails (<i>Aminicola</i>)
Largemouth bass (<i>Micropterus salmoides</i>) ($n = 16$)	100% fish (golden shiner, swamp darter), 13% shrimp, 6% odonata (libellulid)
Bowfin (<i>Amia calva</i>) ($n = 2$)	100% fish

Table 3.5. Mean (\pm SE) trophic position of reptiles and amphibians in the Lake Jackson food web, Leon County, Florida. Isotope samples were obtained from muscle of road-killed individuals on U.S. Highway 27 bisecting Lake Jackson, dead individuals recovered during a dredging operation, and claw clips of live individuals. Trophic position of turtles, snakes, alligators, and frogs was calculated relative to the baseline $\delta^{15}\text{N}$ value with the equation $\text{TP} = ((\delta^{15}\text{N} - \delta^{15}\text{N}_{\text{baseline}}) / 2.3) + 1$, where TP is trophic position and $2.3^{0/00}$ is the mean enrichment of $\delta^{15}\text{N}$ between trophic levels as determined in the laboratory experiment. Trophic position of sirens and amphiumas was estimated relative to the baseline $\delta^{15}\text{N}$ value with the equation $\text{TP} = ((\delta^{15}\text{N} - \delta^{15}\text{N}_{\text{baseline}}) / 3.4) + 1$, where $3.4^{0/00}$ is the mean enrichment of $\delta^{15}\text{N}$ between trophic levels. For turtles, different letters denote significant differences between mean TP of adults of *P. floridana*, *T. scripta*, *A. ferox*, *S. odoratus*, and *C. serpentina* demonstrated with ANOVA and Bonferroni pairwise comparisons.

Species	Trophic position
<i>Turtles</i>	
Yellow-bellied slider (<i>Trachemys scripta</i>)	
Juvenile ($n = 18$)	3.5 (0.1) ^b
Adult ($n = 39$)	3.3 (0.1)
Florida cooter (<i>Pseudemys floridana</i>)	
Juvenile ($n = 22$)	2.4 (0.1)
Adult ($n = 27$)	2.3 (0.1) ^a
Stinkpot (<i>Sternotherus odoratus</i>) ($n = 16$)	3.6 (0.2) ^b
Eastern mud turtle (<i>Kinosternon subrubrum</i>)($n = 1$)	4.0 (-)
Florida softshell (<i>Apalone ferox</i>)	
Juvenile ($n = 14$)	3.2 (0.1)
Adult ($n = 21$)	3.8 (0.1) ^c
Snapping turtle ($n = 3$) (<i>Chelydra serpentina</i>)	3.5 (0.2) ^b
<i>Snakes</i>	
Florida green water snake (<i>Nerodia floridana</i>) ($n = 14$)	3.4 (0.1)
Banded water snake (<i>Nerodia fasciata</i>) ($n = 7$)	3.8 (0.3)
Cottonmouth (<i>Agkistrodon piscivorus</i>)($n = 3$)	3.2 (0.3)
Mud snake (<i>Farancia abacura</i>)($n = 1$)	4.6 (-)

Table 3.5: Continued.

Aquatic salamanders

Greater siren (<i>Siren lacertina</i>) ($n = 13$)	3.1 (0.1)
Two-toed amphiuma (<i>Amphiuma means</i>) ($n = 4$)	4.0 (0.1)

Frogs

Florida cricket frog (<i>Acris gryllus</i>) ($n = 2$)	2.0 (-)
Southern leopard frog (<i>Rana sphenoccephala</i>) ($n = 12$)	3.3 (0.2)
Bullfrog (<i>Rana catesbeiana</i>) ($n = 5$)	3.2 (0.1)
Pig frog (<i>Rana grylio</i>) ($n = 8$)	3.5 (0.2)

American alligator (*Alligator mississippiensis*)

Juvenile (0.5 – 1.3 m) ($n = 21$)	2.7 (0.1)
Adult (1.8 – 2.1 m) ($n = 2$)	3.3 (-)

Table 3.6. Percent occurrence of food items in the diet of juvenile ($n = 14$) and adult ($n = 36$) *Apalone ferox*, juvenile ($n = 18$) and adult ($n = 38$) *Trachemys scripta*, and juvenile ($n = 21$) and adult *Pseudemys floridana* ($n = 35$) at northwestern Lake Jackson and Little Lake Jackson, Leon County, Florida collected during March-October 2001-2003. Data from stomachs of road-killed individuals ($n = 15$) and fecal samples ($n = 97$) are combined, as there were no differences between these samples. Juvenile *Apalone ferox* were <120 mm plastron length and juvenile *Trachemys scripta* and *Pseudemys floridana* were < 100 mm plastron length.

Food Category	<i>A. ferox</i> (juv)	<i>A. ferox</i> (adult)	<i>T. scripta</i> (juv)	<i>T. scripta</i> (adult)	<i>P. floridana</i> (juv)	<i>P. floridana</i> (adult)
Insecta	100	66.7	100	52.6	33.3	2.9
Crustacea		11.1		2.6	4.8	
Gastropoda		30.5		2.6		
Fish		19.4		7.9		
Bird		5.6				
Amphibian larvae	21.4					
Macroalgae	7.1	27.8	16.7	36.8	90.5	97.1
Macrophyte		8.3	33.3	81.6	38.1	37.1
Maidencane grass		2.7	5.6	26.3	9.5	5.7
Seeds		66.7	11.1	13.2	23.8	2.9
Terrestrial leaves				5.3		8.6

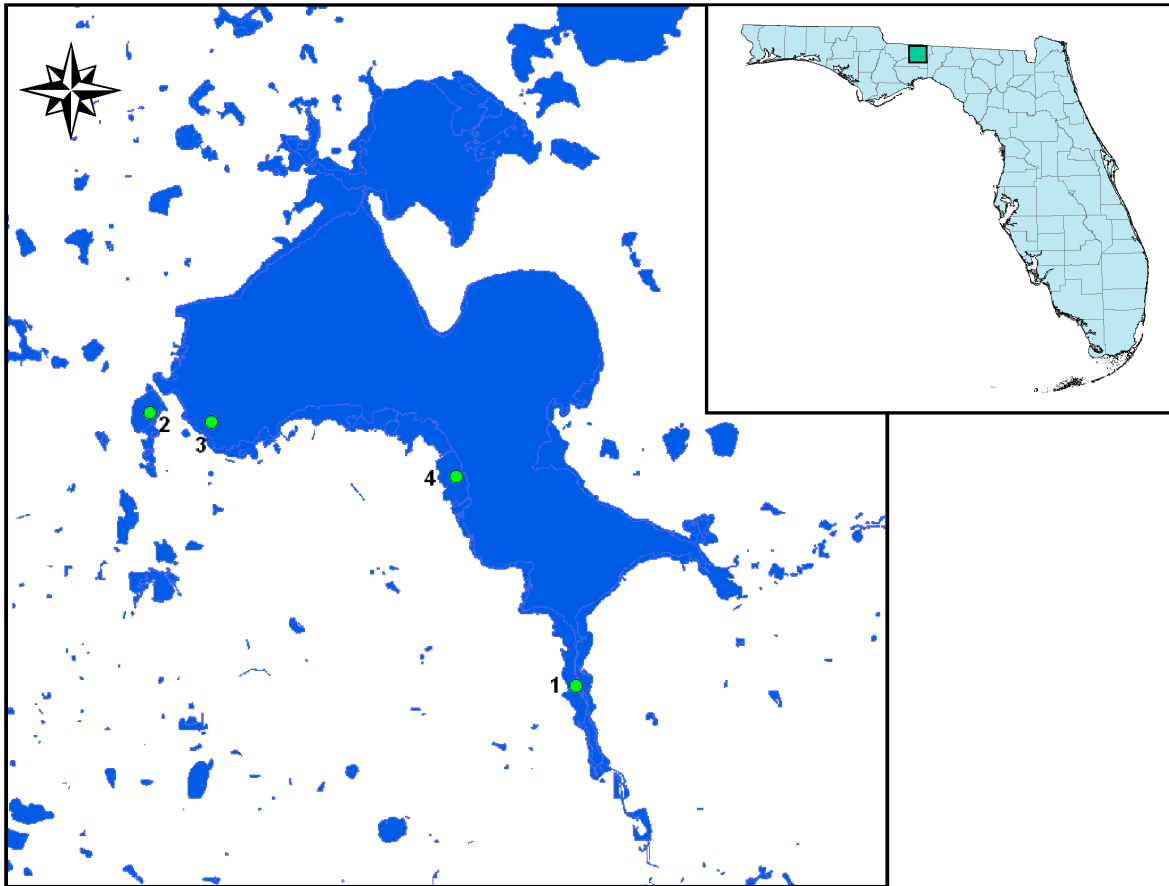


Figure 3.1. Study area at Lake Jackson, Leon County, Florida. 1 = Megginis Arm, 2 = Little Lake Jackson, 3 = Northwest Lake Jackson, 4 = Porter Sink.

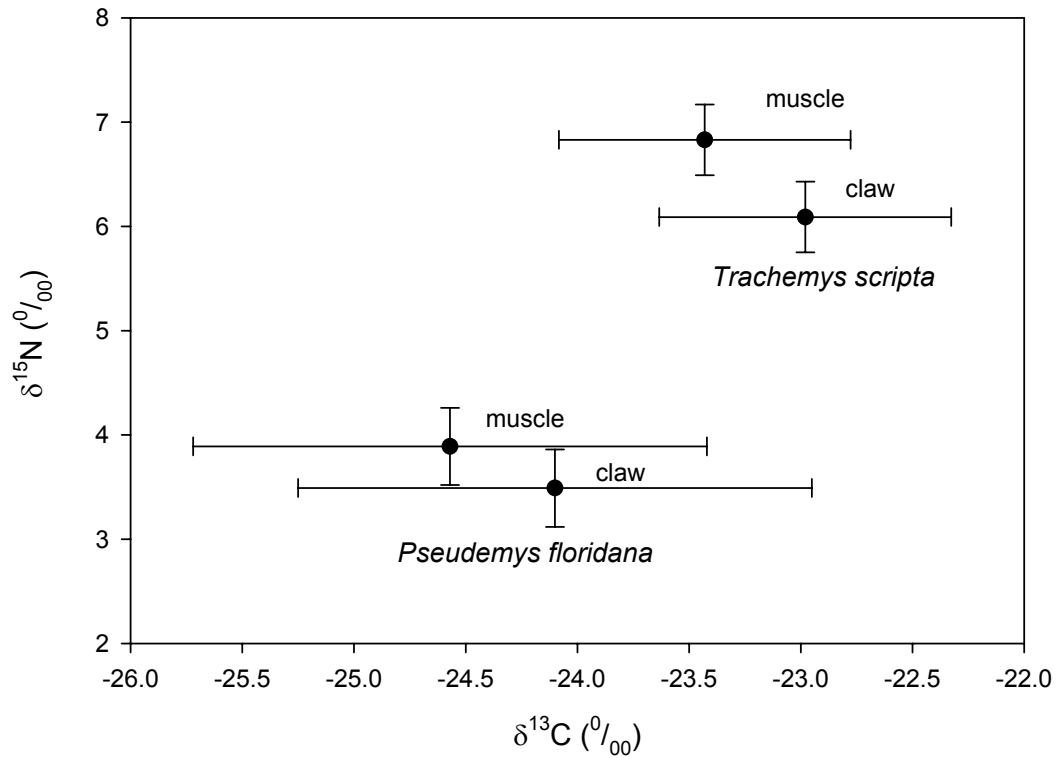


Figure 3.2. Comparison of stable isotope values of claw and muscle tissue from *Trachemys scripta* ($n = 17$) and *Pseudemys floridana* ($n = 11$) collected from road-killed individuals on U.S. Highway 27 at Lake Jackson, Leon County, Florida (2001-2002). There were no significant differences between claw and muscle for $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ in either species.

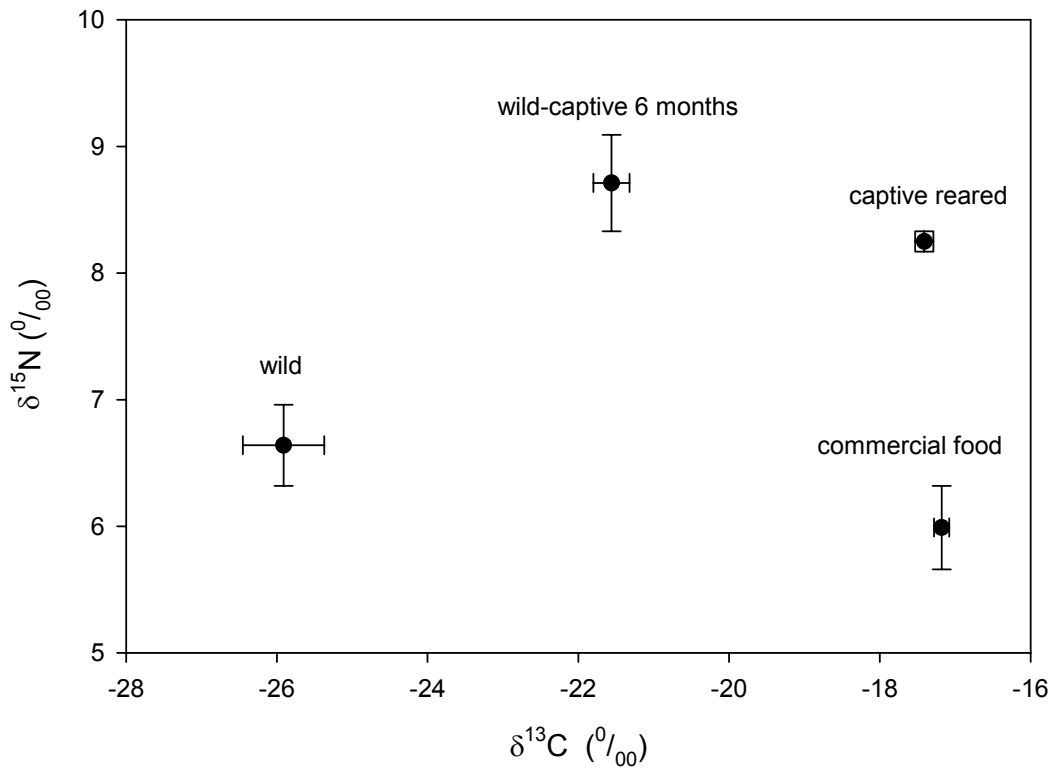


Figure 3.3. Comparison of stable isotope values ($\delta^{15}\text{N}$ and $\delta^{13}\text{C}$) among wild ($n = 18$), captive ($n = 7$), and wild-captive (6 months) ($n = 3$) juvenile *Trachemys scripta* and commercial food (Wardleys™ TEN Reptile food sticks) ($n = 2$ aggregate samples of 20 sticks). Wild turtles were collected at Lake Jackson, Leon County, Florida and captives were hatched from eggs collected at the same location. Fractionation between food and captive turtles is 2.3 for $\delta^{15}\text{N}$ and 0.23 for $\delta^{13}\text{C}$. A diet switch from wild to captive diet required 6 months to be detected by a change in the $\delta^{15}\text{N}$ isotope and 12 months to be detected by a change in the $\delta^{13}\text{C}$ isotope.

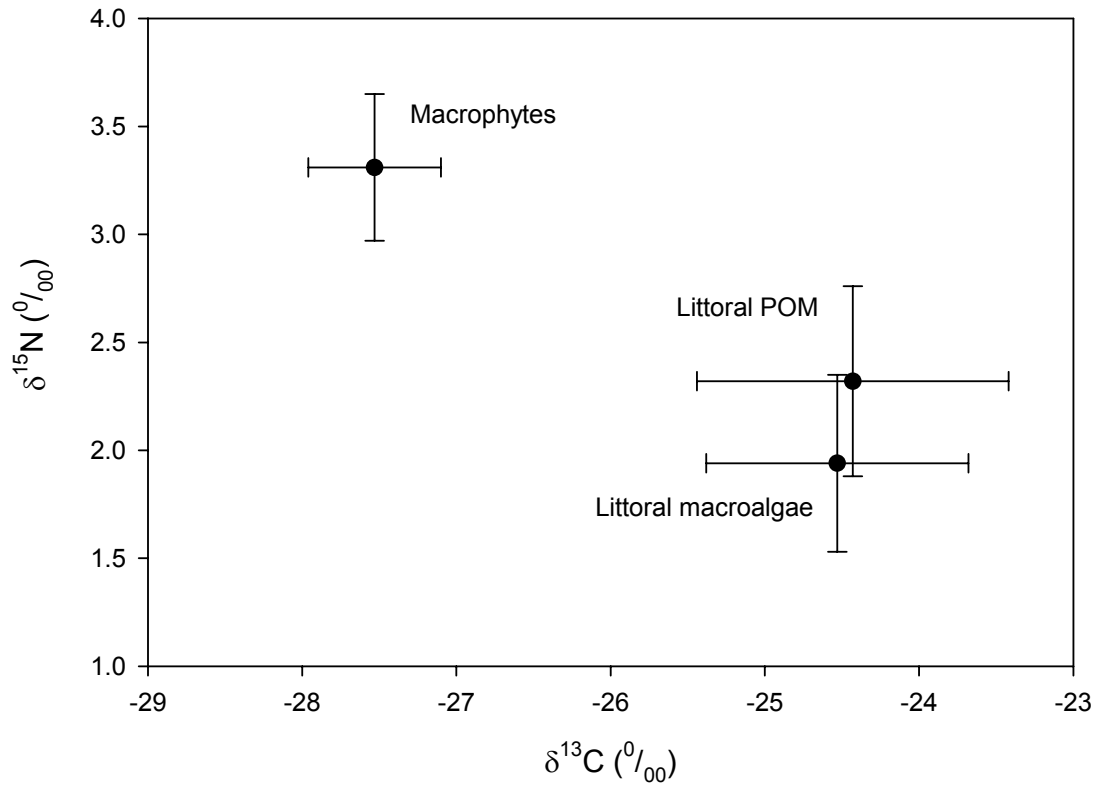


Figure 3.4. Mean $\delta^{15}\text{N}$ vs. mean $\delta^{13}\text{C}$ (± 1 SE) of C3 macrophytes ($n = 30$), particulate organic matter (POM) ($n = 6$), and macroalgae ($n = 32$) from the littoral zone of northwestern Lake Jackson, Leon County, Florida. Floating, submerged, and emergent macrophytes were collected during February 2002 - August 2003. Macroalgae (periphyton and filamentous algae) were collected during November 2001 - June 2004. Particulate organic matter (POM), a mix of phytoplankton, macroalgae, and detritus, was collected during May - August 2003.

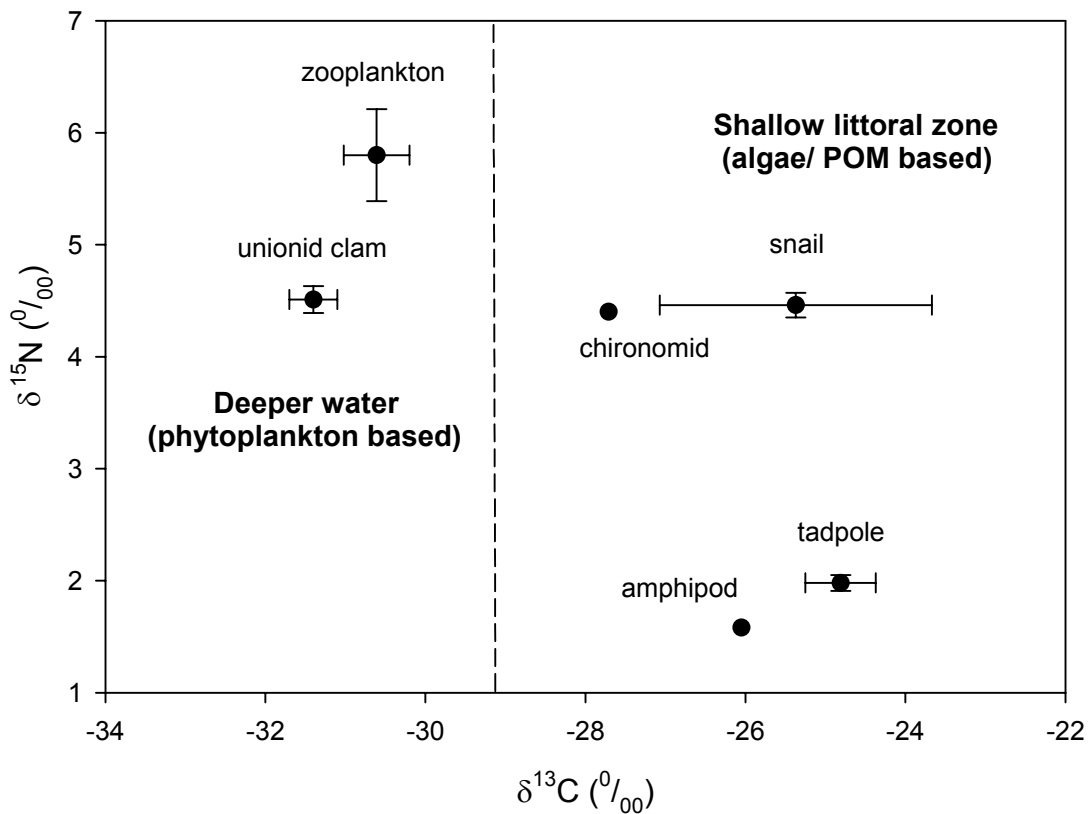


Figure 3.5. Mean $\delta^{15}\text{N}$ vs. mean $\delta^{13}\text{C}$ (± 1 SE) for primary consumers in the shallow littoral zone and pelagic zone at Lake Jackson, Leon County, Florida. Open water zooplankton ($n = 10$ aggregate) was collected at northwestern Lake Jackson using a 250- μm zooplankton tow net during August 2002 – November 2003. Unionid clams (paper pondshell [*Utterbackia imbecillis*]) ($n = 3$) were collected at Porter Sink, Lake Jackson in December 2002 – February 2003. Snails (*Aminicola*), chironomids, amphipods, and tadpoles of *Rana sphenoccephala* were collected by dipnet in 2002 and 2003.

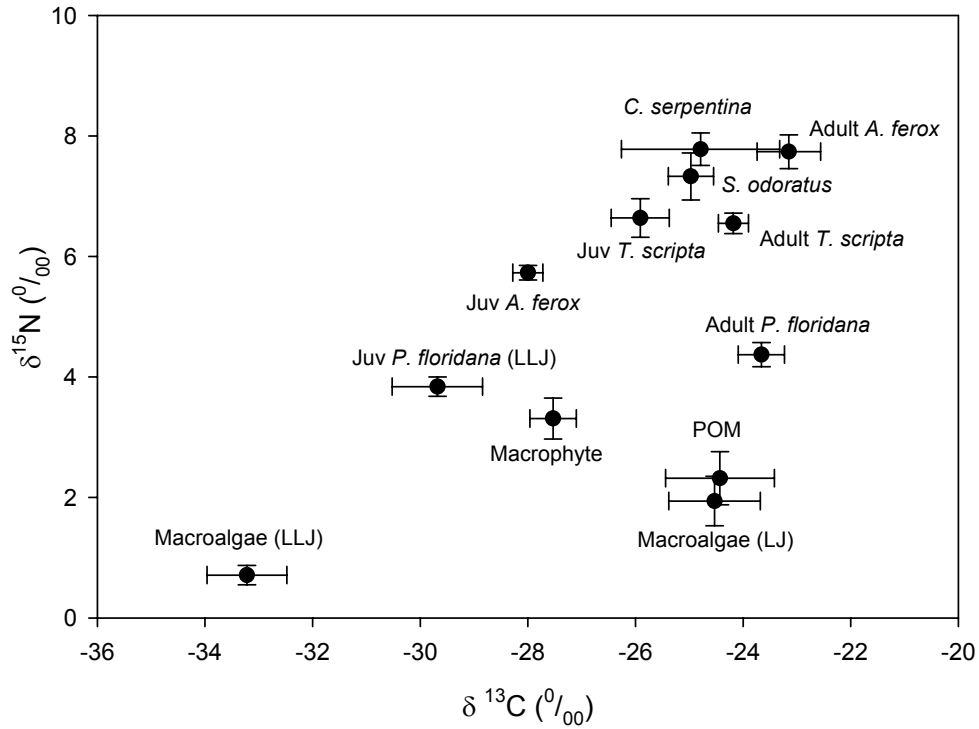


Figure 3.6. Comparison of mean $\delta^{15}\text{N}$ vs. mean $\delta^{13}\text{C}$ (± 1 SE) (± 1 SE) of juvenile and adult *Trachemys scripta*, *Pseudemys floridana*, and *Apalone ferox*, and adult *Sternotherus odoratus* and *Chelydra serpentina* and C4 macrophytes, particulate organic matter (POM), and macroalgae from the littoral zone of Lake Jackson, Leon County, Florida. LLJ = samples were collected from Little Lake Jackson and LJ = samples were collected from northwest Lake Jackson and reflect stable isotope from these respective sites.

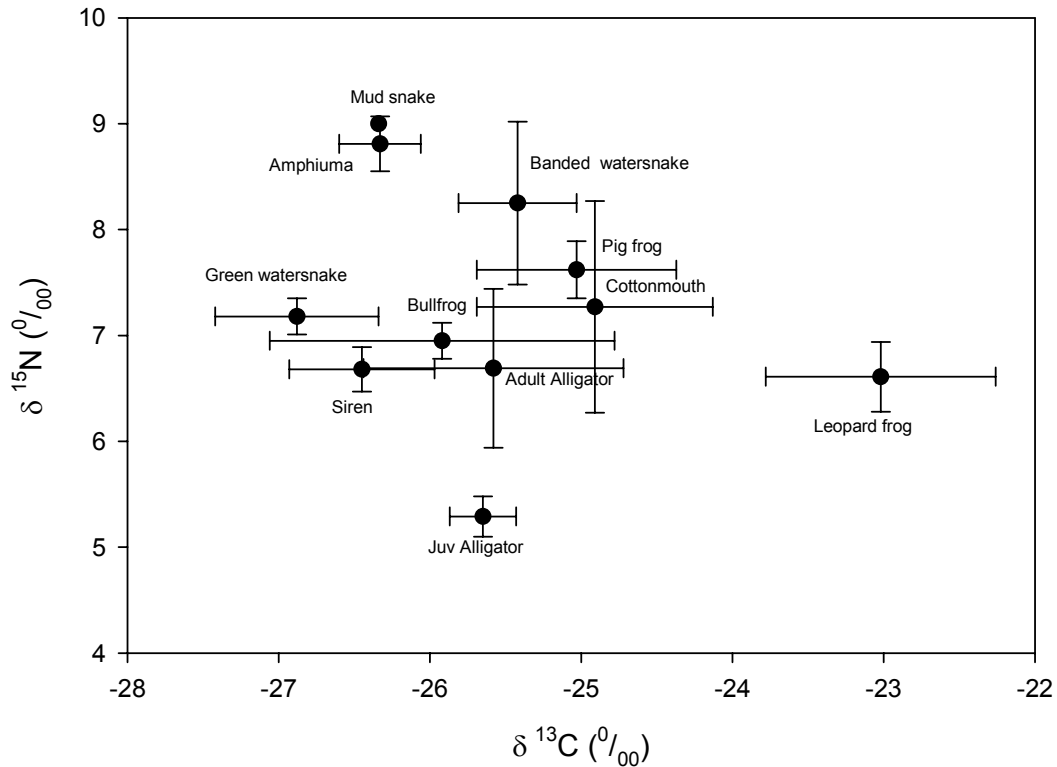


Figure 3.7. Mean stable isotope values (± 1 SE) of snakes, frogs, alligators, and aquatic salamanders at Lake Jackson, Leon County, Florida. Isotope samples were collected in 2001-2004 from muscle of road-killed individuals on U.S. Highway 27 bisecting Lake Jackson, dead individuals recovered during a dredging operation, and claw clips of live individuals. Trophic position of snakes, alligators, and frogs was calculated relative to the baseline $\delta^{15}\text{N}$ value with the equation $\text{TP} = ((\delta^{15}\text{N} - \delta^{15}\text{N}_{\text{baseline}}) / 2.3) + 1$, where TP is trophic position and 2.3‰ is the mean enrichment of $\delta^{15}\text{N}$ between trophic levels as determined in the laboratory experiment. Trophic position of sirens and amphiumas was estimated relative to the baseline $\delta^{15}\text{N}$ value with the equation $\text{TP} = ((\delta^{15}\text{N} - \delta^{15}\text{N}_{\text{baseline}}) / 3.4) + 1$, where 3.4‰ is the mean enrichment of $\delta^{15}\text{N}$ between trophic levels.

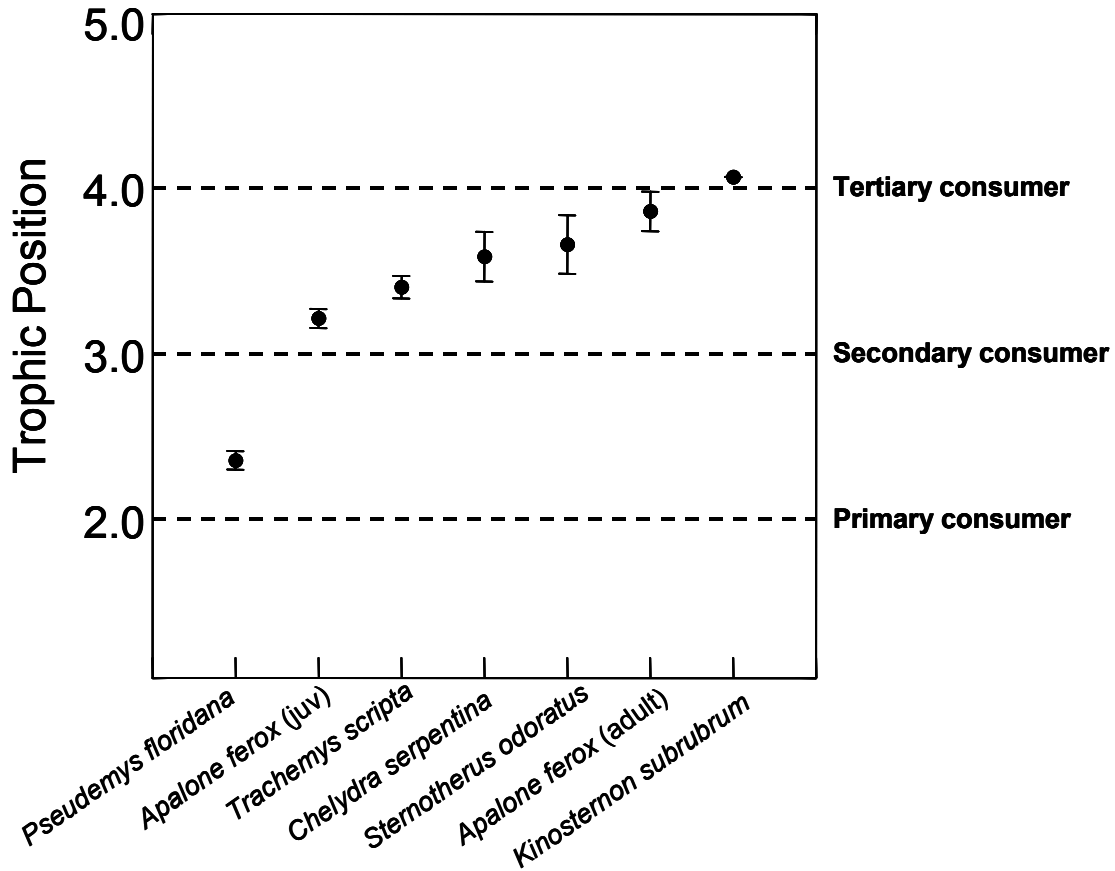


Figure 3.8. Trophic position (± 1 SE) of turtles at Lake Jackson, Leon County, Florida. Isotope samples were collected in 2001-2004 from muscle of road-killed individuals on U.S. Highway 27 bisecting Lake Jackson and claw clips of live individuals. Trophic position of turtles was calculated relative to the baseline $\delta^{15}\text{N}$ value with the equation $\text{TP} = ((\delta^{15}\text{N} - \delta^{15}\text{N}_{\text{baseline}}) / 2.3) + 1$, where TP is trophic position and 2.3‰ is the mean enrichment of $\delta^{15}\text{N}$ between trophic levels as determined in the laboratory experiment.

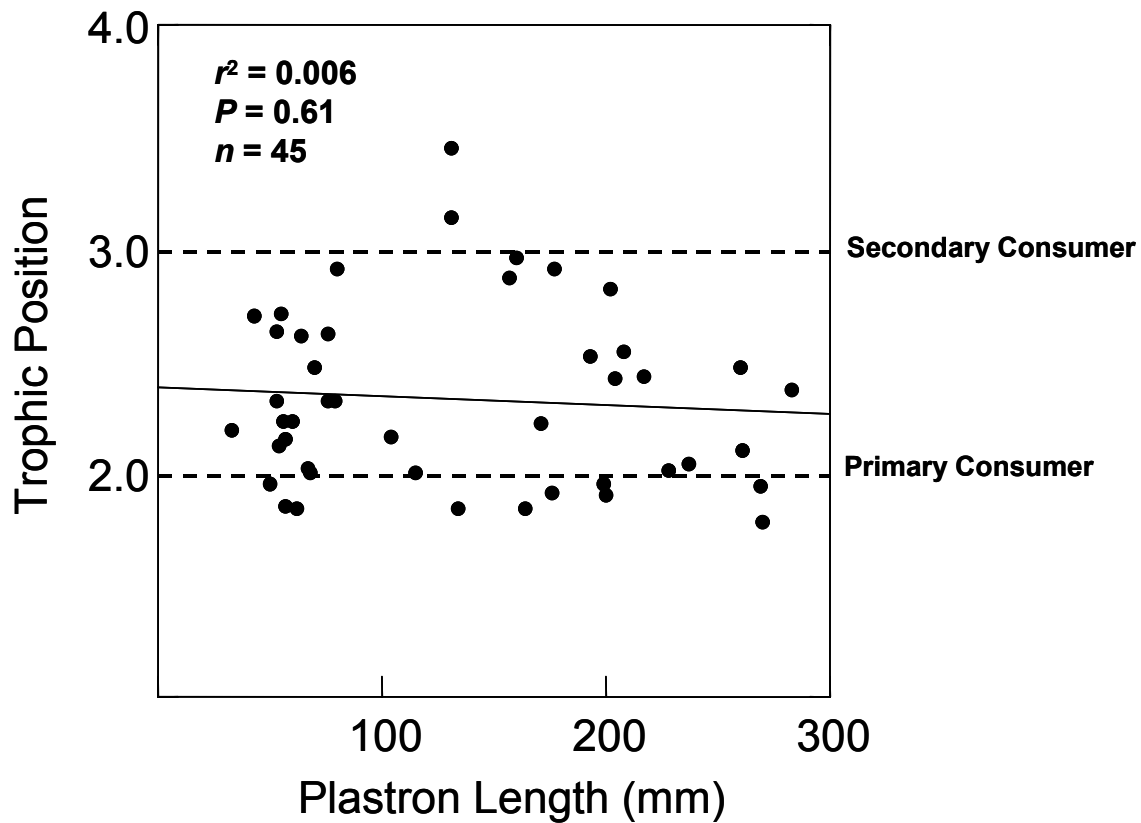


Figure 3.9. Trophic position vs. plastron length of *Pseudemys floridana*. Mean trophic position of adults and juveniles is 2.3 (SE = 0.06) at Lake Jackson, Leon County, Florida. Isotope samples were collected in 2001-2004 from muscle of road-killed individuals on U.S. Highway 27 bisecting Lake Jackson and claw clips of live individuals. Trophic position of turtles was calculated relative to the baseline $\delta^{15}\text{N}$ value with the equation $\text{TP} = ((\delta^{15}\text{N} - \delta^{15}\text{N}_{\text{baseline}}) / 2.3) + 1$, where TP is trophic position and 2.3‰ is the mean enrichment of $\delta^{15}\text{N}$ between trophic levels as determined in the laboratory experiment. Dashed lines denote theoretical TP of a strict “Primary Consumer” (TP = 2.0), “Secondary Consumer” (TP = 3.0), and “Tertiary Consumer” (TP = 4.0).

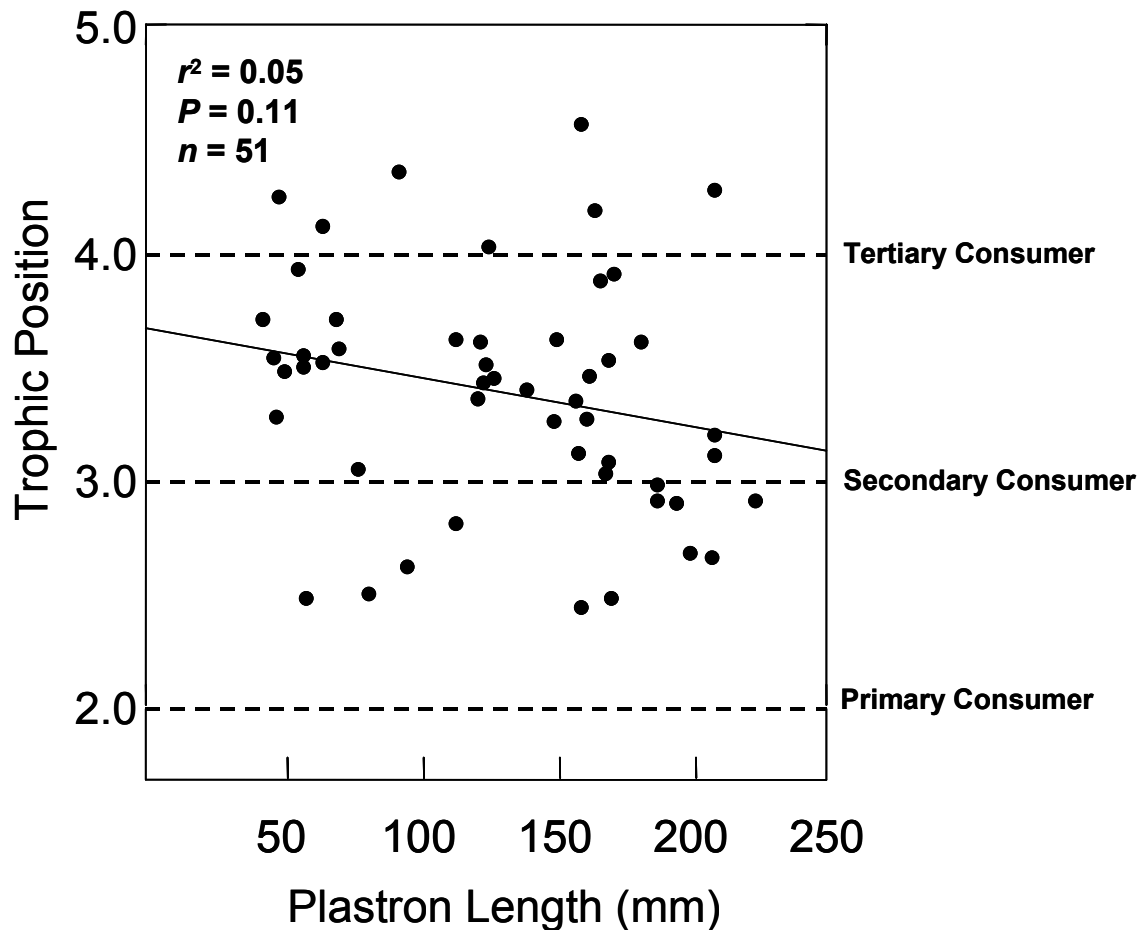


Figure 3.10. Trophic position vs. plastron length of *Trachemys scripta* at Lake Jackson, Leon County, Florida. Isotope samples were collected in 2001-2004 from muscle of road-killed individuals on U.S. Highway 27 bisecting Lake Jackson and claw clips of live individuals. Trophic position of turtles was calculated relative to the baseline $\delta^{15}\text{N}$ value with the equation $TP = ((\delta^{15}\text{N} - \delta^{15}\text{N}_{\text{baseline}}) / 2.3) + 1$, where TP is trophic position and 2.3‰ is the mean enrichment of $\delta^{15}\text{N}$ between trophic levels as determined in the laboratory experiment. Dashed lines denote theoretical TP of a strict “Primary Consumer” (TP = 2.0), “Secondary Consumer” (TP = 3.0), and “Tertiary Consumer” (TP = 4.0).

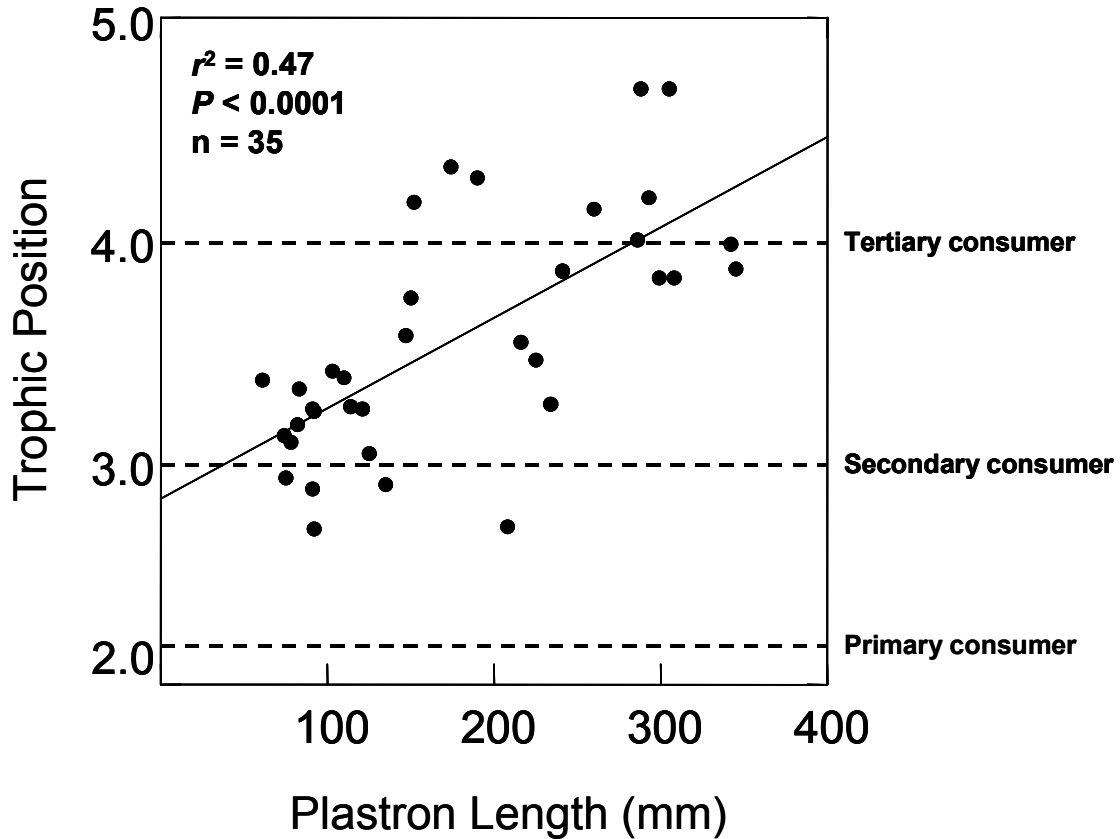


Figure 3.11. Trophic position vs. plastron length of *Apalone ferox* at Lake Jackson, Leon County, Florida. Mean trophic position of adults and juveniles is 3.6 (SE = 0.09). Isotope samples were collected in 2001-2004 from muscle of road-killed individuals on U.S. Highway 27 bisecting Lake Jackson and claw clips of live individuals. Trophic position of turtles was calculated relative to the baseline $\delta^{15}\text{N}$ value with the equation $TP = ((\delta^{15}\text{N} - \delta^{15}\text{N}_{\text{baseline}}) / 2.3) + 1$, where TP is trophic position and 2.3‰ is the mean enrichment of $\delta^{15}\text{N}$ between trophic levels as determined in the laboratory experiment. Dashed lines denote theoretical TP of a strict “Primary Consumer” (TP = 2.0), “Secondary Consumer” (TP = 3.0), and “Tertiary Consumer” (TP = 4.0).

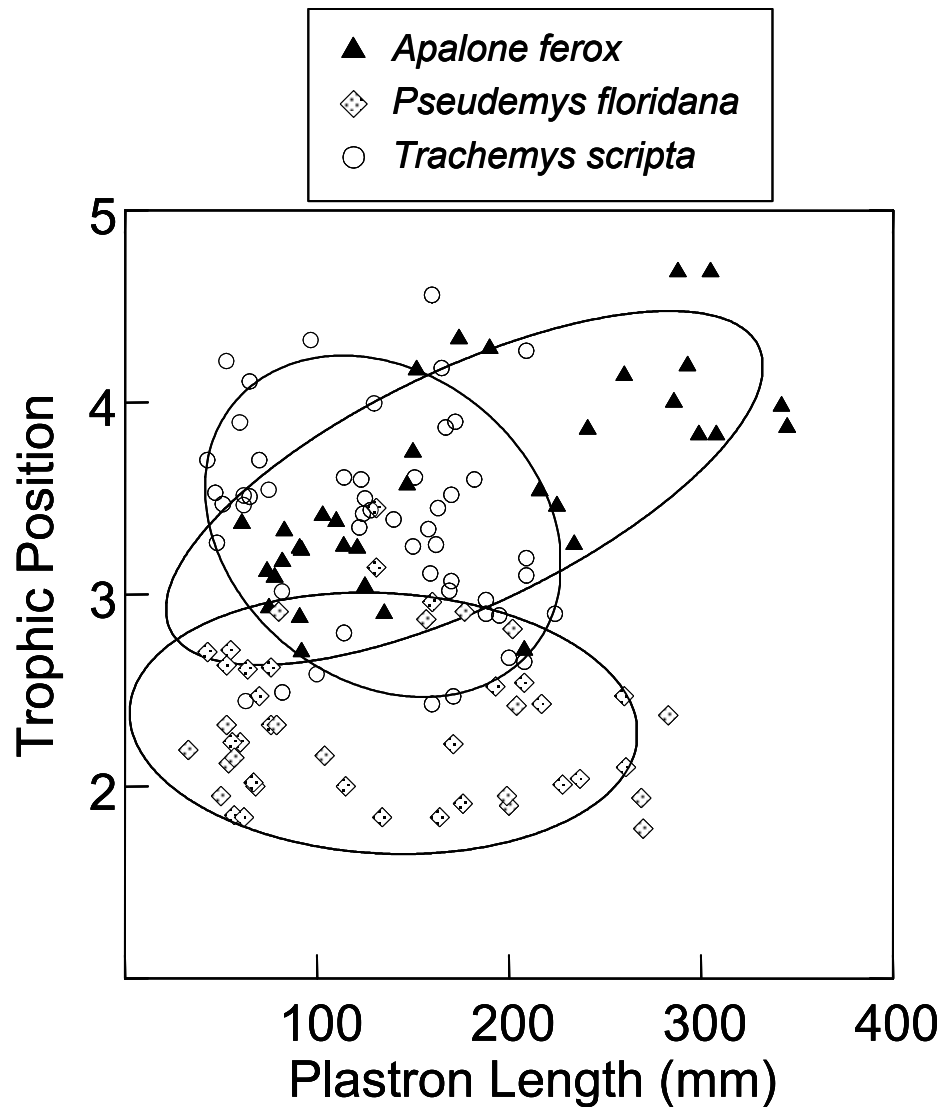


Figure 3.12. Combined plot of trophic position vs. plastron length of all three species with 75% confidence ellipses. Isotope samples were collected in 2001-2004 from muscle of road-killed individuals on U.S. Highway 27 bisecting Lake Jackson and claw clips of live individuals. Trophic position of turtles was calculated relative to the baseline $\delta^{15}\text{N}$ value with the equation $TP = ((\delta^{15}\text{N} - \delta^{15}\text{N}_{\text{baseline}}) / 2.3) + 1$, where TP is trophic position and 2.3‰ is the mean enrichment of $\delta^{15}\text{N}$ between trophic levels as determined in the laboratory experiment. Dashed lines denote theoretical TP of a strict “Primary Consumer” (TP = 2.0), “Secondary Consumer” (TP = 3.0), and “Tertiary Consumer” (TP = 4.0).

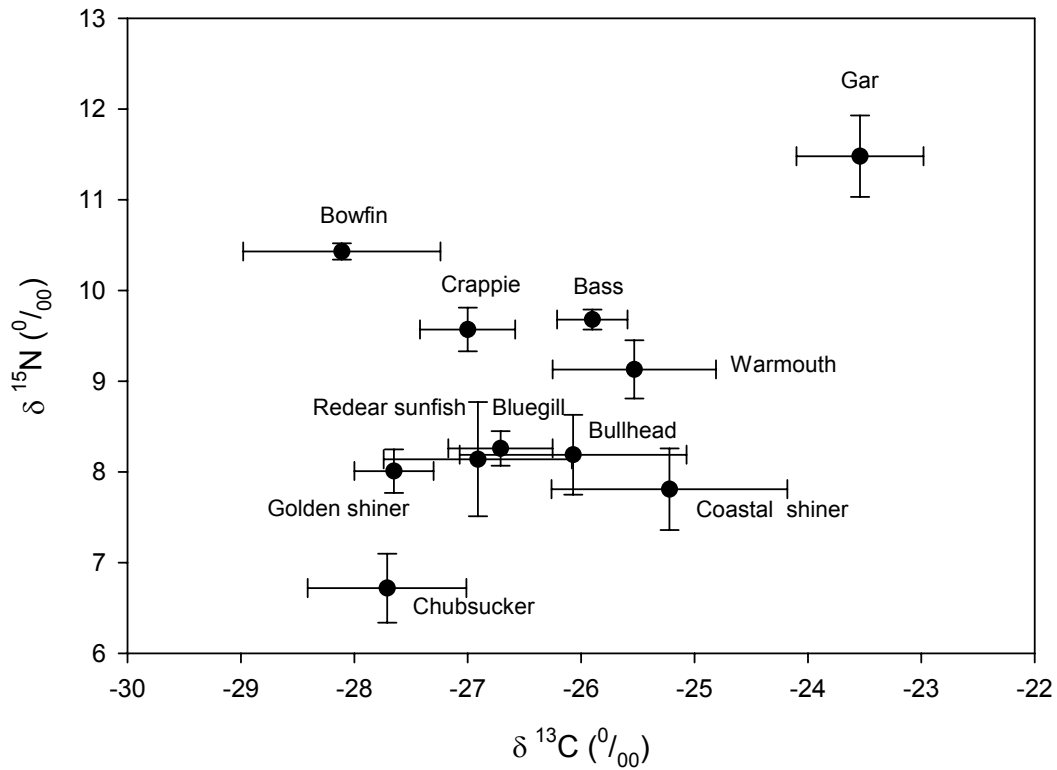


Figure 3.13. Mean stable isotope values (± 1 SE) of fish at Lake Jackson, Leon County, Florida. Fish were collected at Porter Sink, Lake Jackson on 20 December 2002 and 14 February 2003 and in the shallow, littoral zone of northwestern Lake Jackson during May to August 2002-2003.

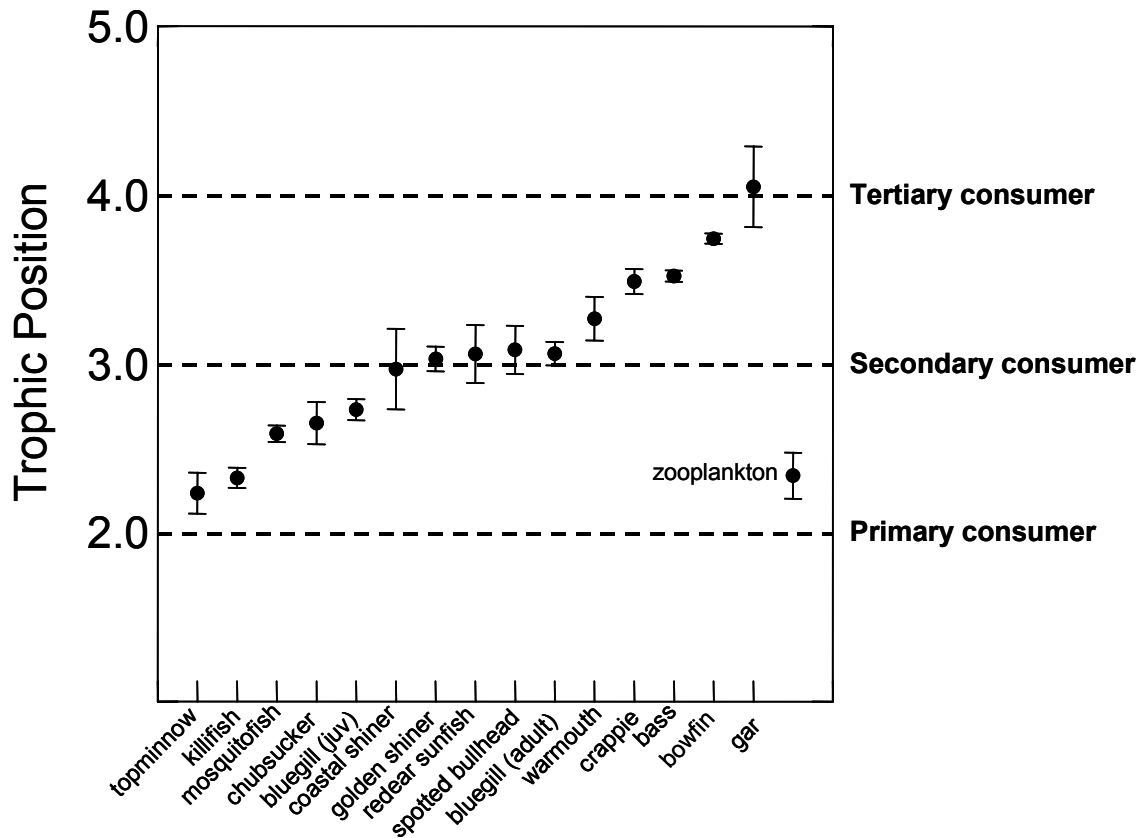


Figure 3.14. Trophic position (± 1 SE) of fish at Lake Jackson, Leon County, Florida. Trophic position of deep-water zooplankton is shown for reference as a primary consumer on phytoplankton and a diet source of some fish. Fish were collected at Porter Sink, Lake Jackson on 20 December 2002 and 14 February 2003 and in the shallow, littoral zone of northwestern Lake Jackson during May to August 2002-2003. Trophic positions were estimated relative to the baseline $\delta^{15}\text{N}$ value with the equation $TP = ((\delta^{15}\text{N} - \delta^{15}\text{N}_{\text{baseline}}) / 3.4) + 1$, where 3.4‰ is the mean enrichment of $\delta^{15}\text{N}$ between trophic levels.

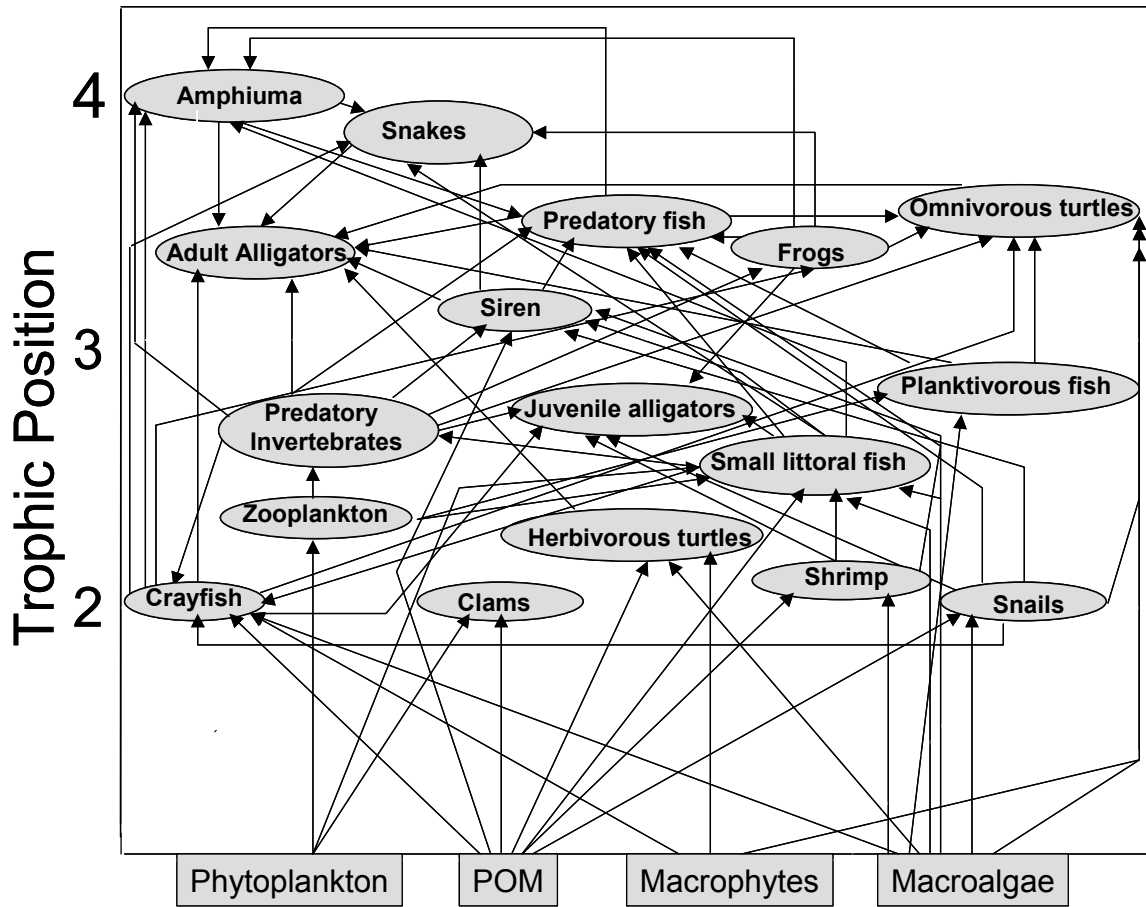


Figure 3.15. Food web diagram of Lake Jackson, Leon County, Florida based on trophic position. Direction of arrows indicates direction of energy flow.

CONCLUSION

Lakes in the Coastal Plain of the southeastern United States have high productivity and species diversity, including many species of reptiles and amphibians. Turtles are abundant in southeastern lakes, but their ecological relationships and role in lake food webs have never been studied. I studied the ecological relationships of turtles in north Florida lakes and the environmental correlates of abundance of three predominant turtle species, the yellow-bellied slider (*T. scripta*), Florida cooter (*P. floridana*), and Florida softshell (*A. ferox*). The species in this assemblage shares a wide habitat distribution but vary substantially in abundance across habitats. Coexistence and variation in abundance may be due to species-specific differences in resource requirements or use (i.e., diet generalist vs. specialist). Therefore, the objectives of this study were to determine whether these species show some consistent pattern of correlation with environmental factors based on trophic position. I evaluated the role of omnivory in regulating abundance, habitat distribution, and trophic dynamics of *T. scripta* and *P. floridana* by quantifying differences in the degree of omnivory and specialization and assessing whether *T. scripta*, an opportunistic omnivore, competes better than a specialist herbivore, *P. floridana*, when forced to share the niche under low resource conditions. I examined sources of primary production and trophic relationships in the food web of Lake Jackson, a large, eutrophic lake in northwestern Florida. Tissues from primary producers, invertebrates, and vertebrates were analyzed for stable isotopes of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ and trophic structure was evaluated in terms of a trophic position (TP) model.

Turtle abundance and environmental characteristics were sampled at 17 lakes in Leon County, Florida. Numbers of turtles captured ranged from 0 to 62 turtles per lake (CPUE = 0.00 - 7.75) of three species: *A. ferox*, *P. floridana*, and *T. scripta*. Mean abundance of *T. scripta* was significantly greater in Tallahassee Red Hill lakes, whereas mean abundance of *P. floridana* and *A. ferox* between physiographic regions was nearly identical. *Trachemys scripta* exhibited substantially greater abundances than that of *P.*

floridana in eutrophic lakes, but was much less abundant than *P. floridana* in oligotrophic lakes. *Pseudemys floridana* occurs in equal abundances in lakes across the primary productivity gradient but never attains the highest densities of *T. scripta*. A principal components analysis indicated major positive covariation among percent area covered by macrophytes (PAC), total phosphorus, chironomid abundance, snail abundance, and macroinvertebrate abundance and negative covariation of periphyton productivity and percent area covered by macrophytes. The first three axes accounted for 81% of the variance. PC 1 was primarily a lake productivity axis and showed covariation between percent surface area covered by macrophytes (PAC), total phosphorus, chironomid abundance, and snail abundance and accounted for 38% of the variation.

Individual Mantel analyses by species revealed significant correlations between abundance of *T. scripta*, *P. floridana*, and *A. ferox* and a suite of environmental variables consisting of both biotic and abiotic factors. Lakes with a higher abundance of *T. scripta* had a mud/muck substrate, no alligators, high periphyton productivity, high abundance of chironomids, and high open water phosphorus (Mantel $r = 0.75$, $P = 0.001$). Similarly, a significant correlation existed between lakes with high abundance of *P. floridana* and those with a mud substrate, no alligators, high periphyton productivity, high abundance of chironomids, and low PAC (Mantel $r = 0.50$, $P = 0.020$). There was a strong association between abundance of *A. ferox* and a set of five environmental variables that included no alligators, high periphyton productivity, high macroinvertebrate abundance, high snail abundance, and high total open water phosphorus (Mantel $r = 0.48$, $P = 0.013$). There was no difference in the results of the Mantel analyses with or without physiographic region included as a variable for any of the three species. A comparison of the results of the Mantel analysis of turtle abundance and DFA for physiographic region demonstrated that, with the exception of phosphorus for *T. scripta* and PAC for *P. floridana*, turtles responded to different variables than the ones that separated physiographic regions. These results suggest that patterns of abundance of sympatric freshwater turtle species can be strongly influenced by environmental variables that are correlated with their trophic position in the food web

A Mantel test based on distance matrices of total turtle abundance of all three species and environmental variables suggested that lakes similar in environmental

characteristics have similar overall turtle abundance. These results revealed a strong correlation between lakes with high turtle abundance and high periphyton productivity, mud/muck substrate, and no alligators (Mantel $r = 0.69$, $P = 0.001$). The strong positive association between turtle abundance and high primary productivity (algae) and no predation by alligators suggests that a combination of bottom-up and top-down controls may be important limiting factors to turtle populations.

Varying levels of omnivory among coexisting species are an overlooked aspect of studies of food web dynamics and niche relationships. This research evaluated the levels of omnivory and competitive interactions between two abundant sympatric emydid turtles, *Trachemys scripta* and *Pseudemys floridana*, that coexist across a productivity gradient in lentic water habitats in northern Florida. First, a foraging experiment indicated that both species were omnivorous in the juvenile stage, but *P. floridana* was more herbivorous and *T. scripta* consumed more insects and carrion. This low level of resource overlap was consistent with studies of gut contents and stable isotope analyses. Second, in a 13-month cage experiment in a natural pond under low resource conditions, the generalist *T. scripta* grew more slowly with conspecifics than with *P. floridana*, and the specialist *P. floridana* grew at the same rate with both *T. scripta* and conspecifics. *Trachemys scripta* with *P. floridana* exhibited the highest growth rate (3.5 mm/yr), slightly faster than *P. floridana* with conspecifics (2.3 mm/yr). *Trachemys scripta* was apparently unable to process macroalgae as well as *P. floridana* and the low abundance of invertebrate prey in the pond was apparently limiting. Gut specializations in *P. floridana* that allow for more efficient digestion and assimilation of nutrients could be the mechanism causing its better performance than that of *T. scripta*, a more generalist omnivore, when only low-quality, basal resources are available. I propose that intraspecific effects can override interspecific effects, reducing interspecific asymmetric competition in cases in which one species can make more efficient use of a limiting resource and influence the abundance of trophic generalists across a productivity gradient. A possible mechanism for competition among conspecifics may be aggressive interactions in habitats with limited resources.

In the Lake Jackson food web, macroalgae represented a small percentage of the biomass of total primary production compared to macrophytes, but was the foundation of

the food web. Stable isotope analyses ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) revealed that macroalgae provided full or partial contribution to the growth of 81% of 42 animal taxa sampled at Lake Jackson. Thus, eutrophication that causes changes in the amount and ratio of nitrogen and phosphorus could cause inedible blue-green algae (cyanobacteria) to displace filamentous macroalgae, resulting in severe changes to the food web.

Omnivory was prevalent in the Lake Jackson food web, and most secondary consumers had a TP of less than 4.0. This result indicates that there were few specialists (TP \geq 4.0) and few strict primary consumers (TP = 2.0). Trophic structure of the fish assemblage at Lake Jackson consisted of several species that were functionally omnivorous predators with trophic positions of only 3.5 – 3.7. Similarly, many other functional predators in the Lake Jackson food web (e.g., alligator, Florida green water snake) had lower than expected TPs. Predation on consumers that occupy lower positions in the food web functions to lower TP of top predators, whereas feeding on predatory insects that occupy a similar or greater trophic position elevated the trophic position of some turtles (e.g., *T. scripta*).

Estimated trophic positions revealed that the turtle assemblage consisted of two foraging patterns: herbivorous (*P. floridana*) and omnivorous (*T. scripta*, *S. odoratus*, *A. ferox*, *C. serpentina*, and *K. subrubrum*). The trophic positions of the omnivorous species ranged from 3.3 to 4.0. Trophic positions of the three predominant species, *P. floridana*, *T. scripta*, and *A. ferox*, were significantly different from each other. Trophic position of adult *Apalone ferox* (TP = 3.8) was significantly higher than that of *T. scripta* (TP = 3.3). Gut contents analysis indicated that adult *A. ferox* consumed primarily insects, snails, fish, and macroalgae, whereas adult *T. scripta* consumed mostly insects (odonate naiads), macrophytes, and macroalgae. Trophic position increased with size in *A. ferox* reflecting an ontogenetic diet shift from mostly insects by juveniles to large predaceous insects, snails, and fish by large adults. Trophic position of juvenile *T. scripta* was 3.5, one position greater than that of juvenile *P. floridana* (TP = 2.4). This difference in trophic position continued in adult *T. scripta* (TP = 3.3) and *P. floridana* (TP = 2.3), with no evidence of a dietary shift towards herbivory in adult *T. scripta*. Gut contents showed that juvenile and adult *P. floridana* consumed primarily macroalgae.

Food webs are complex in Florida lakes and there are many direct and indirect interactions among fish, reptiles, and amphibians. Ninety percent of the consumers in the food web are omnivores and the food web is shortened vertically but expanded horizontally. There were few specialists and few strict primary consumers. Notably, the Lake Jackson web is one trophic position less than in simpler webs in north temperate lake webs that have less species diversity and lower productivity. The results of this study increase our understanding of how the interaction of omnivory and resource limitation controls competitive interactions and trophic dynamics of turtles. One of the principal questions in the history of food web study is whether or not omnivory stabilizes food webs. If omnivory is widespread in lake food webs as this study suggests, other factors probably dictate the stability of food webs. A more important question may be why is anything not omnivorous.

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BIOGRAPHICAL SKETCH

Matthew Joseph Aresco, son of Salvatore V. Aresco and Barbara N. (Dimauro) Aresco, was born June 4, 1963 in Middletown, Connecticut. He graduated from Xavier High School in Middletown, Connecticut in June 1981. He received a Bachelor of Arts degree with a major in English from Fairfield University in Fairfield, Connecticut in June 1985. After working for several years in banking, he returned to school in 1990 to complete the necessary courses to apply to graduate school in biology. He entered the graduate program at Auburn University in September 1994. His major professor at Auburn was Craig Guyer and his thesis was entitled "Growth and burrow abandonment of the gopher tortoise, *Gopherus polyphemus*, in slash pine plantations of southern Alabama". He received a Master of Science degree in Zoology from Auburn University in March 1998. He entered the Ph.D. program in the Department of Biological Science at Florida State University in August 1998. While conducting his Ph.D. research, he founded a non-profit organization, the Lake Jackson Ecopassage Alliance, to develop broad based support and funding for the construction of a wildlife ecopassage on U. S. Highway 27 where it crosses Lake Jackson. He was named Wildlife Conservationist of the Year in 2004 by the Florida Wildlife Federation for his conservation work with Florida turtles.