

Ecological Relationships of Turtles in Northern Florida Lakes: A Study of Omnivory and the Structure of a Lake Food Web

FINAL REPORT

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Abstract: Lakes in 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. The objectives of this study were to determine the environmental correlates of abundance of the predominant turtle species; evaluate the degree of omnivory, trophic position (TP), and competitive interactions of these turtles; and, using stable isotope analyses ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$), describe trophic structure, energy pathways, and sources of primary production in the entire food web in 1 major lake.

In Leon County, Florida, we studied 17 lakes and the abundances of 3 species of turtles: yellow-bellied slider (*Trachemys scripta*), Florida cooter (*Pseudemys floridana*), and Florida softshell (*Apalone ferox*). Mantel analyses demonstrated that abundances of all 3 focal species were strongly correlated with a mud and muck substrate and both top-down (no alligator [*Alligator mississippiensis*] predation) and bottom-up (high periphyton productivity) factors. On a finer scale, abundances of the individual species were correlated with additional factors: *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. A field experiment revealed that intraspecific competition may be more important than interspecific competition in the interactions between the omnivorous *T. scripta* and specialist algivore *P. floridana*. In low resource environments, inefficient digestive physiology and intraspecific competition may limit density of an omnivore compared to that of a low trophic position specialist.

Trophic position based on stable isotopes revealed that the turtle assemblage at Lake Jackson, Leon County, Florida, consisted of 1 herbivore (*P. floridana*) and 5 omnivores (*T. scripta*, *Sternotherus odoratus*, *A. ferox*, *Chelydra serpentina*, *Kinosternon subrubrum*). Among omnivorous species, trophic position ranged from 3.3 to 4.0. The diets of the 3 focal species differed: *P. floridana* was a specialist algivore (TP = 2.3), *T. scripta* was a generalist omnivore (TP = 3.3), and *A. ferox* was an omnivore with some specialization on insects and snails (TP = 3.8). Trophic position increased with size of *A. ferox* and indicated an ontogenetic diet shift from insects to fish and other vertebrates.

Stable isotope analysis of the food web of Lake Jackson revealed that filamentous macroalgae were the foundation of the web despite a much greater biomass of macrophytes. There were few specialists (TP ≥ 4.0) and few strict primary consumers. Omnivory was prevalent (90% of consumers), and the food web is 1 trophic level shorter than those in fish-dominated, north temperate lake webs that have few turtles, less species diversity, and lower productivity. Predation on consumers with lower trophic positions lowered the average trophic position of top predators.

Based on stable isotope analyses of trophic structure, food webs of Florida lakes are complex with many direct and indirect interactions among fish, reptiles, and amphibians. Lake management practices in Florida must consider the role of reptiles and amphibians and important resources such as macroalgae and organic substrates that support these populations.

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TABLE OF CONTENTS

ABSTRACT iii

ACKNOWLEDGMENTS iv

INTRODUCTION 1

 Food Webs and Omnivory 1

 Comparison of North Temperate and Southeastern Lakes 2

 Study System 4

OBJECTIVES 7

METHODS 8

 Study Lakes 8

 Turtle Abundance and Environmental Correlates 9

 Degree of Omnivory of *Trachemys scripta* and *Pseudemys floridana* 12

 Competition Between *Trachemys scripta* and *Pseudemys floridana* 13

 Stable Isotope Analysis of a Whole Lake Food Web 16

RESULTS 22

 Turtle Abundance and Environmental Correlates 22

 Degree of Omnivory of *Trachemys scripta* and *Pseudemys floridana* 27

 Competition Between *Trachemys scripta* and *Pseudemys floridana* 29

 Sources of Primary Production and Trophic Structure of
 the Lake Jackson Food Web 30

 Trophic Relationships of Turtles and Other Herpetofauna 38

 Trophic Relationships of Fish 43

DISCUSSION 45

 Turtle Abundance and Environmental Correlates 45

 Competitive Interactions of *Trachemys scripta* and *Pseudemys floridana* ... 47

 Degree of Omnivory and Trophic Relationships of Turtles 48

 Primary Productivity and Trophic Structure in the
 Lake Jackson Food Web 50

CONCLUSIONS 54

LITERATURE CITED 57

INTRODUCTION

Food Webs and Omnivory

A fundamental goal of ecology is to determine the underlying processes that regulate community composition and explain observed patterns of distribution and abundance. One approach is to study how various producers and consumers are linked in food webs and how these interactions affect community composition and population dynamics of focal species (Paine 1980, Polis 1991, Hairston and Hairston 1993). In the classic tri-trophic interaction, a top predator feeds on both an intermediate consumer and a primary producer in a simple food chain. However, the potential for more complex interactions presented by omnivory in 2 or more connected chains or webs remains a limitation to the general applicability of food chain theory. Furthermore, ontogenetic or environmental diet shifts often prevent assignment of some species to discrete trophic levels and preclude the use of simple food web models (e.g., Hairston et al. 1960, Fretwell 1977, Oksanen et al. 1981).

Omnivory is a special feature of some animals that is broadly defined as feeding on more than 1 trophic level (Pimm and Lawton 1977, Pimm 1982). That is, omnivores either prey on other consumers from different trophic levels or on both plants and animals (Yodzis 1984). Although specialized digestive physiology is required to digest and assimilate both plant and animal tissues, feeding on plants and animals is a type of omnivory that is relatively common in both terrestrial and aquatic systems, especially among vertebrates (Winemiller 1990, Polis 1991, Gu et al. 1997). In addition, many omnivores exhibit “life history omnivory,” a shift in diet during development that is associated with ontogenetic changes in 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 from carnivorous to herbivorous or vice versa. Although the simple effects of predation and herbivory are relatively well understood, the direct and indirect effects of omnivory (feeding at multiple trophic levels) and the additive or non-additive effects of omnivory and herbivory by a guild of trophic species are poorly understood (Diehl 1993, Polis and Strong 1996). 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.

Early studies of food web patterns suggested that omnivory was rare and destabilized food webs (Pimm and Lawton 1977, Pimm 1982, Morin and Lawler 1996). However, more recent empirical and theoretical work has shown that omnivory may be relatively common in nature and it may stabilize food webs in some cases (Polis 1991, Diehl 1993, Fagan 1997, Holt and Polis

1997, McCann and Hastings 1997). Because omnivores feed at multiple trophic levels and can have many alternative food sources, populations of some omnivores may have high carrying capacities, attain high abundance, and exhibit more stable population dynamics than non-omnivores (Morin and Lawler 1996). Thus, omnivores may have greater effects on prey resources and may have top-down control of lower trophic levels, resulting in consumer-mediated community dynamics (Menge and Sutherland 1976, Strong 1992, Polis and Strong 1996). Depending on the number and strength of feeding links in a food web, omnivores can also control the population dynamics of organisms through positive or negative indirect effects (Abrams et al. 1996).

Comparison of North Temperate and Southeastern Lakes

Food webs in freshwater systems have been well studied, primarily in deep, glacial lakes of north temperate regions (Lampert and Sommer 1997). These lakes typically have low species diversity and few macrophytes. In contrast, food webs in southeastern lakes are complex, with high species diversity, high productivity, abundant macrophytes, and many possible direct and indirect interactions (Fig. 1). Northern lake ecosystems are often dominated exclusively by fish, but in the southeastern United States this

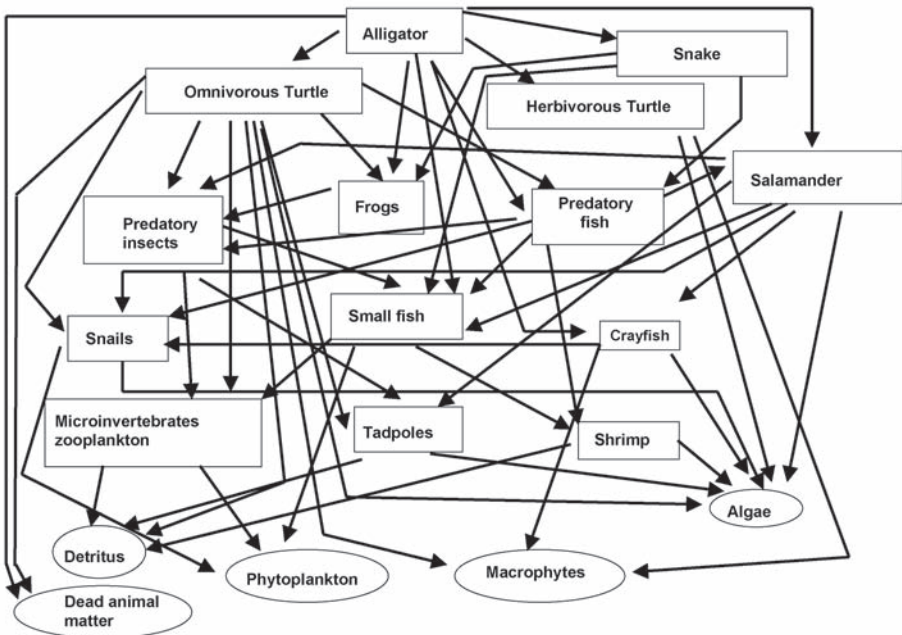


Fig. 1. Generalized food web diagram of a typical Florida lake.

dominance is shared with reptiles, amphibians, and macroinvertebrates. In addition, southeastern lakes differ substantially from northern lakes in physical qualities. For example, southeastern lakes are relatively shallow and occasionally dry during periods of drought (Brenner et al. 1991). Food webs in southeastern lakes have evolved in a dynamic environment that affects food web properties and trophic structure, thus, the structure of food webs may be more complex and variable than that revealed in previous studies of north temperate lakes (Fig. 1). However, no previous studies have examined the trophic structure of food webs and levels of omnivory in southeastern lakes.

In southeastern lakes, the biomass and density of turtles may equal or exceed that of other vertebrates, and the annual productivity of turtles (per area) is apparently exceeded only by some fishes (Iverson 1982, Congdon et al. 1986). Some aquatic turtles grow to relatively large sizes, attain high densities, and have few significant predators as adults. Hence, as with large terrestrial herbivores, many turtle populations may be regulated by primary production (bottom up) rather than predation (top down) (Polis and Strong 1996). However, in some regions predation on freshwater turtles by crocodylians may affect species distribution and abundance. Thus, turtle abundance in Florida lakes may be a function of both American alligator (*Alligator mississippiensis*) abundance and resource productivity.

Omnivory is an important feature of the life histories of some common aquatic and semi-aquatic turtles, and such omnivory may 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 as adults and/or exhibit some form of ontogenetic diet shift (Mahmoud 1968, Clark and Gibbons 1969, Vogt 1981, Vogt and Guzman 1988). The level of omnivory is known to vary within and among species, often depending on a complex interaction between resource availability, energy requirements, and foraging efficiency. Therefore, the degree of omnivory can vary both temporally and spatially, but the propensity towards carnivory or herbivory is likely to be constrained by phylogeny.

Both abiotic and biotic factors influence landscape-level patterns of diversity and species richness in freshwater communities (Leitman et al. 1991). Specifically, factors such as type of wetland (e.g., fast- vs. slow-moving water), wetland size, hydroperiod, and primary and secondary productivity may be important habitat features that structure the composition of turtle communities (Bodie et al. 2000). Within a defined niche of abiotic factors, turtle populations can be limited by resources (bottom-up control) and/or predation (top-down control) (Bury 1979, Polis and Strong 1996). Estimates of abundance among populations are more difficult to determine, and, thus,

few studies have examined the environmental characteristics that influence turtle abundance in populations across habitats (Congdon and Gibbons 1996, Marchand and Litvaitis 2004). Intraspecific (density-dependent regulation) and interspecific competition may interact with key environmental factors to affect turtle abundance and composition of turtle communities. However, other than anecdotal observations and correlative studies, the importance of competition on structuring turtle populations is unknown (Bury 1979, Congdon and Gibbons 1996, Bodie et al. 2000).

Study System

The most abundant large freshwater turtles in lentic water habitats of northern Florida are the yellow-bellied slider (*Trachemys scripta scripta*), the Florida cooter (*Pseudemys floridana*), and the Florida softshell (*Apalone ferox*). All 3 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. 1944). Thus, *T. s. scripta* and *P. floridana* coexist in lakes and ponds of the Coastal Plain from southeastern Virginia to north-central Florida, while all 3 species co-occur throughout the range of *A. ferox*, excluding the extreme southern portion of the Florida peninsula (Ernst et al. 1994).

Although *T. scripta* and *P. floridana* are closely related and often coexist, their feeding ecology differs. *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). However, the degree of herbivory of adult *T. scripta* may vary with differences in the availability of plant and animal foods (Clark and Gibbons 1969, Hart 1983). For example, Moll (1977) found that adults were more carnivorous in habitats where aquatic plants were less abundant than insects. *Trachemys scripta* may also change their diet seasonally from summer omnivory to winter herbivory, a shift that may be related to food availability (Parmenter 1980). In contrast, adults of *P. floridana* are reported to be entirely herbivorous, preferring filamentous algae and vascular aquatic plants (Allen 1938, Marchand 1942, Carr 1952). Adult *P. floridana* feed exclusively on the predominant aquatic plants in a given habitat, although the predominant plant may vary among lakes and seasonally within lakes (Thomas 1972). Feeding

experiments demonstrated that adult *P. floridana* can consume an average of 14 g of aquatic macrophytes per day (5.3 times their average body mass per year) (Aresco, unpublished data). *Pseudemys floridana* is more specialized to digest macrophytes and algae 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) was 18% longer in *P. floridana* than in *T. scripta* of the same size. As with other herbivorous reptiles, it is likely that both *T. scripta* and *P. floridana* rely on symbiotic gut microflora to digest plant cell walls, but longer gut length in *P. floridana* provides a greater volume of microflora (Bjorndal and Bolten 1990, Bjorndal 1991).

Although the feeding ecology of adult *P. floridana* and *T. scripta* is relatively well known (Allen 1938, Marchand 1942, Thomas 1972), hatchlings and small juveniles are often difficult to capture, and their diet in nature is poorly understood. Furthermore, diet studies that do not include all size classes may not detect an ontogenetic diet shift if the shift occurs at a small size. Even so, it is known that *T. scripta* exhibits an ontogenetic shift in diet from carnivory toward herbivory with an increase in body size in some populations (Clark and Gibbons 1969, Hart 1983).

Both *T. scripta* and *P. floridana* are found in lakes, ponds, slow-flowing rivers, and floodplain swamps, but their relative abundance may vary widely among these habitats (Gibbons and Coker 1978, Ernst et al. 1994). Variation in relative abundance may be due to differences in habitat characteristics, diet requirements, competition, and/or predation. In addition to its omnivorous food habits, *T. scripta* is apparently a habitat generalist and can be found in virtually any freshwater habitat (Cagle 1950, Mount 1975). Because of dietary differences, habitats with sparse aquatic plants and low productivity may not support high densities of *P. floridana* in relation to *T. scripta*. However, aquatic vegetation may not be essential to *T. scripta*, and omnivory may allow it to exploit habitats that are unsuitable or only marginally suitable for *P. floridana*.

Under low-resource conditions the outcome of competition between a generalist omnivore and a more specialized species is not clear. A generalist omnivore, such as *T. scripta*, that can easily switch between herbivory, carnivory, and scavenging, depending on the quality and quantity of resources, may grow faster and survive better than a competitor. Alternatively, a more specialized herbivore such as *P. floridana* may outcompete a generalist omnivore if only low-quality, basal resources are available and unique specializations allow for more efficient assimilation of nutrients needed for growth and survival. These predictions set up the potential for competition

between *P. floridana* and *T. scripta* when they are forced to share the niche under low-resource conditions, and the outcome may depend on the type of limiting resource.

This research used a combination of field surveys, field experiments, laboratory experiments, and stable isotope analyses. A field survey determined covariation between abundance of *T. scripta*, *P. floridana*, and *A. ferox*, and environmental variables. We conducted a laboratory experiment to quantify differences in the degree of omnivory between young of the predominant species, *T. scripta* and *P. floridana*. A field experiment determined if an omnivorous turtle, *T. scripta*, competes better than a specialist herbivore, *P. floridana*, when forced to share the niche under low-resource conditions. We used stable isotopes ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) and gut contents to describe trophic structure, energy pathways, and sources of primary production in the entire lake food web in 1 major lake, and to evaluate ontogenetic shifts in diet and trophic position among the 5 most common turtle species.

OBJECTIVES

The objectives of this study were to

1. determine turtle abundance in north Florida lakes and its environmental correlates;
2. quantify differences in the degree of omnivory between young of the predominant species, *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 1 major lake.

METHODS

Study Lakes

This study was conducted at 17 lakes located in Leon County in northwestern Florida, ranging in size from 0.6 to 2,330 ha (Fig. 2, Table 1). Five lakes are within the Munson Sandhills (MSH) physiographic region and the Norfleet/Spring Hill Ridge lake region dominated by deeply weathered beach and dune sand. Lakes in this region are clear and acidic ($\text{pH} < 5.5$). Twelve lakes are within the Tallahassee Red Hills (TRH) physiographic region and the Tifton/Tallahassee lake region dominated by phosphatic sand, silty sand, and clay and underlying karst formations (Table 1). Lakes in this region have slightly acidic to neutral ($\text{pH} 6.0\text{--}7.0$), colored, soft water.

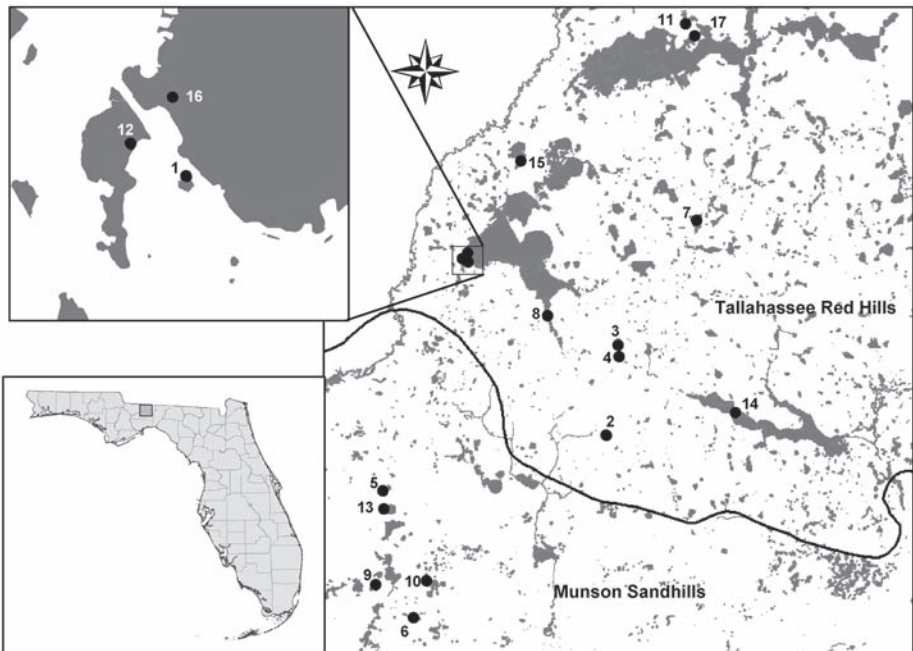


Fig. 2. Location of 17 study lakes in Leon County, Florida. Dark line indicates separation of the Tallahassee Red Hills and Munson Sandhills physiographic regions. 1 = Coolview Pond, 2 = Chapman Pond, 3 = Waverly Pond, 4 = McCord Pond, 5 = Andrew Lake, 6 = Trout Pond, 7 = Lake Tom John, 8 = Megginis 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.

Table 1. Summary data of lake area and primary productivity as measured by open-water nutrients and chlorophyll *a*, periphyton, and macrophyte biomass and percent area covered (PAC) for 17 study lakes in Leon County, Florida. Environmental variables were measured at each lake during May–September 2003.

Lake	Lake area (ha)	Phosphorus (ug/L)	Nitrogen (ug/L)	Chlorophyll <i>a</i> (ug/L)	Periphyton (g/m ² y)	Macrophyte biomass (kg wet/m ²)	PAC
Tallahassee Red Hills							
Coolview Pond	0.6	72	650	7	0.38	4.85	100
Chapman Pond	1	47	380	10	3.39	6.54	100
Waverly Pond	1.5	98	1,240	40	4.00	2.84	5
McCord Pond	2	33	830	33	4.64	6.49	98
Lake Tom John	6	54	920	32	7.56	1.65	12
Megginnis Arm	8	62	390	11	2.23	10.7	70
Gannett Pond	21	52	880	68	0.09	10.8	100
Little Lake							
Jackson	21	24	535	12	0.28	17.1	40
Lake Piney Z	78	25	480	7	1.16	3.82	90
Orchard Pond	85	10	400	6	0.99	7.97	65
Lake Jackson	1,620	23	780	9	0.80	5.88	80
Lake Iamonia	2,330	19	860	19	1.37	11.4	88
Munson Sandhills							
Andrew Lake	4	5	330	2	1.05	2.10	5
Trout Pond	5	11	504	6	2.83	2.26	12
Clear Lake	11	3	290	3	5.05	4.28	10
Lofton Ponds	11	5	430	3	1.13	1.59	10
Moore Lake	27	5	350	3	2.52	2.78	1

Turtle Abundance and Environmental Correlates

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 2002 and 2003. The large mesh size precluded capture of small turtle species (e.g., common musk turtle [*Sternotherus odoratus*] and eastern mud turtle [*Kinosternon subrubrum*]) and small individuals of larger species. Traps were unbaited to reduce the possibility of trapping bias towards species that may prefer fish bait (e.g., *T. scripta*). 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.

Traps were set for 1 5-day period at each locality (96 trap hours x 2 traps = 192 trap hours) to obtain a standardized abundance for each species. Raw capture data were converted to catch per unit effort (CPUE = number of each species caught divided by trap hours). For each turtle collected, we 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 biases among species, we compared the relative abundance of each species captured during the 5-day trapping period to the relative abundance of each species captured by all methods, including hand collection, during the complete drawdown and sediment removal at 3 ponds: Waverly Pond, Chapman Pond, and McCord Pond (Aresco and Gunzburger 2004). For each species, we compared, using Spearman rank correlation analysis, the relative abundance of turtles trapped to actual abundance at each pond. We compared abundance (CPUE) of each species between physiographic regions (TRH vs. MSH) using ANOVA.

The biotic and abiotic factors chosen for measurement at each lake were considered a priori to be those most important to the abundance of turtles. Lake primary productivity was measured in terms of standing crop biomass of macrophytes (kg wet weight/m²); periphyton productivity (g/m²/y dry mass); concentrations (ug/L) of chlorophyll *a*, nitrogen, and phosphorus; and percent lake surface area covered with macrophytes (PAC). Macrophytes and macroalgae comprise a large proportion of the nutrient pool in Florida lakes and are not considered when only measuring chlorophyll *a* content of open water (Canfield et al. 1983). Furthermore, macrophytes and periphyton may be a more relevant measure of primary productivity in this study because some turtle species feed on macrophytes and macroalgae.

Standing crop biomass of macrophytes was determined by establishing at each lake 5 transects that spanned 3 depth zones: shallow (0.1–0.5 m), medium depth (>0.5–1.0 m), and deep water (>1.0 m). All plants within 0.25-m² quadrats located in each zone were harvested and separated as emergent, floating, and submerged. Plants from each category were placed in a mesh bag that was shaken vigorously to remove excess water and weighed to the nearest gram 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 was visually estimated at each lake.

We determined periphyton productivity from May to July 2004 by establishing 2 periphyton samplers in the littoral zone at each lake. We placed 2 stakes at least 100 m apart, each with 4 glass microscope slides affixed 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 and dried. We scraped the dried periphyton from each slide with a razor blade onto pre-weighed GF filter paper, weighed each

sample to the nearest milligram, and calculated mean periphyton productivity at each lake as $\text{g/m}^2/\text{y}$. We 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.

We sampled each lake in May–September 2003 and determined the abundance of macrofauna 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). We collected all macrofauna within the box sampler by performing 10 D-net sweeps within the box sampler. The net was swept vigorously through any macrophytes and the substrate to ensure collection of epiphytic and benthic macroinvertebrates. All macrofauna were counted and identified to the lowest possible taxon. We summed the number of macroinvertebrates (excluding snails and chironomids), small fish, chironomids, and snails collected in each of the 5 box samples at each site to yield an abundance value per 1.25 m^2 for each category. The presence or absence of amphipods was also recorded. Maximum surface area of each lake was determined using the GIS program ArcMap and 1999 digital ortho quarter quads available from the Florida Department of Environmental Protection. Primary substrate was classified into 1 of 3 categories: sand, mud/silt, or organic (peat/muck).

A turtle predator variable consisted of American alligator presence/absence at each lake. American alligators may be the primary aquatic predators of adult turtles and can reduce the abundance of some turtle species. We determined presence or absence of alligators by visiting each lake ≥ 5 nights between May and July 2003 and used a spotlight that produces detectable red eye reflection at approximately 200 m (Woodward and Marion 1978). Surveys were conducted from shore. An estimation of alligator density at each lake was not possible due to thick aquatic vegetation at some lakes.

In order to determine environmental correlates of turtle abundance, we first examined the correlation structure of the data by performing a Spearman rank correlation analysis among CPUE (turtles/trap hour) of 3 turtle species (*T. scripta*, *P. floridana*, and *A. ferox*) and 14 continuous environmental variables at 17 lakes: LAKE AREA, EMERGENT (mean emergent macrophyte biomass), FLOATING (mean floating macrophyte biomass), SUBMERGED (mean submerged macrophyte biomass), BIOMASS (mean total macrophyte biomass), PAC (percent lake surface area covered with macrophytes), PERIPHY (mean periphyton productivity), CHLA (mean chlorophyll *a* concentration), NITR (mean open-water total nitrogen concentration), PHOS (mean open-water total phosphorus concentration), INVERT (total macroinvertebrate

abundance), FISH (total small fish abundance), CHIRON (total chironomid abundance), and SNAIL (total snail abundance).

Second, we examined whether sites that were similar in abundance of turtles were similar in environmental characteristics. We constructed matrices of distances between sites based on turtle abundance data (3 individual species matrices and a turtle community matrix with all species) and 17 environmental variables. A distance matrix of abundance of the snapping turtle (*Chelydra serpentina*) was not constructed because it was only trapped at 2 sites. Each matrix was constructed by calculating Euclidean distances between all pairwise combinations of lakes (Legendre and Legendre 1998). We performed Mantel tests using the *R* program to determine if 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 test is a nonparametric procedure that allows for analysis of both continuous and categorical data. The Mantel test 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 environmental variable was sequentially eliminated from that matrix such that the final matrix represents only the set of variables with nonrandom correlations (*r*) with the turtle abundance matrix. A significant correlation (Mantel *r*) between the turtle abundance matrix and the environmental matrix demonstrates that lakes similar in abundance of turtles were similar in environmental characteristics and identifies the suite of environmental variables that are important for each species separately and combined.

Degree of Omnivory of *Trachemys scripta* and *Pseudemys floridana*

Hatchling *T. scripta* and *P. floridana* were obtained from nests at Lake Jackson, Leon County, Florida, in July 2001. Turtles were housed in 55-L plastic containers filled with well water to 10 cm. Hatchling *T. scripta* and *P. floridana* forage in shallow water (<20 cm) of the littoral zone at Lake Jackson, and we surveyed this area for potential plant and animal foods. Duckweed (*Spirodela polyrhiza*) and filamentous and epiphytic algae (e.g., *Spirogyra*, *Cladophora*) were the most abundant plants available as food for hatchling turtles. The most common invertebrate prey were hemipterans (*Belostoma lutarium*), odonate naiads (libellulids and aeshnids), coleopterans (dytiscids), and grass shrimp (*Palaemonetes paludosis*). The least killifish (*Heterandria*

formosa), mosquitofish (*Gambusia affinis*), and golden topminnow (*Fundulus chrysotus*) were the most abundant small vertebrates.

Eggs of *T. scripta* and *P. floridana* were collected from nests at Lake Jackson, Leon County, Florida, in July 2001. The laboratory experiment was initiated 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 the following treatments: turtles (either 1 *T. scripta* or 1 *P. floridana*), 2 g duckweed, and 1 of 4 prey types (either 3 small *B. lutarium*, 7 libellulid odonate naiads, 3 grass shrimp, or 5 dead least killifish). Live prey were added to 55-L experimental containers (glass aquaria) 24 hours prior to the addition of a hatchling turtle. Trials were conducted for 24 hours for each turtle, and remaining duckweed was weighed and prey animals were counted.

We calculated the proportion of duckweed, invertebrates, and dead least killifish eaten by each species. First, the proportion of *B. lutarium*, libellulids, and shrimp eaten was pooled under a single category: invertebrate prey. We used ANOVA to compare the proportion eaten of duckweed, pooled invertebrates, and dead fish between *T. scripta* and *P. floridana*. Second, we examined differences in the proportion of the type of animal prey consumed by *T. scripta* and *P. floridana* using 2-sample *t*-tests.

Competition Between *Trachemys scripta* and *Pseudemys floridana*

We designed a field experiment to test the predictions that competition between *P. floridana* and *T. scripta* may occur when they are forced to share the niche under low-resource conditions, and the outcome may depend on the type of the limiting resource. Because we were limited by the number of juvenile turtles available for proper replication of a competition experiment, we instead designed a substitution experiment where densities were kept equal in each replicate but one species was substituted for another to maintain the same overall density in the mixed species treatment. This design tested whether one species exhibited slower growth or lower survival under intraspecific versus interspecific competition (= competitive equivalence) with a priori comparisons that analyzed 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 were in the same cages, they were not independent and could not be directly compared to each other.

The experiment was conducted from 11 July 2002 to 3 August 2003 at Gannett Pond, a 21-ha pond on Tall Timbers Research Station located near Lake Iamonia, Leon County, Florida (Fig. 3). Gannett Pond is relatively shallow (1- to 2-m depth) with an organic substrate and has a littoral zone dominated by emergent macrophytes (maidencane grass [*Panicum hemitomon*], arrowhead [*Sagittaria latifolia*], pickerelweed [*Pontedaria cordata*]) and a deeper-water zone completely covered with water lilies (*Nymphaea odorata*, *Nelumbo lutea*). Submerged plants are primarily bladderworts (*Utricularia* sp). The experiment was set up under low-resource, drought conditions where water levels had receded from the normal littoral zone. Juvenile (1–2 years old) *P. floridana* and *T. scripta* were used in the experiment because growth rate during this stage is measurable over relatively short time periods (e.g., 1 year)

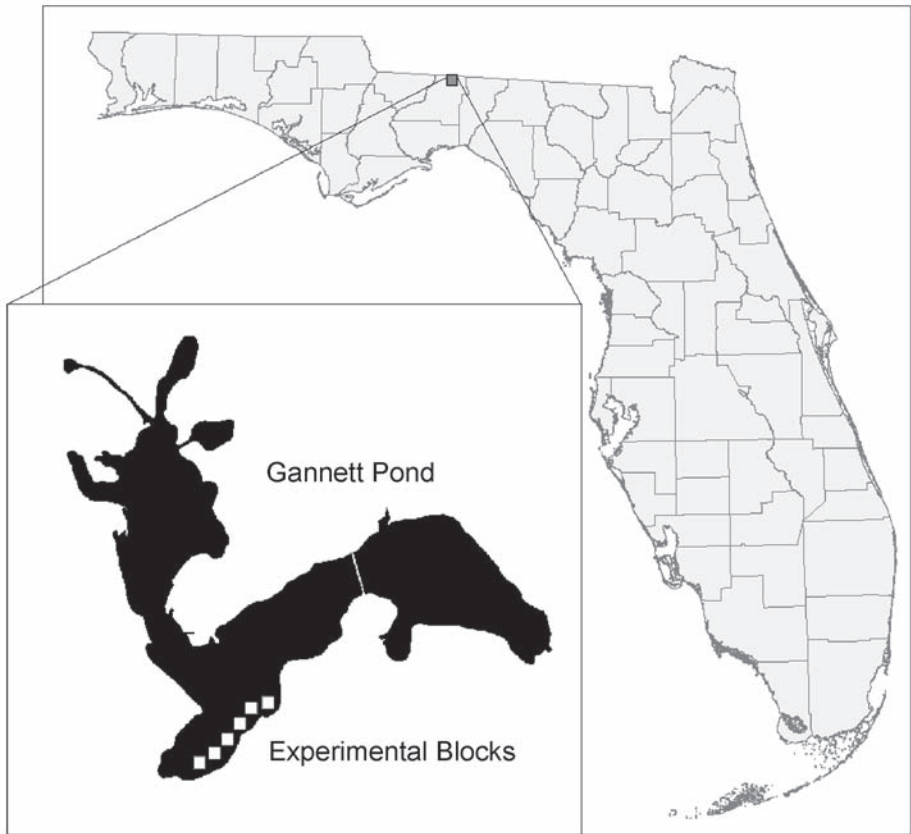


Fig. 3. Location of Gannett Pond on Tall Timbers Research Station in northern Leon County, Florida. The location of 6 experimental blocks (3 cage treatments per block) is shown in the southwestern part of the pond.

and is a key demographic variable that directly determines age at maturity in turtles. The experiment consisted of 6 replicates of 3 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, and stocking densities of turtles were consistent with field densities of juveniles as produced after several good reproductive years (i.e., several cohorts in the juvenile size range) (Aresco, unpublished data). We constructed 18 1-m² enclosures using hardware cloth. 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 blocks were located 5 m apart. Equal amounts of aquatic vegetation (e.g., maidencane grass, bladderworts, frog's bit [*Limnobium spongia*]) were added to each cage. Cages were stocked with turtles on 11 July 2002, and each turtle was individually marked by notching the rear marginal scutes.

Water level and cages were monitored weekly, and drying from lack of rain required relocating the cages 6 times during July–September 2002 to maintain a cage depth of 30–40 cm. Because of the necessity of frequent cage movement, we installed bottoms on the cages on 16 August using hardware cloth in order to facilitate recapturing the turtles and quickly moving cages. Low water levels required that we move all 18 cages to deeper water on 26 July, 10 August, 16 August, 24 August, 5 September, 29 September, 13 October, and 17 December 2002 and on 23 January, 9 February, 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 (block 2/cage 3, 1 *T. scripta*; block 3/cage 2, 3 *P. floridana*; block 4/cage 2, 2 *T. scripta*; block 4/cage 3, 1 *P. floridana*; block 5/cage 2, 3 *T. scripta*). 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 block 2/cage 3, block 4/cage 1, and block 4/cage 3 were replaced to restore the proper cage density for the final 4 months of the experiment, but not used in the analysis. Thus, the final design consisted of the following replication of treatments: SS ($n = 4$), CC ($n = 4$), CS ($n = 5$), and SC ($n = 5$).

Subsequent drying required moving cages to deeper water on 27 April, 8 May, and 26 May 2003 and heavy rains in early June required moving all cages to shallower water on 13 June 2003, where they remained until 2 August 2003.

Plastron length and mass of each turtle were measured at the start of the experiment on 11 July 2002 and at the end of the experiment on 2 August 2003 (387 days). Growth rates (final PL – initial PL) among 4 treatment levels (CC,

CS, SS, 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.

Fecal samples were 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. We determined the number of insects in each sample by matching wings, thorax, and head parts. Data were square root transformed to meet the assumptions of normality. Mean number of insects per turtle among treatments was compared with ANOVA. We also scored whether or not each fecal sample contained macroalgae and compared number of turtles with and without algae among treatments using a Pearson chi-square.

Stable Isotope Analysis of a Whole Lake Food Web

We examined the sources of primary production and trophic relationships in the food web at Lake Jackson, a large, eutrophic lake in northern Florida (Fig. 2). 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 model. Stable isotopes of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ are excellent indicators of average diet and actual trophic links because they reflect assimilation of energy sources integrated over long time-scales (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).

Isotope samples of turtles, snakes, frogs, and alligators were obtained from either muscle of road-killed individuals or by claw clips of live individuals. Road-killed animals were collected from U.S. Highway 27 at Lake Jackson, Leon County, Florida, 2001–2002. Claw clips were obtained from animals captured in aquatic hoop traps or at drift fences at Lake Jackson, Leon County, Florida, 2001–2002. 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 and by hand 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 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 algae may vary temporally, so samples were collected over time to determine average values. Open-water zooplankton was collected at

northwest Lake Jackson using a 250- μ m zooplankton tow net pulled from a boat. We collected 10 aggregate zooplankton samples during August 2002–November 2003. Macroalgae (periphyton and filamentous algae) was collected during November 2001–June 2004 ($n = 29$) at northwest Lake Jackson, during October 2001–August 2003 ($n = 17$) at Little Lake Jackson, and June 2002–June 2004 at Megginnis Arm ($n = 11$). Algae 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 [*Bacillaria* sp.]). In addition, we compared stable isotope values of periphyton collected during the same time-period at 3 different sites at Lake Jackson (Little Lake Jackson, northwest Lake Jackson, and Megginnis Arm) (Fig. 2) in order to evaluate spatial variation in isotope values of algae within a large lake. 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 on a mass spectrometer at the University of California Davis Stable Isotope Facility.

No previous studies have examined stable isotope values of turtles. Therefore, preliminary experiments were necessary in order to use more than 1 tissue type interchangeably in the analysis (e.g., claw vs. muscle), to independently 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, we compared claw vs. muscle tissue in 28 road-killed *T. scripta* ($n = 14$) and *P. floridana* ($n = 14$) and demonstrated that these 2 different tissues did not differ in stable isotope values (ANOVA, $P = 0.66$) (Fig. 4.). Second, we 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 experiment indicated that $\delta^{13}\text{C}$ of food (-17.18‰, SE = 0.10) and of turtles (-17.41‰, SE = 0.12) were almost identical (Fig. 4). Third, we 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. To better understand the effect of a diet change and tissue turnover rate on stable isotope values, we compared stable isotope values among 3 sets of juvenile *T. scripta*: wild only diet ($n = 18$), wild fed a captive diet for 6 months ($n = 3$), and captive only diet ($n = 7$). 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. 5), 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‰, SE = 0.24) were intermediate between wild-only turtles (-25.91‰, SE = 0.54) and captive-only turtles (17.41‰, SE = 0.12) (Fig. 5). Thus, this preliminary experiment suggests that for turtles, a diet switch requires 6 months to be detected by a change in the $\delta^{15}\text{N}$ isotope and 12

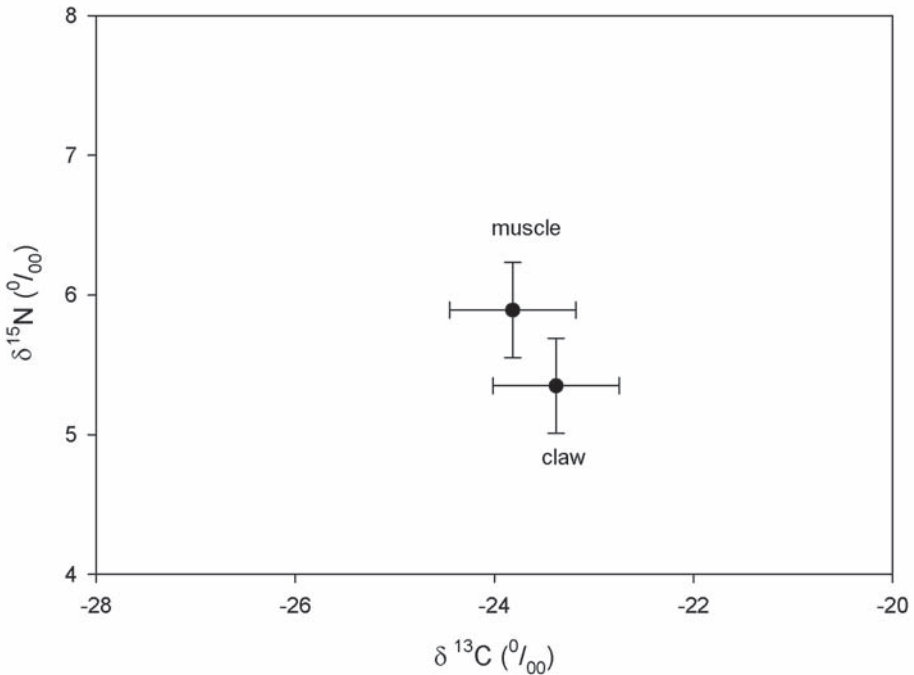


Fig. 4. Comparison of stable isotope values of claw and muscle tissue from 28 pairs of *Trachemys scripta* ($n = 14$) and *Pseudemys floridana* ($n = 14$) collected 2001–2002 from road-killed individuals on U.S. Highway 27 at Lake Jackson, Leon County, Florida.

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 a food web. In freshwater systems, food webs may be based on macroalgae, macrophytes, detritus (terrestrial or aquatic), POM, phytoplankton, or some combination of each of these sources. Thus, organisms that feed directly on these primary producers or on prey that feed on them, will match the $\delta^{13}\text{C}$ values of that source of primary production. Stable isotope values of several species of macrophytes (C3 plants) were averaged to 1 value. Maidencane grass, a C4 plant, was analyzed separately. We were not able to collect pure, open-water phytoplankton for analysis at Lake Jackson, so as a surrogate we used isotope values of a unionid clam (paper pondshell [*Utterbackia imbecillis*]) that feeds

exclusively on open-water phytoplankton (Vander Zanden and Rasmussen 1999). We 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. Where the 95% confidence interval of a consumer overlapped with that of more than 2 primary producers, this method was not informative and suggested multiple sources of primary production through that energy link. Overlapping 95% confidence intervals among different species indicated that they directly or indirectly utilized the same source of primary production in the food web. In order to determine which source(s) were the most important basal resources, we calculated the percent of consumers in the food web that overlapped with each category of primary producers.

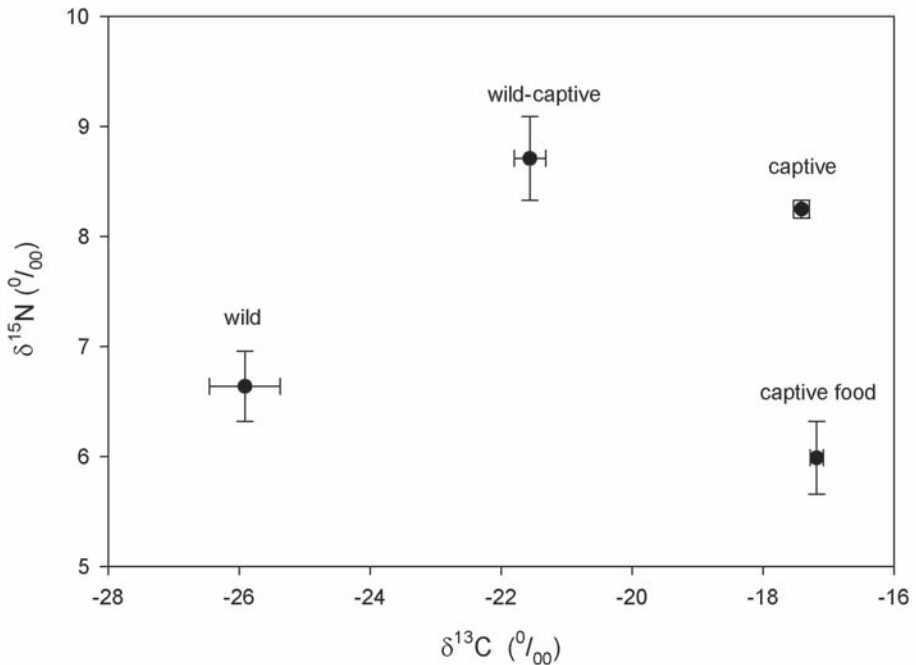


Fig. 5. Comparison of stable isotope values ($\delta^{15}\text{N}$ and $\delta^{13}\text{C}$) among wild ($n = 18$), captive ($n = 7$), and wild-captive (6 months) ($n = 3$) juvenile *Trachemys scripta* and captive food (Wardleys™ TEN Reptile food sticks) ($n = 2$ aggregate samples of 20 sticks). Wild 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 $\delta^{13}\text{C}$.

There are 2 conceptual approaches to understanding trophic relationships: food chain versus food web (Paine 1980). Food chains are oversimplified with discrete trophic levels and no omnivory (Polis and Strong 1996). In contrast, trophic position (TP) is a continuous variable and includes omnivory and the complexity of real food webs. Trophic position is defined as a noninteger value reflecting the energy-weighted mean number of trophic transfers between basal resources and a consumer (Vander Zanden and Rasmussen 1999). For example, a strict primary consumer has a TP of 2.0. Omnivores that exhibit an ontogenetic diet shift from carnivory to herbivory may vary in TP from primary to higher consumers depending on resource levels across a productivity gradient. The $\delta^{15}\text{N}$ isotope will be used to quantify within-population variation in TP of *T. scripta*, *P. floridana*, and *A. ferox*.

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 TP (Vander Zanden and Rasmussen 1999, Post 2002). Trophic position of reptiles, amphibians, and fish was estimated using a 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) or a primary consumer (unionid mussel) (Table 2). 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 TPs 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 (DeNiro and Epstein 1981, Minagawa and Wada 1984, Vander Zanden et al. 1999, Post 2002).

We determined how TPs inferred from stable isotope analysis compared to gut contents in turtles ($n = 172$), alligators ($n = 7$), and fish ($n = 83$) at Lake Jackson. Turtles captured at northwest Lake Jackson, Little Lake Jackson, and Megginis Arm were held individually in water-filled, plastic containers for 24 hours to collect 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 TP as determined from stable isotope analysis. We classified juvenile *A. ferox* as those individuals <120 mm PL and juvenile *T. scripta* and *P. floridana* as those individuals

<100 mm PL. 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., arthropods, gastropods, crustaceans, macroalgae, macrophytes) and percent occurrence of diet items was calculated.

Table 2. Baseline $\delta^{15}\text{N}$ values used to estimate trophic position of vertebrates at Lake Jackson. Macroalgae was collected November 2001–June 2004 ($n = 29$) at northwestern Lake Jackson and 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, 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, 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	particulate organic mater	2.32

^aLJ = Lake Jackson, LLJ = Little Lake Jackson.

RESULTS

Turtle Abundance and Environmental Correlates

Turtles were trapped at 16 of 17 lakes, yielding 4 species: *A. ferox*, *C. serpentina*, *P. floridana*, and *T. scripta*. Numbers of turtles captured ranged from zero to 62 turtles per lake (CPUE = 0.00–0.32) (Table 3). Mean CPUE of all turtles was 0.08 (SE = 0.021). *Trachemys scripta* had the greatest overall abundance (mean CPUE = 0.05, SE = 0.015) and was trapped at 71% of lakes (median CPUE = 0.02, range 0–0.23) (Fig. 6). In contrast, mean CPUE of *P. floridana* at all lakes was only 0.02 (SE = 0.01), but this species was widely and more evenly distributed and was trapped at 76% of all lakes (median CPUE = 0.01, range 0–0.08) (Fig. 6). *Apalone ferox* was trapped at 53% of lakes, mean CPUE = 0.01 (SE = 0.002) (median CPUE = 0.01, range 0–0.04) (Fig. 6). The presence of *A. ferox* was also confirmed by other methods (direct observation, dead on road, excavated during pond dredging, or captured at drift fences) at 7 other lakes, so this species was actually present at 95% of lakes in this study. Likewise, *C. serpentina* was trapped at only 2 of 17 lakes (12%) (mean CPUE = 0.002, SE = 0.002), but its presence was confirmed by other methods at 4 other study lakes, so despite its low abundance it was actually present at 35% of lakes.

Table 3. Catch per unit effort (no./hour) of turtles trapped at lakes and ponds in Leon County, Florida, 2002–2003. Numbers in parentheses are actual numbers of turtles trapped.

Location ^a	All turtles	<i>Pseudemys floridana</i>	<i>Trachemys scripta</i>	<i>Apalone ferox</i>
Lake Tom John (TRH)	0.32 (62)	0.08 (16)	0.23 (45)	0.01 (1)
Coolview Pond (TRH)	0.17 (32)	0.02 (4)	0.14 (26)	0.01 (2)
McCord Pond ^b (TRH)	0.17 (32)	0.00 (0)	0.09 (18)	0.04 (7)
Waverly Pond (TRH)	0.15 (28)	0.05 (10)	0.07 (14)	0.02 (4)
Chapman Pond ^c (TRH)	0.14 (26)	0.01 (2)	0.10 (20)	0.02 (3)
Lake Jackson (TRH)	0.07 (13)	0.02 (3)	0.05 (10)	0.00 (0)
Megginnis Arm (TRH)	0.07 (13)	0.02 (3)	0.05 (10)	0.00 (0)
Moore Lake (MSH)	0.06 (11)	0.04 (8)	0.00 (0)	0.02 (3)
Lake Iamonia (TRH)	0.04 (8)	0.02 (4)	0.02 (4)	0.00 (0)
Lofton Ponds (MSH)	0.03 (6)	0.02 (3)	0.01 (1)	0.01 (2)
Little Lake Jackson (TRH)	0.03 (6)	0.01 (1)	0.03 (5)	0.00 (0)
Andrew Lake (MSH)	0.02 (4)	0.01 (2)	0.01 (2)	0.00 (0)
Lake Piney Z (TRH)	0.02 (3)	0.00 (0)	0.02 (3)	0.00 (0)
Gannett Pond (TRH)	0.01 (2)	0.00 (0)	0.00 (0)	0.01 (2)
Clear Lake (MSH)	0.01 (2)	0.01 (1)	0.00 (0)	0.01 (1)
Orchard Pond (TRH)	0.01 (1)	0.01 (1)	0.00 (0)	0.00 (0)
Trout Pond (MSH)	0.00 (0)	0.00 (0)	0.00 (0)	0.00 (0)

^aTRH = Tallahassee Red Hills region, MSH = Munson Sandhills region.

^bAlso trapped 7 *Chelydra serpentina*.

^cAlso trapped 1 *C. serpentina*.

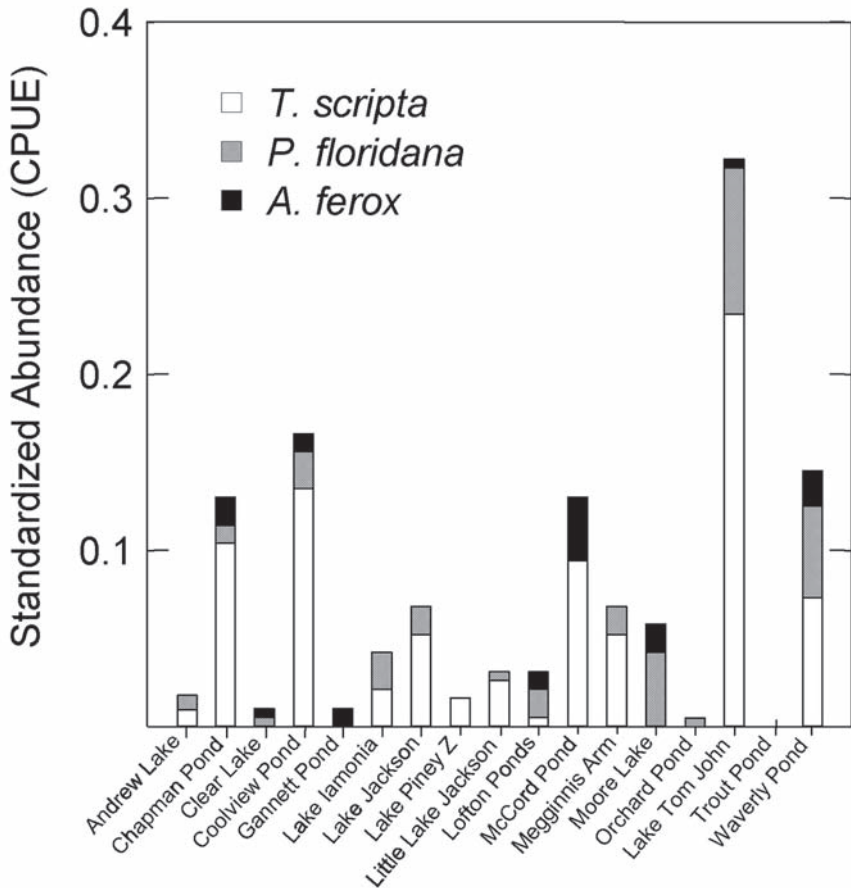


Fig. 6. Comparison of abundance (standardized to catch per unit effort [CPUE]) (no./hour) of *Trachemys scripta*, *Pseudemys floridana*, and *Apalone ferox* trapped 2002–2003 at 17 lakes and ponds in Leon County, Florida.

Overall turtle abundance was greater in lakes in the Tallahassee Red Hills (mean CPUE = 0.10, SE = 0.02, $n = 12$) than in the Munson Sandhills (mean CPUE = 0.02, SE = 0.04, $n = 5$), but this difference was not statistically significant (ANOVA, $P = 0.11$, $F = 2.98$). Mean abundance of *T. scripta* was significantly greater in Tallahassee Red Hill lakes (ANOVA, $P < 0.001$, $F = 13.9$) (Table 4). Mean abundance of *P. floridana* and *A. ferox* between physiographic regions was nearly identical (Table 4).

We found no evidence of a trapping bias, leading us 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 5).

Spearman rank correlation analysis demonstrated that the strongest correlations among environmental variables were between open-water nutrients and chlorophyll *a* (Tables 1, 6). However, periphyton productivity was not related to nutrients or chlorophyll *a* and was negatively correlated with each of the aquatic macrophyte categories. There was a strong positive correlation between lake area and floating macrophytes, 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 6).

Table 4. Mean catch per unit effort of *Trachemys scripta*, *Pseudemys floridana*, and *Apalone ferox* trapped in Tallahassee Red Hills lakes ($n = 12$) and Munson Sandhills lakes ($n = 5$), Leon County, Florida, 2002–2003. Standard errors are shown in parentheses.

Region	<i>T. scripta</i>	<i>P. floridana</i>	<i>A. ferox</i>
Tallahassee Red Hills	0.07 (0.02)	0.02 (0.01)	0.01 (0.003)
Munson Sandhills	0.003 (0.03)	0.01 (0.01)	0.01 (0.01)

Table 5. Comparison of relative abundance of *Trachemys scripta*, *Pseudemys floridana*, *Apalone ferox*, and *Chelydra serpentina* captured in Leon County, Florida, by trapping during a 5-day period (Trapped) vs. overall relative abundance determined by hand capture, trapping, and mechanical excavation (Actual) 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	Trapped	Actual
Waverly Pond	<i>T. scripta</i>	0.50	0.42
	<i>P. floridana</i>	0.36	0.29
	<i>A. ferox</i>	0.14	0.27
	<i>C. serpentina</i>	0	0.02
Chapman Pond	<i>T. scripta</i>	0.77	0.73
	<i>P. floridana</i>	0.07	0.10
	<i>A. ferox</i>	0.12	0.12
	<i>C. serpentina</i>	0.04	0.05
McCord Pond	<i>T. scripta</i>	0.56	0.63
	<i>P. floridana</i>	0	0.09
	<i>A. ferox</i>	0.22	0.08
	<i>C. serpentina</i>	0.22	0.20

Table 6. Spearman rank correlations among abundance of *Trachemys scripta*, *Pseudemys floridana*, and *Apalone ferox* and 14 environmental variables^a measured 2002–2003 at 17 lakes in Leon County, Florida.

	<i>T. scripta</i>	<i>P. floridana</i>	<i>A. ferox</i>	AREA	EMERGENT	FLOATING	SUBMERGED	BIOMASS	PAC
<i>T. scripta</i>									
<i>P. floridana</i>	0.44								
<i>A. ferox</i>	0.27	0.21							
AREA	-0.51	-0.10	-0.54						
EMERGENT	0.06	-0.20	-0.06	0.34					
FLOATING	-0.25	-0.49	-0.22	0.53	0.27				
SUBMERGED	-0.08	0.24	-0.44	0.16	-0.26	-0.01			
BIOMASS	0.05	-0.28	-0.19	0.32	-0.02	0.70	0.23		
PAC	0.37	-0.36	0.04	-0.04	0.31	0.46	0.03	0.61	
PERIPHY	0.23	0.21	0.38	-0.35	-0.07	-0.28	-0.33	-0.40	-0.31
CHLA	0.50	0.02	0.25	-0.08	0.78	0.13	-0.48	0.49	0.48
NITR	0.44	0.20	0.19	-0.02	0.54	-0.12	-0.42	0.15	0.30
PHOS	0.75	0.10	0.37	-0.47	0.46	-0.19	-0.28	0.28	0.54
INVERT	-0.16	0.07	-0.22	0.28	-0.20	0.06	0.02	-0.08	0.16
FISH	0.10	0.39	0.23	0.10	0.44	-0.02	-0.09	0.26	-0.10
CHIRON	0.60	0.70	0.34	-0.15	-0.01	-0.41	0.06	-0.14	0.04
SNAIL	0.55	0.06	0.50	-0.47	-0.03	0.04	0.07	0.18	0.44
	PERIPHY	CHLA	NITR	PHOS	INVERT	FISH	CHIRON		
PERIPHY									
CHLA	0.08								
NITR	-0.04	0.82							
PHOS	0.10	0.80	0.66						
INVERT	-0.13	-0.16	-0.13	-0.26					
FISH	0.22	0.44	0.14	0.22	0.01				
CHIRON	0.19	0.34	0.62	0.46	-0.04	0.12			
SNAIL	0.09	0.25	0.19	0.52	-0.47	0.02	0.36		

^aAREA = lake area, EMERGENT = mean emergent macrophyte biomass, FLOATING = mean floating macrophyte biomass, SUBMERGED = mean submerged macrophyte biomass, BIOMASS = mean total macrophyte biomass, PAC = percent lake surface area covered with macrophytes, PERIPHY = mean periphyton productivity, CHLA = mean chlorophyll *a* concentration, NITR = mean open-water total nitrogen concentration, PHOS = mean open-water total phosphorus concentration, INVERT = total macroinvertebrate abundance, FISH = total small fish abundance, CHIRON = total chironomid abundance, SNAIL = total snail abundance.

Chironomids were strongly correlated with open-water nutrients. 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 zero to 135 individuals per 1.25 m² (mean = 36.8, SE = 9.4) and was correlated with emergent macrophytes and chlorophyll *a* (Tables 6 and 7). Abundance of macroinvertebrates varied widely across all lakes and ranged from zero to 69 individuals per 1.25 m² (mean = 31.2, SE = 5.5) but showed no strong correlations with any of the environmental variables (Tables 6 and 7). The Spearman *r* between *T. scripta* and *P. floridana* (*r* = 0.44) was greater than that between *A. ferox* and *T. scripta* (*r* = 0.27) or *A. ferox* and *P. floridana* (*r* = 0.21).

Individual Mantel tests by species revealed significant correlations between abundance of *T. scripta*, *P. floridana*, and *A. ferox* and a suite of 5 environmental variables consisting of both biotic and abiotic factors. Lakes with a higher abundance of *T. scripta* had a mud/organic 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/organic substrate, no alligators, high periphyton

Table 7. 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 collected May–September 2003 from 17 study lakes in Leon County, Florida.

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

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 5 environmental variables that included no alligators, high periphyton productivity, high macroinvertebrate abundance, high snail abundance, and high total open-water phosphorus (Mantel $r = 0.48$, $P = 0.013$).

A Mantel test based on distance matrices of turtle community abundance (total abundance of 3 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/organic substrate, and no alligators (Mantel $r = 0.688$, $P = 0.001$).

Degree of Omnivory of *Trachemys scripta* and *Pseudemys floridana*

When offered a choice between duckweed and invertebrate prey, naïve hatchling *P. floridana* ate significantly more duckweed than did *T. scripta*, and hatchling *T. scripta* ate over 3 times more invertebrate prey than duckweed (ANOVA, $P = 0.029$, $F = 4.04$, $df = 2, 27$) (Fig. 7). *Trachemys scripta* also scavenged on dead least killifish significantly more than on duckweed compared to *P. floridana* (ANOVA, $P = 0.001$, $F = 54.5$, $df = 2, 7$). These results indicate that both species are omnivorous in the juvenile stage, but *T. scripta* is more carnivorous than *P. floridana*.

Although both species were omnivorous, there were striking differences in the proportion of the type of prey consumed between *P. floridana* and *T. scripta* (Fig. 8). Two-sample t -tests indicated that *T. scripta* consumed a significantly greater proportion of *Belostoma lutarium* ($t = -2.496$, $P = 0.037$), libellulids ($t = -3.40$, $p = 0.047$), and dead fish ($t = -1.294$, $P = 0.046$) than did *P. floridana* (Fig. 8). However, fewer shrimp were consumed by both species, with no difference in mean proportion eaten.

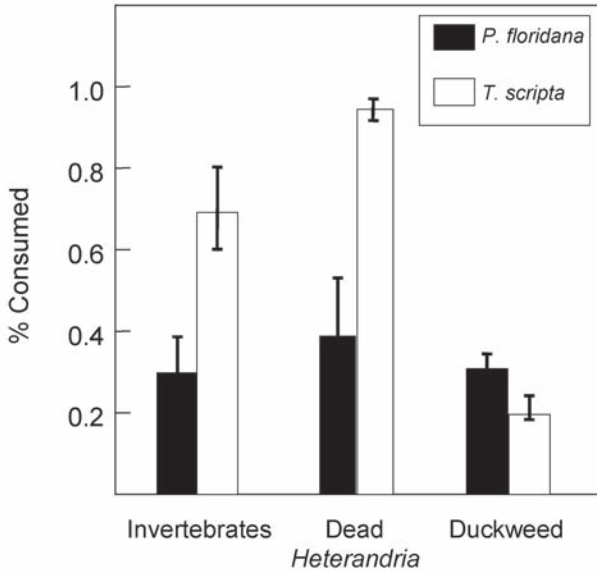


Fig. 7. Comparison of percent invertebrates, fish carrion (least killifish), and duckweed eaten by hatchling *Trachemys scripta* and *Pseudemys floridana* in a laboratory experiment conducted August 2001. Invertebrates included 1 of 3 prey types: either 3 small *Belostoma lutarium*, 7 libellulid odonate naiads, or 3 grass shrimp. Error bars equal ± 1 SD.

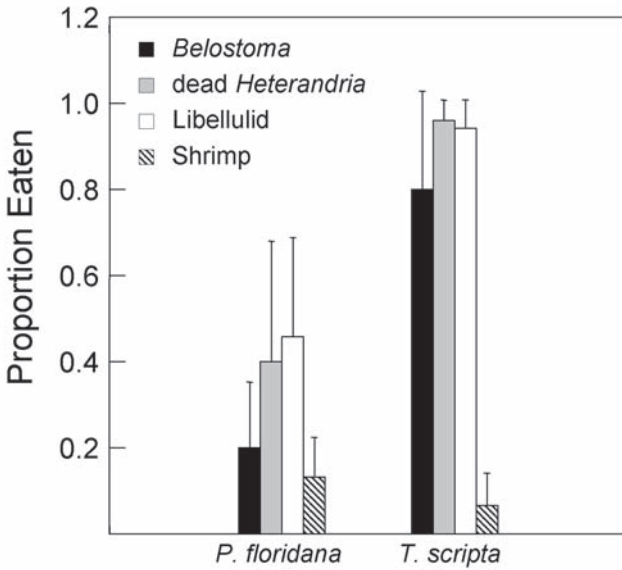


Fig. 8. Comparison of proportion eaten of each category of invertebrate and fish carrion between hatchling *Trachemys scripta* and *Pseudemys floridana* in a laboratory experiment conducted August 2001. Error bars equal ± 1 SD.

Competition Between *Trachemys scripta* and *Pseudemys floridana*

Differences in growth rates among the 4 treatments were marginally significant ($P = 0.11$, $F = 2.37$, $df = 3, 14$). More importantly, a posteriori contrast tests indicated that mean growth of *T. scripta* in combination with *P. floridana* was significantly greater than growth of *T. scripta* under intraspecific competition ($P = 0.028$, $F = 5.98$, $df = 1, 14$) (Fig. 9). However, there was no difference in growth between *P. floridana* in the presence of *T. scripta* and *P. floridana* alone (Fig. 9).

Overall ANOVA of mean number of insects eaten by turtles demonstrated a significant treatment effect ($P = 0.013$, $F = 4.95$, $df = 3, 16$). The a posteriori contrasts tested the hypothesis that turtles in treatments with greater growth rates consumed more insects. Although the contrast of number of insects eaten by *T. scripta* with *P. floridana* versus *T. scripta* alone was not statistically significant ($P = 0.11$, $F = 2.83$, $df = 1, 16$) (Fig. 10), the trend in the data followed that observed in the growth rate comparison. *Trachemys scripta* with conspecifics ate fewer insects per turtle and also had slower growth than did *T. scripta* with *P. floridana*. Seventy-four percent of turtles at the end of the experiment had eaten some macroalgae, but there were no differences in the number of turtles with and without algae among treatments.

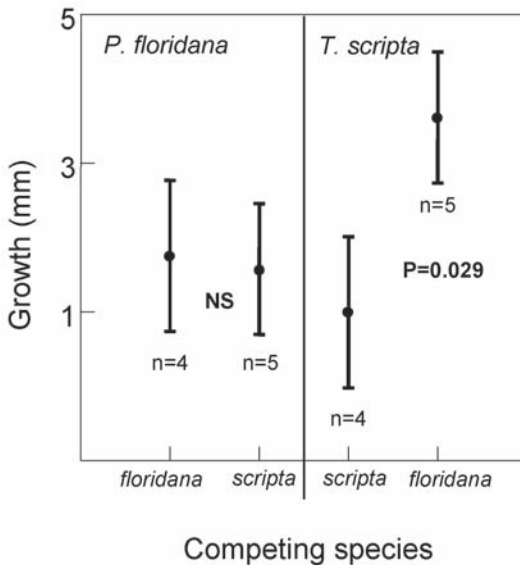


Fig. 9. Differences in growth of *Trachemys scripta* and *Pseudemys floridana* among 4 treatments in an experiment conducted 11 July 2002–3 August 2003 at Gannett Pond, Leon County, Florida

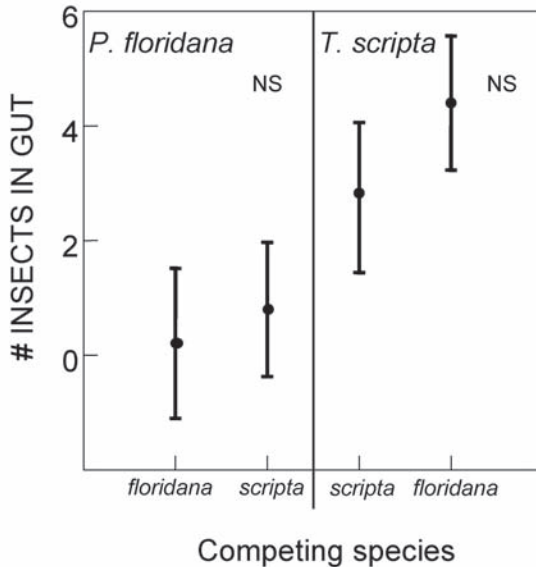


Fig. 10. Differences in the number of insects found in fecal samples of *Trachemys scripta* and *Pseudemys floridana* collected 11 July 2002–3 August 2003 at Gannett Pond, Leon County, Florida.

Sources of Primary Production and Trophic Structure of the Lake Jackson Food Web

The sources of primary production in the Lake Jackson food web are phytoplankton, POM, macroalgae (periphyton and filamentous algae), C3 macrophytes, and C4 maidencane grass. Primary producers had $\delta^{13}\text{C}$ values that indicated 3 distinct signatures of basal resources in the food web, with non-overlapping 95% confidence intervals: phytoplankton, C4 grass and C3 macrophytes, and POM and macroalgae (Table 8, Fig. 11). Algae and POM had the most enriched values of $\delta^{13}\text{C}$, phytoplankton was the least enriched, and macrophytes and maidencane grass intermediate between these other sources. There was significant variation in stable isotope values of macroalgae from 3 different locations (Fig. 12).

Lake Jackson is a relatively shallow lake with no deep-water, pelagic zone except for the area surrounding 2 sinkholes. The food web consists of 3 overlapping subwebs: terrestrial/shore, shallow vegetated littoral (<0.5 m), and deep vegetated littoral (0.5–2 m). Stable isotope values of selected primary consumers in the deep littoral and shallow littoral zones indicate a distinct difference in $\delta^{13}\text{C}$ signatures (Fig. 13). In deeper water, zooplankton

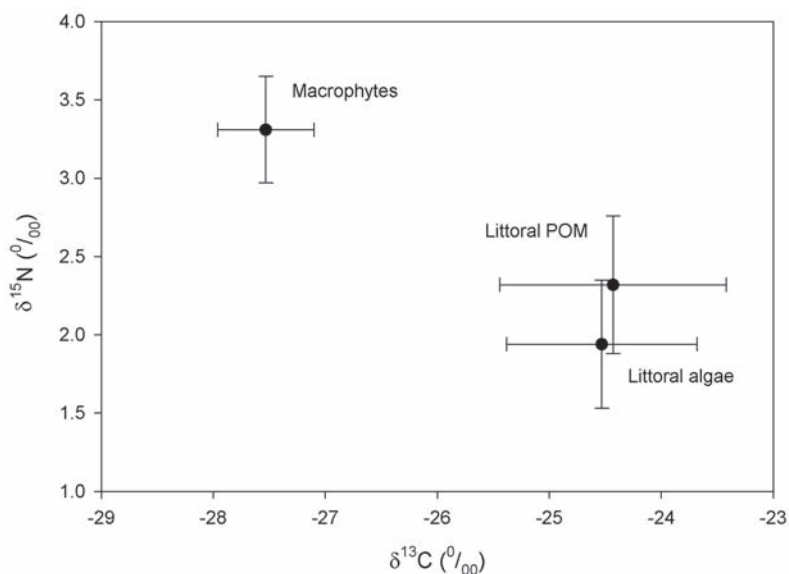


Fig. 11. Mean $\delta^{15}\text{N}$ vs. mean $\delta^{13}\text{C}$ (± 1 SE) for macrophytes, particulate organic matter (POM), and algae collected 2001–2004 from the littoral zone of northwest Lake Jackson, Leon County, Florida.

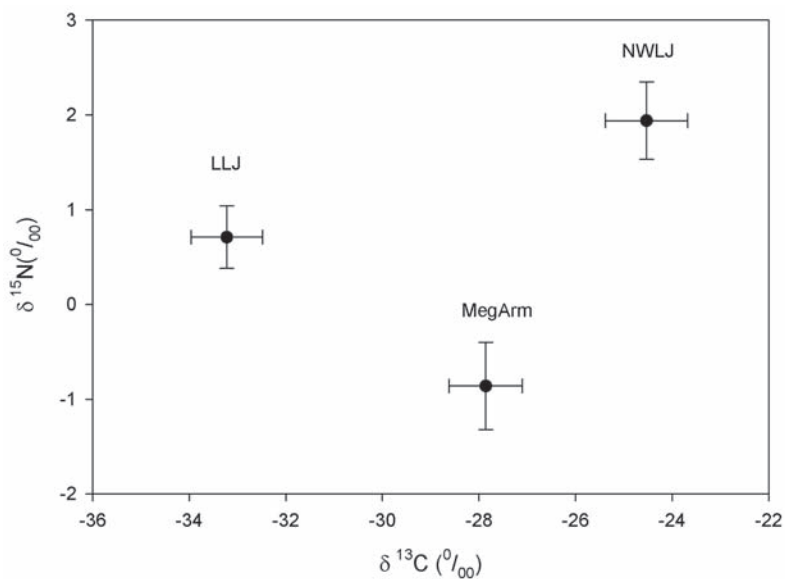


Fig. 12. Mean $\delta^{15}\text{N}$ vs. mean $\delta^{13}\text{C}$ (± 1 SE) for littoral algae collected 2001–2004 from 3 different sites at Lake Jackson, Leon County, Florida: northwest Lake Jackson (NWLJ), Little Lake Jackson (LLJ), and Megginis Arm (MegArm).

Table 8. 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 in northwest Florida in 3 different subwebs.

Taxon (<i>n</i>)	Subweb ^a	$\delta^{15}\text{N}$ (‰)	$\delta^{13}\text{C}$ (‰) ^b	Source ^c
Primary producers				
Maidencane grass (7)	SL	4.44 (0.83)	-27.81 (0.43) [-26.0 – -29.5]	
All macrophytes (23)	SL, DL	2.96 (0.42)	-27.44 (0.54) [-26.3 – -28.6]	
Particulate organic matter (POM) (6)				
Periphyton (48)	SL	1.94 (0.41)	-24.53 (0.85) [-22.8 – -26.3]	
Phytoplankton	DL	1.10 (-)	-30.17 (-)	
Herbivorous invertebrates				
Bivalvia (Unionid) (3)	DL	4.51 (0.12)	-30.40 (0.30) [-30.1 – -32.7]	phytoplankton
Zooplankton (10)	DL	5.80 (0.41)	-30.61 (0.41) [-29.7 – -31.5]	phytoplankton
Amphipoda (1)	SL	1.58 (-)	-26.05 (-)	
Coleoptera (Hydrophilid) (3)	SL	5.64 (1.05)	-24.79 (0.03) [-24.5 – -25.1]	POM, algae
Chironomid (1)	SL	4.40 (-)	-27.71 (-)	
Gastropoda (<i>Aminicola</i>) (4)	SL	4.46 (0.11)	-25.37 (1.70) [-20.0 – -30.8]	multiple sources
Shrimp (3)	SL, DL	4.72 (0.36)	-25.54 (0.57) [-23.1 – -28.0]	multiple sources
Crayfish (5)	SL	3.16 (0.25)	-27.12 (0.73) [-25.1 – -29.2]	grass
Carnivorous invertebrates				
Odonata (Libellulid) (8)	SL	4.19 (0.16)	-27.88 (0.30) [-27.2 – -28.6]	macrophyte, grass
Odonata (<i>Coryphechna</i>) (3)	SL	5.72 (0.31)	-25.88 (0.88) [-22.1 – -29.7]	multiple sources
Coleoptera (Dytiscid) (2)	SL	4.21 (0.32)	-29.17 (0.01) [-29.1 – -29.3]	grass
Hemiptera (Belostomatid) (5)	SL	4.64 (0.21)	-26.12 (0.38) [-25.1 – -27.2]	POM
Hemiptera (Naucorid) (3)	SL	3.65 (0.24)	-25.86 (2.70) [-14.3 – -37.2]	NA
Arachnida (<i>Dolomedes</i>) (3)	SL	7.72 (0.28)	-25.00 (0.34) [-23.5 – -26.5]	algae
Fish				
Florida gar (2)	DL	11.48 (0.45)	-23.54 (0.56) [-16.4 – -30.7]	NA
Bowfin (5)	DL	10.43 (0.09)	-28.11 (0.87) [-25.7 – -30.5]	multiple sources
Largemouth bass				
Adult (14–49 cm) (17)	DL	9.68 (0.11)	-25.9 (0.31) [-25.3 – -26.6]	POM
Juvenile (4 cm) (1)	SL	7.78 (-)	-24.46 (-)	
Black crappie				
Adult (15.0–30 cm) (10)	DL	9.57 (0.24)	-27.00 (0.42) [-26.1 – -27.9]	macrophyte, grass
Juvenile (3 cm) (1)	SL	6.30 (-)	-23.80 (-)	
Warmouth (15–17 cm) (5)	DL	9.13 (0.32)	-25.53 (0.72) [-23.5 – -27.5]	multiple sources
Bluegill				
Adult (7–18 cm) (19)	DL	8.26 (0.19)	-26.71 (0.46) [-25.8 – -27.7]	multiple sources
Juvenile (1.5–6 cm) (8)	SL	7.00 (0.20)	-26.17 (0.58) [-24.5 – -27.8]	multiple sources
Spotted bullhead (6)	DL	8.19 (0.44)	-26.07 (1.00) [-23.5 – -28.6]	multiple sources
Redear sunfish (7)	DL	8.11 (0.54)	-26.16 (1.04) [-23.6 – -28.7]	multiple sources
Golden shiner (11–19 cm) (11)				
DL		8.01 (0.24)	-27.65 (0.35) [-26.9 – -28.4]	macrophyte, grass
Coastal shiner (2)	DL	7.81 (0.45)	-25.22 (1.04) [-12.1 – -38.4]	NA
Mosquitofish (13)	SL	7.72 (0.16)	-25.51 (0.55) [-24.3 – -26.7]	POM, algae
Least killifish (9)	SL	7.01 (0.08)	-24.96 (0.67) [-23.4 – -26.5]	POM, algae
Chain pickerel				
Juvenile (7 cm) (1)	SL	7.08 (-)	-22.10 (-)	

Table 8. Continued.

Taxon (n)	Subweb ^a	$\delta^{15}\text{N}$ (‰)	$\delta^{13}\text{C}$ (‰) ^b	Source ^c
Fish (continued)				
Golden topminnow (5)	SL	6.80 (0.31)	-23.79 (1.24) [-20.3 – -27.3]	multiple sources
Lake chubsucker (6)	DL	6.72 (0.38)	-27.71 (0.70) [-25.9 – -29.5]	grass
Turtles				
Yellow-bellied slider				
Juvenile (18)	SL, DL	6.64 (0.32)	-25.91 (0.54) [-23.6 – -28.2]	multiple sources
Adult (39)	SL, DL	6.55 (0.17)	-24.18 (0.28) [-22.4 – -25.9]	algae
Florida cooter				
Juvenile (22)	SL, DL	3.84 (0.16)	-29.68 (0.84) [-25.8 – -33.6]	multiple sources
Adult (27)	SL, DL	4.37 (0.20)	-23.66 (0.43) [-22.8 – -24.5]	algae
Stinkpot (16)	SL, DL	7.33 (0.39)	-24.97 (0.42) [-24.1 – -25.9]	algae
Eastern mud turtle (1)	SL	8.89 (-)	-25.94 (-)	
Florida softshell				
Juvenile (14)	SL, DL	5.73 (0.12)	-28.00 (0.28) [-26.4 – -29.2]	grass
Adult (21)	SL, DL	7.74 (0.28)	-23.15 (0.59) [-22.0 – -24.6]	POM, algae
Snapping turtle (3)	SL	7.78 (0.27)	-24.79 (1.47) [-18.5 – -31.1]	multiple sources
Snakes				
Florida green watersnake (14)				
	SL, DL	7.18 (0.17)	-26.88 (0.54) [-25.7 – -28.1]	macrophyte
Banded watersnake (7)	TS, SL	8.25 (0.77)	-25.42 (0.39) [-24.5 – -26.4]	POM, algae
Cottonmouth (3)	TS, SL	7.27 (1.00)	-24.91 (0.78) [-21.6 – -28.3]	multiple sources
Mud snake (1)	SL	9.00 (-)	-26.34 (-)	
Aquatic salamanders				
Siren (13)	SL, DL	6.68 (0.21)	-26.45 (0.48) [-25.4 – -27.5]	algae
Amphiuma (4)	SL, DL	8.81 (0.26)	-26.33 (0.27) [-25.5 – -27.2]	algae
Frogs				
Florida cricket frog (2)	TS, SL	2.96 (1.00)	-28.23 (1.54) [-26.1 – -30.4]	terrestrial
Southern leopard frog				
Tadpole (3)	SL	1.98 (0.07)	-24.81 (0.44) [-22.9 – -26.7]	algae
Adult (12)	TS, SL	6.61 (0.33)	-23.02 (0.76) [-21.3 – -24.7]	POM, terrestrial
Southern toad (3)	TS	7.12 (0.44)	-24.25 (0.08) [-23.9 – -24.6]	terrestrial
Bullfrog (5)	TS, SL, DL	6.95 (0.17)	-25.92 (1.14) [-22.8 – -29.1]	multiple sources
Pig frog (8)	SL, DL	7.62 (0.27)	-25.03 (0.66) [-23.5 – -26.6]	algae
Alligator				
Juvenile (0.5–1.3 m) (21)	TS, SL	5.29 (0.19)	-25.65 (0.22) [-25.2 – -26.1]	algae
Adult (1.8–2.1 m) (2)	TS, SL, DL	6.69 (0.75)	-25.58 (0.86) [-14.6 – -36.8]	NA
Birds				
Anhinga (1)	DL	5.51 (-)	-16.45 (-)	
Mammals				
Marsh rice rat (1)	TS	5.84 (-)	-25.03 (-)	

^aTS = terrestrial/shore, SL = shallow vegetated littoral (<0.5 m), DL = deep vegetated littoral (0.5–2 m).

^b95% confidence intervals of $\delta^{13}\text{C}$ values are shown in brackets.

^cSource = basal source of primary production for a consumer based on 95% confidence intervals within that of producer and adjusted for trophic fractionation of $\delta^{13}\text{C}$; multiple = overlap with some combination of 2 or more sources, but uninformative for specific sources; POM = particulate organic matter; NA = undetermined basal resource, low sample size, wide variation.

and unionid clams have mean $\delta^{13}\text{C}$ values $>-30\text{‰}$, which indicates that they feed on phytoplankton. In the shallow littoral zone, primary consumers such as chironomids, amphipods, snails, and tadpoles indicated either a macrophyte or algae/POM-based web (Fig. 13).

A comparison of 95% confidence intervals of $\delta^{13}\text{C}$ values of primary producers and 41 animal taxa indicated that macroalgae, either by itself or in combination with POM, was the most important source of primary production in the food web (Table 9). Thirty-four percent of animal taxa had $\delta^{13}\text{C}$ signature values of primarily algae only or algae+POM. The most prevalent macroalgae found in Lake Jackson were 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 19.5% of animal taxa had $\delta^{13}\text{C}$ signature values of primarily C3 macrophyte only, C4 maidencane only, or macrophyte+maidencane (Table 9). Detritus of macrophytes and maidencane were other basal resources with similar $\delta^{13}\text{C}$ signature values. Some wider-ranging consumers (34% of animal taxa sampled) had $\delta^{13}\text{C}$ values that reflected multiple sources of primary production (including macroalgae), as they forage in different subwebs (e.g., deep-shallow zones or shore-shallow zones) or on prey with different $\delta^{13}\text{C}$ signature values. Overall, macroalgae provided full or partial contribution to the growth of 31 of 41 animal taxa.

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 8, Figs. 14 and 15). These carbon ratios indicated that they fed in an algae-based portion of the food web, either directly on algae or on prey that fed on algae. In contrast, juvenile *T. scripta* and *P. floridana* had $\delta^{13}\text{C}$ values that demonstrated they fed

Table 9. Percentage of 41 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	4.9
Algae	9	22.0
Particulate organic matter	3	7.3
Algae + particulate organic matter	5	12.0
Macrophyte	1	2.4
Maidencane grass	4	9.8
Macrophyte + maidencane	3	7.3
Multiple sources ^a	14	34

^aMultiple sources = overlap with some combination of >2 sources, but uninformative for specific sources.

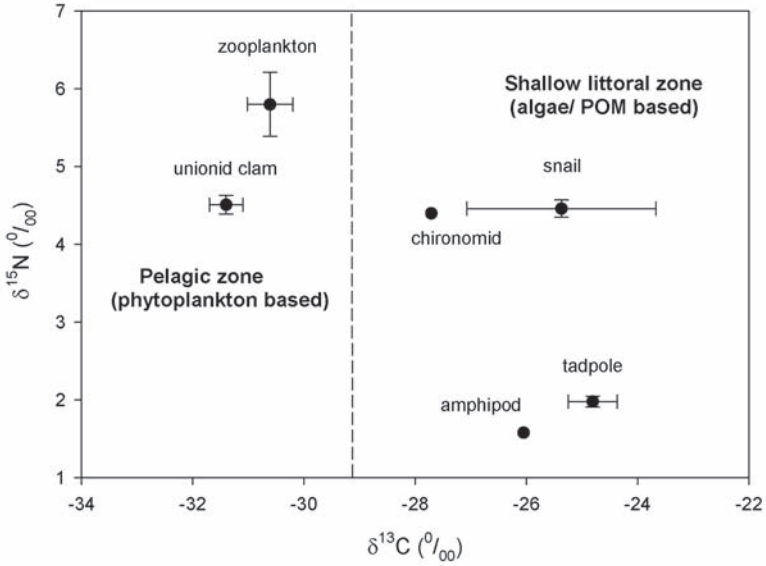


Fig. 13. Mean $\delta^{15}\text{N}$ vs. mean $\delta^{13}\text{C}$ (± 1 SE) for primary consumers collected 2002–2003 in the shallow littoral zone and pelagic zone at Lake Jackson, Leon County, Florida.

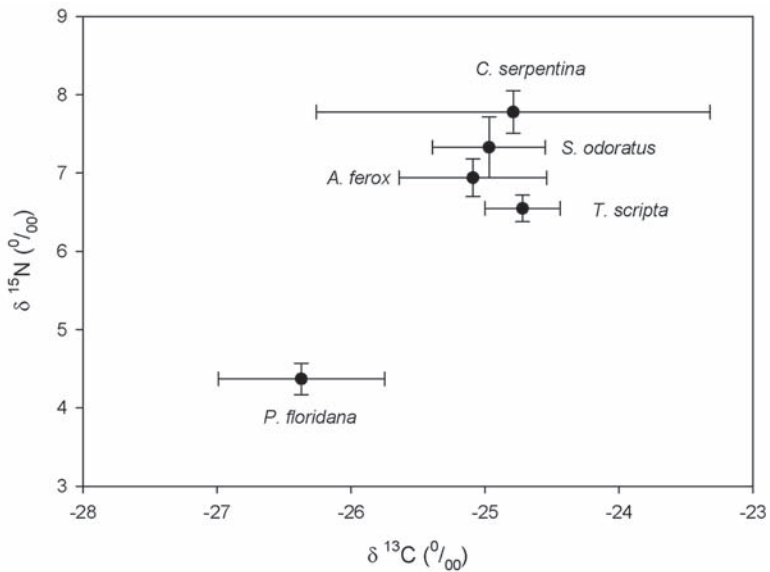


Fig. 14. Mean stable isotope values (± 1 SE) of *Trachemys scripta*, *Pseudemys floridana*, *Apalone ferox*, *Chelydra serpentina*, and *Sternotherus odoratus*, collected 2001–2004, at Lake Jackson, Leon County, Florida.

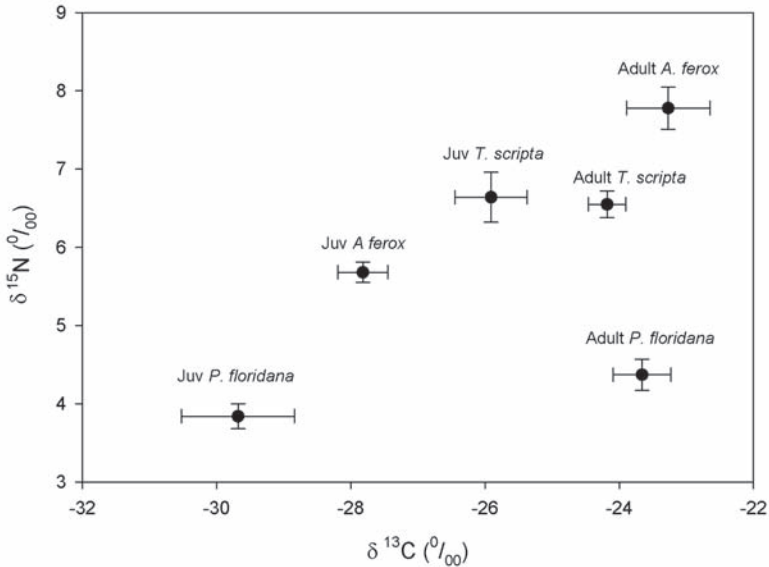


Fig. 15. Comparison of mean stable isotope values (± 1 SE) of juvenile and adult *Trachemys scripta*, *Pseudemys floridana*, and *Apalone ferox* collected 2001–2004 at Lake Jackson, Leon County, Florida.

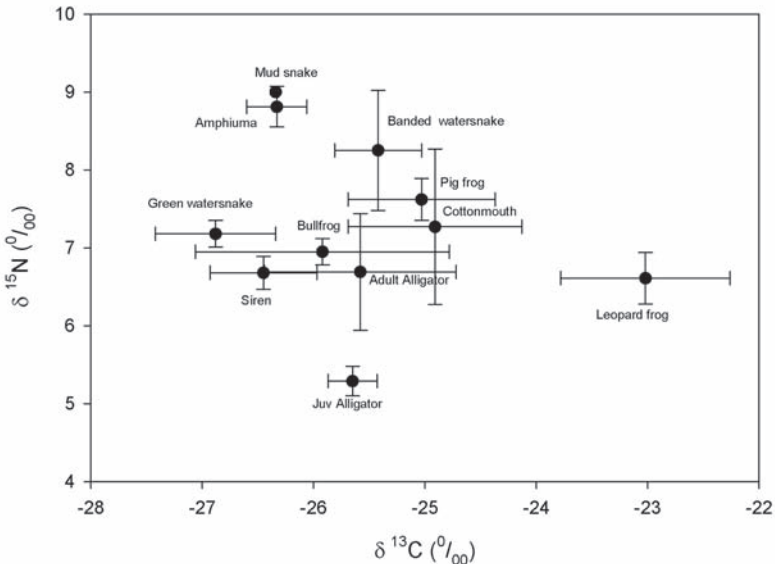
in a macrophyte-based part of the food web (-26 to -29 ppt) (Fig. 15). Juvenile *A. ferox* had $\delta^{13}\text{C}$ values indicating that maidencane was the important basal resource for its feeding links.

Despite the dominance of C3 macrophytes in the shallow littoral zone of Lake Jackson, 2 abundant, herbivorous, aquatic invertebrates (amphipods and hydrophilid beetles), and littoral fish (least killifish and mosquitofish) had signatures indicating significant contribution of algae in the form of periphyton and POM (Table 8). Diet data from these fish species indicated that least killifish fed primarily on algae and POM, and mosquitofish fed on zooplankton (Table 10). Two common shallow littoral zone predators, the fishing spider (*Dolomedes* sp.) and the banded watersnake (*Nerodia fasciata*), which prey heavily on small littoral fish, also had $\delta^{13}\text{C}$ signatures consistent with those of macroalgae and POM. Likewise, greater siren (*Siren lacertina*), two-toed amphiuma (*Amphiuma means*), and pig frog (*Rana grylio*) were other common predatory species in the littoral zone with $\delta^{13}\text{C}$ signatures consistent with those of macroalgae (Fig. 16).

Most fish species in the deep-water, littoral zone had stable isotope values that reflected multiple sources of primary production, indicating that they forage in different subwebs (e.g., deep-shallow zones or shore-shallow zones) or on prey with different $\delta^{13}\text{C}$ signature values (Table 8). Lake chubsucker

Table 10. Frequency of occurrence of diet items in gut contents of fish ($n = 83$) collected 20 December 2002 and 14 February 2003 at Porter Sink, Lake Jackson, Leon County, Florida.

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

**Fig. 16.** Mean stable isotope values (± 1 SE) of snakes, frogs, alligators, and aquatic salamanders. Samples were collected 2001–2004 at Lake Jackson, Leon County, Florida, from muscle of road-killed individuals and claw clips of live individuals.

(*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 TP model of the Lake Jackson food web based on stable isotopes demonstrated 2 major divisions among the trophic structure of turtles—herbivores (*P. floridana*) versus omnivores (*T. scripta*, *S. odoratus*, *A. ferox*, *K. subrubrum*, and *C. serpentina*) (ANOVA, $F = 37.7$, $P < 0.0001$) (Table 11, Fig. 17). Mean TP of *T. scripta* (adults and juveniles combined) was significantly greater than that of *P. floridana*, whereas TPs of *T. scripta*, *A. ferox*, *S. odoratus*, and *C. serpentina* were not significantly different from each other.

Table 11. Mean (\pm SE) trophic position of reptiles and amphibians in the Lake Jackson food web, Leon County, Florida, determined from isotope samples collected 2001–2004. Samples were obtained from muscle of road-killed individuals and claw clips of live individuals.

Species	Trophic position (\pm SE)
Turtles	
Yellow-bellied slider (<i>Trachemys scripta</i>)	
Juvenile ($n = 18$)	3.5 (0.1)
Adult ($n = 39$)	3.3 (0.1)
Florida cooter (<i>Pseudemys floridana</i>)	
Juvenile ($n = 22$)	2.3 (0.1)
Adult ($n = 27$)	2.3 (0.1)
Stinkpot (<i>Sternotherus odoratus</i>) ($n = 16$)	3.6 (0.2)
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)
Snapping turtle (<i>Chelydra serpentina</i>) ($n = 3$)	3.5 (0.2)
Snakes	
Florida green watersnake (<i>Nerodia floridana</i>) ($n = 14$)	3.4 (0.1)
Banded watersnake (<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 (-)
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 (0.4)
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 (<i>Alligator mississippiensis</i>)	
Juvenile (0.5–1.3 m) ($n = 21$)	2.7 (0.1)
Adult (1.8–2.1 m) ($n = 2$)	3.3 (0.3)

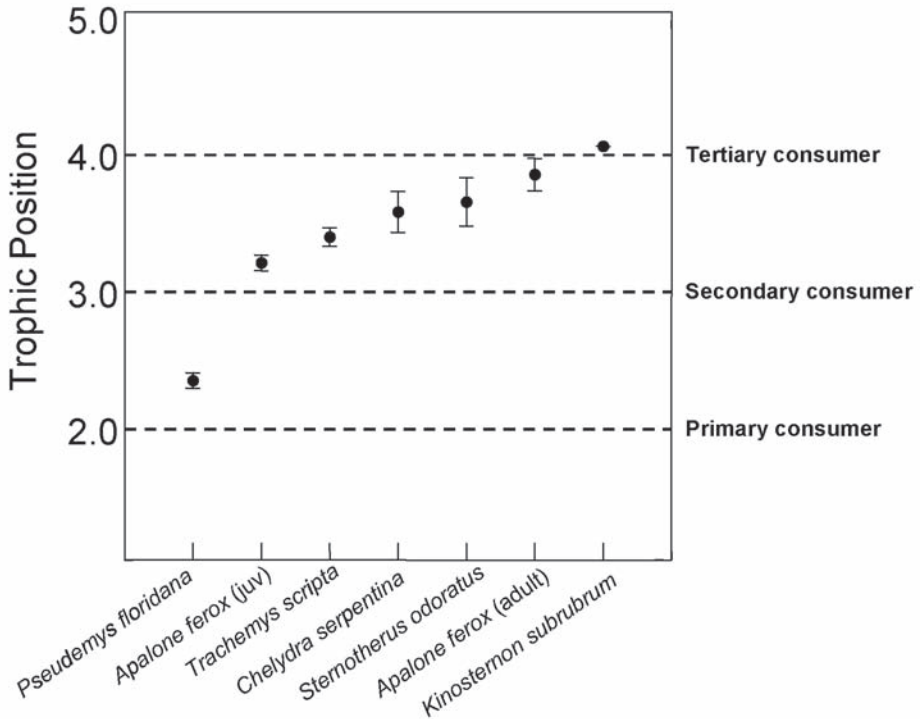


Fig. 17. Trophic position (± 1 SE) of turtles at Lake Jackson, Leon County, Florida, determined from isotope samples collected 2001–2004 from muscle of road-killed individuals and claw clips of live individuals.

Kinosternon subrubrum ($n = 1$) was the only turtle species with a TP ≥ 4.0 . 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. Adult and juvenile *P. floridana* both had a TP of 2.3, only slightly above the theoretical TP (2.0) of a strict herbivore (Table 11, Fig. 17). There was no relationship between size of *P. floridana* and TP ($r^2 = 0.006$, $P = 0.61$, $n = 45$) (Fig. 18), indicating that there was no ontogenetic shift in TP. Trophic positions of adult and juvenile *T. scripta* were 3.3 and 3.5, respectively (Table 11). 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. 19). 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. 20).

Gut contents of *A. ferox*, *T. scripta*, and *P. floridana* closely matched their respective TP inferred from stable isotopes (Table 12). Juvenile *A. ferox* ($n = 18$) almost exclusively consumed arthropods, whereas diet of adult *A. ferox*

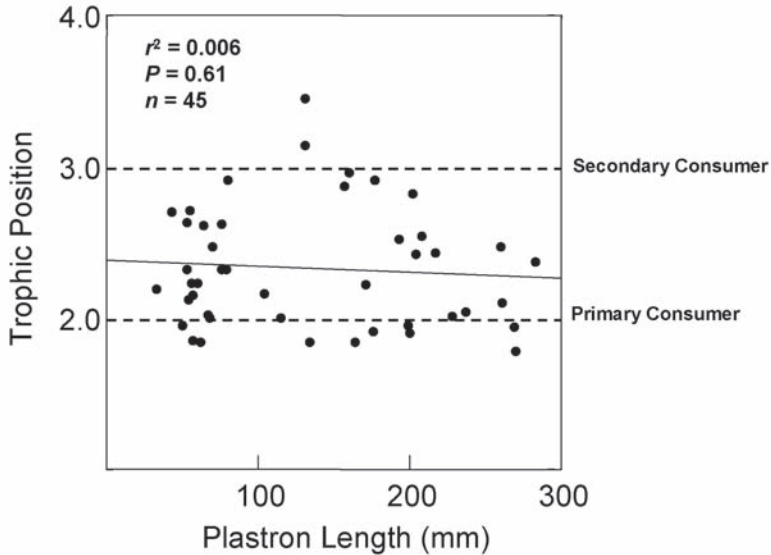


Fig. 18. Trophic position (TP) vs. plastron length of *Pseudemys floridana* at Lake Jackson, Leon County, Florida, determined from isotope samples collected 2001–2004 from muscle of road-killed individuals and claw clips of live individuals. Mean TP is 2.3 (SE = 0.06). Dashed lines denote theoretical TP of a strict primary consumer (2.0) and secondary consumer (3.0).

Table 12. Percent occurrence of food items in the diet of juvenile (juv) and adult *Apalone ferox*, *Trachemys scripta*, and *Pseudemys floridana* at northwest Lake Jackson, Little Lake Jackson, and Megginnis Arm, Leon County, Florida, collected March–October 2001–2003. Data from stomachs of road-killed individuals ($n = 15$) and fecal samples ($n = 97$) are combined. Juvenile *A. ferox* were <120 mm plastron length; juvenile *T. scripta* and *P. floridana* were <100 mm plastron length.

Food Category	<i>A. ferox</i> (juv) ($n = 14$)	<i>A. ferox</i> (adult) ($n = 35$)	<i>T. scripta</i> (juv) ($n = 18$)	<i>T. scripta</i> (adult) ($n = 38$)	<i>P. floridana</i> (juv) ($n = 21$)	<i>P. floridana</i> (adult) ($n = 35$)
Arthropoda	100	65.7	100	52.6	33.3	2.9
Crustacea		11.4		2.6	4.8	
Gastropoda		28.6		2.6		
Fish		20.0		7.9		
Bird		5.7				
Amphibian larvae	21.4					
Macroalgae	7.1	28.6	16.7	36.8	90.5	97.1
Macrophyte		8.6	33.3	81.6	38.1	37.1
Maidencane grass		2.9	5.6	26.3	9.5	5.7
Seeds		68.6	11.1	13.2	23.8	2.9
Terrestrial leaves				5.3		8.6

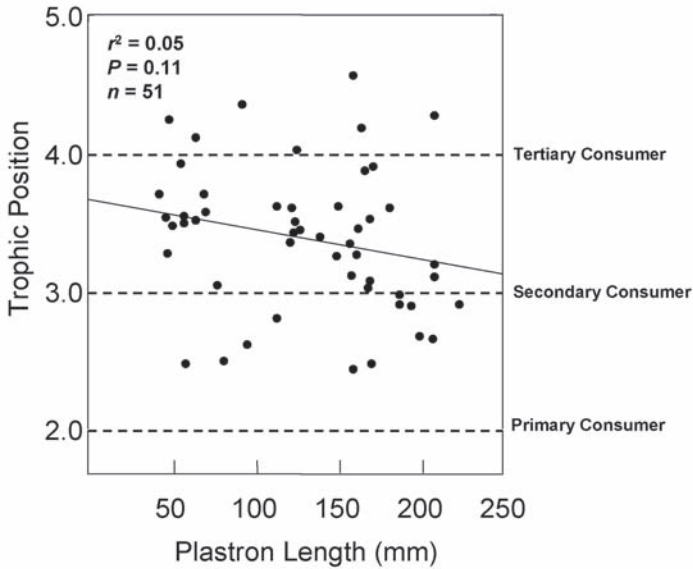


Fig. 19. Trophic position (TP) vs. plastron length of *Trachemys scripta* at Lake Jackson, Leon County, Florida, determined from isotope samples collected 2001–2004 from muscle of road-killed individuals and claw clips of live individuals. Mean TP is 3.4 (SE = 0.07). Dashed lines denote theoretical TP of a strict primary consumer (2.0), secondary consumer (3.0), and tertiary consumer (4.0).

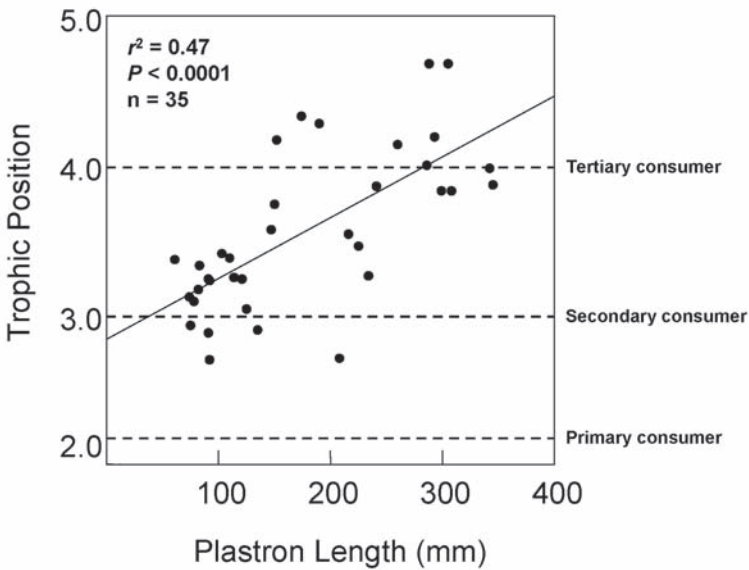


Fig. 20. Trophic position (TP) vs. plastron length of *Apalone ferox* at Lake Jackson, Leon County, Florida, determined from isotope samples collected 2001–2004 from muscle of road-killed individuals and claw clips of live individuals. Mean TP is 3.6 (SE = 0.09). Dashed lines denote theoretical TP of a strict primary consumer (2.0), secondary consumer (3.0), and tertiary consumer (4.0).

($n = 35$) consisted primarily of arthropods (e.g., giant water bug [*Lethocerus americanus*]), snails, macroalgae, and fish (Table 12). In addition, 69% 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 composed mostly of insects (e.g., odonate naiads) and macrophytes (e.g., bladderwort [*Utricularia* sp.]). The diet of adult *T. scripta* ($n = 38$) was similar to that of juveniles, with macrophytes (e.g., bladderwort, pickerelweed [*Pontedaria cordata*]), insects, and macroalgae (*Chara*) consumed most frequently. Three adult *T. scripta* had fish scales in guts. In contrast, both juvenile ($n = 21$) and adult ($n = 35$) *P. floridana* specialized on macroalgae (e.g., *Chara*, *Nitella*) (Table 12). Only 7 of 21 (33%) juvenile *P. floridana* and 1 of 35 (3%) 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 12). In gut contents of 6 *S. odoratus*, 4 individuals ate insects, 3 ate maidencane grass 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 arthropods (giant water bug). One individual also consumed macroalgae and seeds.

The mud snake (*Farancia abacura*) had the greatest TP (4.6) among reptiles and amphibians in the lake food web, indicating that it specialized on other consumers (e.g., amphiuma) (Fig. 16). Similarly, the two-toed amphiuma, with a mean TP of 4.0, was also considered one of the top predators in the littoral zone food web and fed primarily on secondary consumers. In contrast, mean TP of the greater siren was 3.1, a TP lower than that of the amphiuma because it directly consumes algae. Aquatic and semi-aquatic frogs (pig frog, bullfrog [*Rana catesbeiana*], and leopard frog [*Rana sphenoccephala*]) had trophic positions of 3.2–3.5, indicating that they fed on both primary and secondary consumers (Table 11). Trophic position of 3 semi-aquatic snakes (Florida green watersnake [*Nerodia floridana*], banded watersnake, and cottonmouth [*Agkistrodon piscivorus*]) ranged from 3.2 to 3.8 (Table 11). Trophic position of juvenile alligators (2.7) was slightly lower than that of adult alligators (3.3). Gut contents of juvenile alligators ($n = 6$) consisted primarily of predatory arthropods (e.g., *Belostoma lutarium*, giant water bug, predaceous diving beetle [*Dytiscus* sp.], odonate naiads, adult odonates), along with crayfish, snails, and frogs (*Acris gryllus*, *Rana* spp.), whereas stomach contents of 1 adult alligator (1.8 m total length) contained an American coot and musk turtle. 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 (*Amia calva*) (TP = 3.7) were the top fish predators in the food web and fed primarily on fish (Figs. 21 and 22). Trophic position of largemouth bass (*Micropterus salmoides*) (3.5), black crappie (3.5), and warmouth (*Lepomis gulosus*) (3.3) were slightly lower, indicating that they fed 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 10). Bluegill (*Lepomis macrochirus*) had a TP of 3.1 and fed on a diversity of prey including zooplankton, small fish (least killifish and mosquitofish), grass shrimp, and odonate naiads. Spotted bullhead (*Ameiurus serracanthus*) had the same TP as bluegill but fed exclusively on snails. Gut contents indicated that the golden shiner and mosquitofish fed mostly on zooplankton (Table 10). Differences in TP of the golden shiner (3.0) and mosquitofish (2.6), however, suggest that the mosquitofish was more herbivorous (algae or POM). Similarly, lake chubsucker had a TP of 2.6, indicating that it likely fed on a combination of zooplankton and macrophyte detritus. Stable isotopes indicated a low TP of the golden topminnow (2.3) and least killifish (2.4) and gut contents indicated that least killifish were primarily herbivores (algae/POM) in the shallow littoral zone (Table 10, Fig. 22).

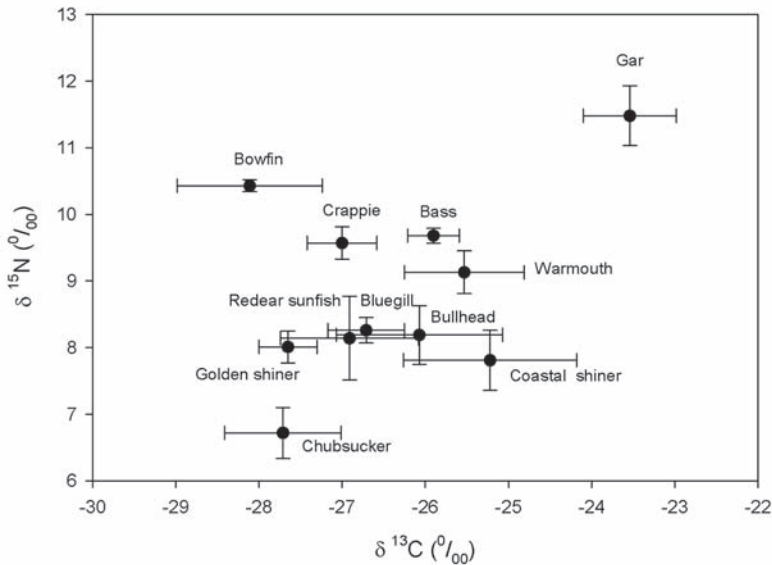


Fig. 21. Mean stable isotope values (± 1 SE) of fish collected 2002–2004 from Lake Jackson, Leon County, Florida.

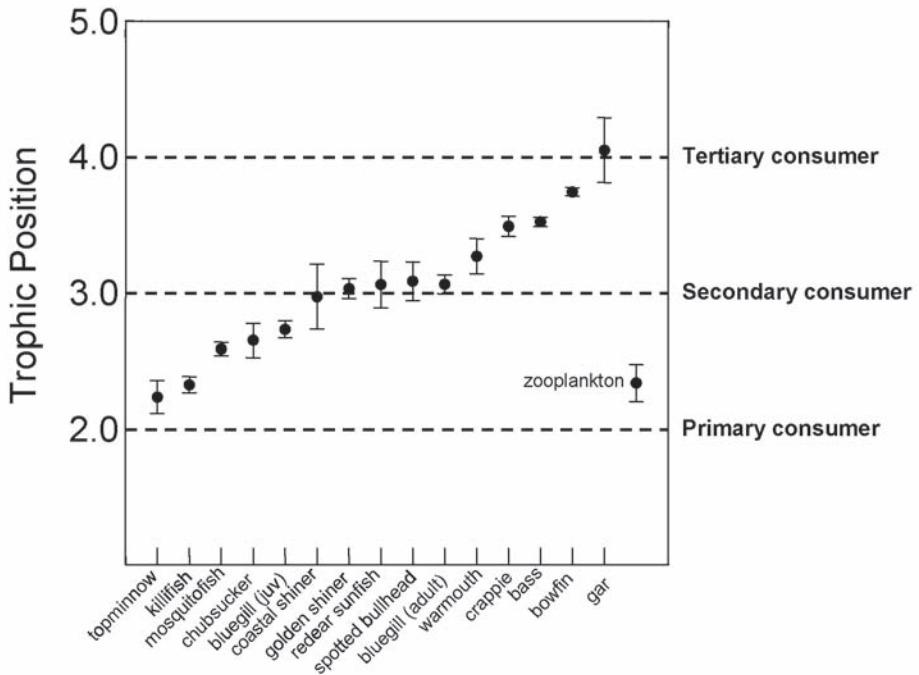


Fig. 22. Trophic position (± 1 SE) of fish collected 2002–2003 from Lake Jackson, Leon County, Florida. Trophic position of deep-water zooplankton is shown for reference as a primary consumer on phytoplankton and a diet source of some fish.

DISCUSSION

Turtle Abundance and Environmental Correlates

In this study, overall turtle abundance was highest in lakes with high periphyton productivity, a mud/organic substrate, and no alligators. Lakes with a higher abundance of *T. scripta* had a mud/organic substrate, no alligators, high periphyton productivity, high abundance of chironomids, and high open-water phosphorus. Similarly, lakes with high abundance of *P. floridana* had a mud/organic substrate, no alligators, high periphyton productivity, high abundance of chironomids, and low macrophyte cover. The overlap of 4 out of 5 environmental variables associated with the abundance of both *T. scripta* and *P. floridana* suggests wide niche overlap between these species. There was a strong association between abundance of *A. ferox* and a set of 5 environmental variables that included no alligators, high periphyton productivity, high macroinvertebrate abundance, high snail abundance, and high total open-water phosphorus. *Apalone ferox* shared a suite of environmental variables with *T. scripta* and *P. floridana*, but the correlation between lakes with high snail abundance and high macroinvertebrate abundance and high *A. ferox* abundance suggests a unique niche variable for this species (see Dalrymple 1977).

Studies of bird and fish communities in Florida lakes indicated 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 explained the abundance of *T. scripta* and *A. ferox*. However, overall turtle abundance was most positively correlated with a different measure of primary productivity: macroalgae in the form of periphyton. Periphyton was an important food source of *T. scripta* and *P. floridana* in this study and represented up to 90% of the diet of these species. In addition, as demonstrated by a stable isotope analysis of the Lake Jackson food web in this study, periphyton is the primary basal resource of the lake food web despite the prevalence of macrophytes. 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 biomass and abundance of aquatic macrophytes.

A mud or organic (muck) 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 an organic substrate than in ponds with an inorganic substrate. Substrate may indirectly affect turtle populations in 2 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, type of substrate 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 lake bottoms than in sandy bottoms.

There was a strong positive association between turtle abundance and high primary productivity (algae) and no predation by alligators. This result suggests that a combination of bottom-up and top-down controls may be important limiting factors to turtle populations. At Lake Jackson, macroalgae (e.g., *Nitella*, *Chara*) were a primary food of *T. scripta* and *P. floridana*. In other studies, macroalgae (e.g., *Cladophora* spp.) were a large portion of the diet of *Pseudemys* spp. and *T. scripta* (Parmenter 1980, Lagueux et al. 1995, Bondavalli and Ulanowicz 1999). Algae are easily digestible compared to fibrous macrophytes and are high in protein (Boyd and Lawrence 1967). In lakes where algae are 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.

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). *Pseudemys nelsoni* (Florida red-bellied turtles), *P. floridana peninsularis* (peninsula cooters), *T. scripta*, *Kinosternon baurii* (striped mud turtles), *Apalone ferox*, and *Sternotherus 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. Where turtles occur within the range of crocodylians, freshwater turtle populations 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,

and 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 some parts of the southeastern United States may add a limiting factor on 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 this effect.

Competitive Interactions of *Trachemys scripta* and *Pseudemys floridana*

Omnivory with an ontogenetic diet shift is a relatively common feeding pattern in freshwater systems and may be 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). Thus, generalist omnivores may be equally abundant and competitively superior in both high- and low-productivity environments if they can maintain equal growth rates compared to algal specialists. In contrast, a specialist may require specific minimum resources and grow too slowly in marginal habitats to maintain a stable population and/or compete with an omnivore. 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). Interspecific competition may be most important for juvenile *T. scripta* and *P. floridana* because growth during juvenile stages affects survival probability and age at maturity, and such interactions may have long-term effects on population demography. *Trachemys scripta* and *P. floridana* occur across a range of habitats that vary in quantity and quality of food. The mechanism for competition between similar turtle species (such as *T. scripta* and *P. floridana*) may be competitive exclusion through aggressive interactions, greater foraging efficiency on fast-moving (high protein) prey, or greater digestive efficiency (Webb 1962, Lardie 1965, Auth 1975, Leibold 1989, Bjorndal and Bolten 1990, Jackson 1996).

When forced to share the niche under low-resource conditions in this study, *P. floridana* grew equally well with both *T. scripta* and with conspecifics. However, *T. scripta* grew more slowly with conspecifics than with *P. floridana*. This experimental result suggests that the intraspecific effect of *T. scripta* on conspecifics is stronger than the interspecific effect. 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 insect 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 *T. scripta* and conspecifics. Thus, in this study, 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*. A possible mechanism for intraspecific competition in *T. scripta* for limited resources is aggressive interactions among conspecifics (Cahn 1937, Lardie 1983, Kramer 1986).

Omnivores may have an advantage over specialists in high-productivity environments, but inefficient conversion rates and intraspecific competition may limit density in low-resource environments (Diehl and Feibel 2000). However, to attain equal abundances across a productivity gradient, an optimal foraging strategy can be low levels of omnivory and high specialization on minimum basal resources (Persson et al. 1996). The trade-off may be that population density of a specialist equals but never exceeds that of species with high levels of omnivory.

Degree of Omnivory and Trophic Relationships of Turtles

Trachemys 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 differences in the availability of plant and animal foods (Clark and Gibbons 1969, Parmenter 1980, Hart 1983). 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). In contrast, *P. floridana* is herbivorous, preferring macroalgae and vascular aquatic plants (Allen 1938, Marchand 1942, Carr 1952). Adult *P. floridana* feed exclusively on the dominant aquatic plants in a given habitat, which may vary among lakes and seasonally within lakes (Thomas 1972).

In this study, a foraging experiment indicated that although both *P. floridana* and *T. scripta* were omnivorous in the juvenile stage, there were

striking differences in the proportion of the type of prey consumed and the degree of omnivory. *Trachemys scripta* ate significantly more insects and scavenged more on dead fish than did *P. floridana*. This result demonstrated a low level of resource overlap between these species and was consistent with the analysis, using stable isotopes, of TP of turtles. At Lake Jackson, TP of juvenile *T. scripta* was 3.5, >1 position higher than that of *P. floridana* (2.3). This difference in TP continued in adult *T. scripta* (3.3) and *P. floridana* (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 arthropods 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 on 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, unpublished data). Stable isotope ratios of some turtle species represent long-term assimilation of diet sources, so tissue samples collected post-drydown at Lake Jackson reflect foraging on large quantities of carrion. Hence, TP of turtles such as *T. scripta* and *S. odoratus* are elevated by scavenging on predatory fish or by feeding on predatory arthropods that occupy a similar or greater TP.

Based on TP, the turtle assemblage at Lake Jackson can be divided into 2 foraging groups: herbivorous (*P. floridana*) and omnivorous (*T. scripta*, *S. odoratus*, *A. ferox*, *C. serpentina*, *K. subrubrum*). *Pseudemys floridana* is a specialist on macroalgae in both the juvenile and adult stages. 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 algae. 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 giant water bug), fish, and other vertebrates (e.g., American coot) 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 [*Procambarus* spp.]) 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, TP of *C. serpentina* (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 (Punzo 1975). Aquatic plants are a major component of the diet of snapping turtles. In this study, a fecal sample of an adult male (31 cm CL) contained 95% duckweed and 5% stems of American lotus, and the stomach of a 28-cm-CL female contained 100% bladderwort (Aresco et al., in press).

Sternotherus odoratus functioned as both a predator and processor of organic material, and its 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 (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 TP. 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. 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 by facultative scavenging of turtles may represent important links in the food web that increase system stability (McCann et al. 1998, DeVault et al. 2003).

Primary Productivity and Trophic Structure in the Lake Jackson Food Web

Lake Jackson is a high productivity lake. Much of the primary production was accounted for by macrophytes and ranged from 6,000 g/m² in the main lake to 11,000–17,000 g/m² in the arms of the lake (e.g., Little Lake Jackson, Megginnis Arm). In contrast, filamentous algae (e.g., *Chara* spp.) and periphyton contributed much less to total primary production. Periphyton

that grows on the stems and roots of macrophytes ranged from only 1 to 2 g/m²/y (dry mass). At Lake Jackson, the ¹³C signatures of algae differed from those of macrophytes, and the tissues of a consumer reflect the basal sources of organic carbon. An abundance of vascular plant detritus occurred on the lake bottom and had 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 (microalgae). Forty-one percent of animal taxa sampled had ¹³C signatures that indicated macroalgae-based sources, compared to only 17% for macrophytes (including maidencane grass). Further, 34% of animals sampled exhibited a wide range of ¹³C signatures that overlapped with multiple sources of primary production, including macrophytes and algae. Therefore, stable isotope analysis revealed that macroalgae provided full or partial contribution to the growth of 75% of 41 animal taxa sampled at Lake Jackson.

The pattern of a macroalgae-based food web in a macrophyte or terrestrial-litter dominated system has been shown in some riverine 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). In contrast, most previous studies of lake systems with few macrophytes showed that they were phytoplankton-based food webs (Kling et al. 1992, Gu et al. 1997). 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. Our results from Lake Jackson were consistent with the overall conclusion of other studies—that algae represented a small fraction of the biomass of producers but was the primary energy source to consumers. This finding is likely to extend to other shallow, macrophyte-dominated lakes in Florida.

In this study, stable isotopes were used to determine trophic structure of a complex food web in a high-productivity lake in northern Florida. Lake Jackson is representative of lakes in this region with high species richness, diversity, and biomass of macroinvertebrates (including mollusks, insects, true bugs, spiders, crayfish, shrimp), fish (15 species), amphibians (11 species), and reptiles (15 species). Reptile diversity included 8 species of aquatic and semi-aquatic turtles, 6 species of aquatic and semi-aquatic snakes, and the American alligator (Aresco 2005). Most lake food web studies have been conducted in north temperate regions where species richness and diversity is much lower than in Florida lakes, but where much current food web theory is

based (Vander Zanden et al. 1999, Vander Zanden and Rasmussen 1999). For example, in the Great Lakes region of Ontario and Quebec, there are fewer species of fish than in Florida lakes and only a few species of reptiles and amphibians (e.g., *Chelydra serpentina*, painted turtle, northern watersnake [*Nerodia sipedon*], bullfrog, northern leopard frog [*R. pipiens*]). Thus, energy links and trophic interactions in Florida lakes are more complex and can be difficult to resolve.

Omnivory was prevalent in the Lake Jackson food web and most secondary consumers had a TP < 4.0. This result indicates that there were few specialists (TP ≥ 4.0) that forage on particular groups except for the Florida gar, a strict piscivore; the mud snake, which specializes on sirens and amphiumas; and the amphiuma (Mount 1975, Gibbons and Dorcas 2004). Likewise, at the bottom of the food web, only 2 vertebrate species were considered strict primary consumers—*P. floridana* and least killifish—along with southern leopard frog (*Rana sphenoccephala*) tadpoles. Thus, 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 studies have shown that increasing productivity adds trophic levels and increases stability (Yodzis et al. 1984, Polis and Strong 1996, McCann and Hastings 1997, Holyoak and Sachdev 1998). In our study, moderate to high levels of open-water nutrients produced high macrophyte biomass, but stable isotopes showed that algae was the primary energy source, and this resource may be limiting. Omnivory is common in natural food webs (Polis 1991, Diehl 1993) and combined with high species richness can increase feeding links and connectivity in the food web (Winemiller 1990). Omnivory may also stabilize food webs in variable environment such as Lake Jackson (e.g., seasonally fluctuating water levels), where feeding links may change significantly during drought (Winemiller 1990).

In food webs with widespread omnivory, food web length may be limited to fewer than 4 trophic levels. In a series of Great Lakes food webs, Vander Zanden et al. (1999) 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 4.5 (Vander Zanden et al. 1999, 2000). In contrast, trophic structure of the fish assemblage at Lake Jackson consisted of several species that are functionally top predators (in addition to the Florida gar), including largemouth bass, bowfin, and black crappie, but with TPs of only 3.5–3.7. Similarly, many other functional predators in the Lake Jackson food web (e.g., alligator, Florida green watersnake) 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 watersnake had a mean TP of 3.4, slightly lower than the TP of the banded watersnake (3.8). Although *Nerodia* species eat primarily frogs and a variety of small fish, the inclusion of tadpoles and herbivorous fish (e.g., least killifish) in their diet functions to decrease their actual TP to < 4.0. Aquatic frogs (pig frog, bullfrog, and leopard frog) are functionally secondary consumers with a mean TP of 3.3–3.5. However, feeding on predatory insects with a similar TP elevates their own TP to > 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 algae and primary consumers (e.g., least killifish).

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 $\delta^{15}\text{N}$ 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 $\delta^{15}\text{N}$ 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., Florida cricket frog [*Acris gryllus*]), predatory arthropods, and odonates. Interestingly, a study that examined stable isotope values of fossil alligators found that $\delta^{15}\text{N}$ values were also lower than expected compared to softshell turtles and other species found together in the fossil beds (Ostrom et al. 1993, 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.

CONCLUSIONS

Stable isotope analysis of the food web of Lake Jackson, Florida, revealed that filamentous macroalgae were the foundation of the web despite the much greater biomass of macrophytes. Similarly, in the oligotrophic Florida Everglades, periphyton mats are the base of the food web where biomass is dominated by cattails (*Typha* spp.), sawgrass (*Cladium jamaicense*), and spikerush (*Eleocharis* spp.) (Geddes and Trexler 2003). This result contrasts with previous studies of lake systems in other regions where phytoplankton was the base of the food web. The finding that macroalgae controls the biodiversity of Lake Jackson will likely extend to other shallow, macrophyte-dominated lakes in Florida.

Environmental changes, such as anthropogenic eutrophication that causes inedible cyanobacteria (e.g., blue-green algae [*Lyngbya* sp.]) to outcompete and displace filamentous macroalgae, can cause severe changes to the food web. Increases in nitrogen and phosphorus input that alter the N:P ratio can affect algal species composition. Therefore, under phosphorus-rich conditions, when nitrogen may be limiting, cyanobacteria has a competitive advantage over green filamentous algae because it can fix nitrogen directly. Further, cyanobacteria can successfully compete against green algae and diatoms because it can store phosphorus for later use, but is inedible to zooplankton, larval fish, or turtles that frequently graze on other types of algae. Lake Apopka in central Florida is a well-known example of a lake where hypereutrophication has resulted in a dominance of cyanobacteria and alteration of the food web. In addition, if macrophytes compete with macroalgae for nutrients, and that balance is changed by the mode and rate of nutrient deposition in the lake, the food web can also be altered. Prior to the natural drydown of Lake Jackson in 1999–2000, the lake was shifting towards a dominance of cyanobacteria because of eutrophication associated with increases in dissolved inorganic phosphorus and nitrogen entering the lake in stormwater runoff (Livingston 1997). The successional shift in dominance from green filamentous macroalgae to cyanobacteria was slowed by the drydown and demonstrated the ecological importance of natural hydrologic fluctuations in sinkhole lakes. Such fluctuations are often not possible in lakes where water levels have been stabilized by control structures. Although the beneficial filamentous green algae have returned since the lake refilled in 2001, this condition may only be temporary as polluted stormwater from urbanization and new development still enters the lake.

The importance of macroalgae in lake food webs is further emphasized by the finding in this study 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 periphyton by 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.

In the Lake Jackson food web, 90% of the consumers were omnivores and there were few specialists and few strict primary consumers. Notably, the Lake Jackson food web is 1 TP less than in simpler webs in north temperate lake systems, which have less species diversity and lower productivity. Omnivores may buffer the food web against environmental variability and, combined with high species richness, can increase feeding links, connectivity, and stability of the food web. Thus, in lake food webs with a high degree of omnivory, the effects of productivity and consumption are diffused across the web rather than at specific trophic levels. Further, the results of this study increase our understanding of how the interaction of omnivory and limitation of important resources such as macroalgae can control competitive interactions and trophic dynamics.

Despite the potential importance of turtles in food webs, these long-lived vertebrates have been generally overlooked in studies of freshwater communities. 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. 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.

Based on the analyses of trophic structure, food webs are complex in Florida lakes and there are many direct and indirect interactions among macroinvertebrates, fish, reptiles, and amphibians. Lake management practices

in Florida must consider the role of reptiles and amphibians in food webs and important resources such as macroalgae and organic substrates that support these populations. For example, this study demonstrated that turtle abundance was greater in lakes with mud/muck substrates. Many species of herpetofauna in the southeastern United States, including the two-toed amphiuma, siren, snapping turtle, mud snake, north Florida swamp snake (*Seminatrix pygaea*), and Florida green watersnake, are primarily associated with habitats of thick organic sediment and dense stands of macrophytes for foraging, reproduction, or aestivation. Thus, many species are negatively affected by large-scale muck removal operations, either through direct mortality or habitat alteration that leaves the littoral zone with a hard, graded, sand substrate devoid of organic material and macrophytes (Aresco and Gunzburger 2004). Future studies should evaluate the effects of lake management practices such as the removal of organic substrate and macrophytes on lake food webs and ecosystem functioning.

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