This is to certify that the

thesis entitled

THE DISTRIBUTION, DIEL MIGRATION, AND GROWTH OF THE GRASS SHRIMP PALAEMONETES PALUDOSUS IN THE KISSIMMEE RIVER FLOODPLAIN ECOSYSTEM

presented by

Kelly James Wessell

has been accepted towards fulfillment of the requirements for

M S degree in Fisheries and Wildlife

Major professor

Date 16 December 1999

THE DISTRIBUTION, DIEL MIGRATION, AND GROWTH OF THE GRASS SHRIMP *PALAEMONETES PALUDOSUS* IN THE KISSIMMEE RIVER FLOODPLAIN ECOSYSTEM

By

Kelly James Wessell

A THESIS

Submitted to
Michigan State University
in partial fulfillment of the requirements
for the degree of

MASTER OF SCIENCE

Department of Fisheries and Wildlife

1999

ABSTRACT

THE DISTRIBUTION, DIEL MIGRATION, AND GROWTH OF THE GRASS SHRIMP *PALAEMONETES PALUDOSUS* IN THE KISSIMMEE RIVER-FLOODPLAIN ECOSYSTEM

By

Kelly James Wessell

Historically, the Kissimmee River meandered over an extensive floodplain wetland. In response to catastrophic flooding and settlement pressures in Central Florida, the Kissimmee was channelized, converting the complex, braided channel into a straightened canal. The result has been a sharp decrease in fringing wetland habitat and the associated biota. Soon after channelization was completed, environmental concerns prompted the State of Florida to start examining options for restoration to reestablish the river's natural hydrology and restore lost wetland habitat. The grass shrimp, *Palaemonetes paludosus* has been identified as a keystone invertebrate species in this system, and this study was designed to examine its distribution, diel migration, and growth within the two dominant macrophyte communities of the Kissimmee River riparian marsh: *Nuphar* and *Polygonum*. Results indicated that grass shrimp were more abundant in *Polygonum* beds. This species also showed no well-defined diel migration, although I have found a significant vertical pattern in some instances. *P. paludosus* growth is highest on periphyton and *Polygonum* leaves. Grass shrimp distribution may be explained by their decreased susceptibility to predation because of the higher stem densities inherent in *Polygonum* beds.

ACKNOWLEDGMENTS

I wish to first thank my major professor, Dr. Richard W. Merritt for the incredible opportunity to work on the Kissimmee River and for all of his guidance on this project. I am truly lucky to have such a supportive mentor and advisor. Special thanks go to my committee members, Dr. Thomas Burton and Dr. Thomas Coon, for their leadership and support throughout this research and for providing valuable suggestions in reviewing this manuscript.

I am indebted to Ngoc Kieu for her tireless help in the field and with sample processing. I am also grateful to many other people for help with my field and lab work: Eric Naguski, Tom Burton, Don Uzarski, Michael Higgins, Becky Blasius, John Wallace, and Osvaldo Hernandez.

Thanks also go to Dr. Carlos de la Rosa, Dr. David Anderson, and the rest of the crew at Riverwoods Field Laboratory for the use of lab space and living quarters and to the South Florida Water Management District for providing travel funds.

Bridgette VandenEeden did biomass calculations, and Jim Brock provided data loggers and sondes for measuring dissolved oxygen. I also wish to extend my thanks to Dr. Ken Cummins, who provided invaluable help in every stage of this study. Without his guidance and knowledge, this study would not have been possible.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

THE DISTRIBUTION, DIEL MIGRATION, AND GROWTH OF THE GRASS SHRIMP *PALAEMONETES PALUDOSUS* IN THE KISSIMMEE RIVER-FLOODPLAIN ECOSYSTEM

HISTORY AND MANAGEMENT OF THE KISSIMMEE RIVER

THE PRE-CHANNELIZED KISSIMMEE RIVER

The Kissimmee River originates in the Kissimmee Lakes region of central Florida just south of Orlando and makes up the northern portion of the Kissimmee-Lake Okeechobee-Everglades watershed (Figure 1). Historically, the river was a complex braided channel that meandered approximately 166 km within a 1.5-3 km wide floodplain. In its historical condition, water levels fluctuated on a seasonal basis and discharge exceeded 11 m^3 / second during 90%-95% of the period of record, with highest discharges typically occurring at the end of the wet season (September-November) (Koebel 1995). Prior to channelization, 94% of the floodplain (16,920 ha) was inundated over 50% of the time (Shen et al. 1994). When inundated, water depths on the floodplain were generally 0.3-0.7 m, with depths over 1 m occurring on over 40% of the floodplain for at least one-third of the period of record (Toth 1990).

This system was unique to North American river-floodplain ecosystems in that it had an extremely well-developed fringing floodplain wetland that occurred along most of the river's length (Koebel 1995). This wetland habitat along with the seasonal fluctuation in water levels and nearly constant river-floodplain connectivity sustained a highly diverse invertebrate community including caddisflies, dragonflies, damselflies, water bugs, water beetles, isopods, amphipods, decapods, midges, and mollusks (Koebel 1995).

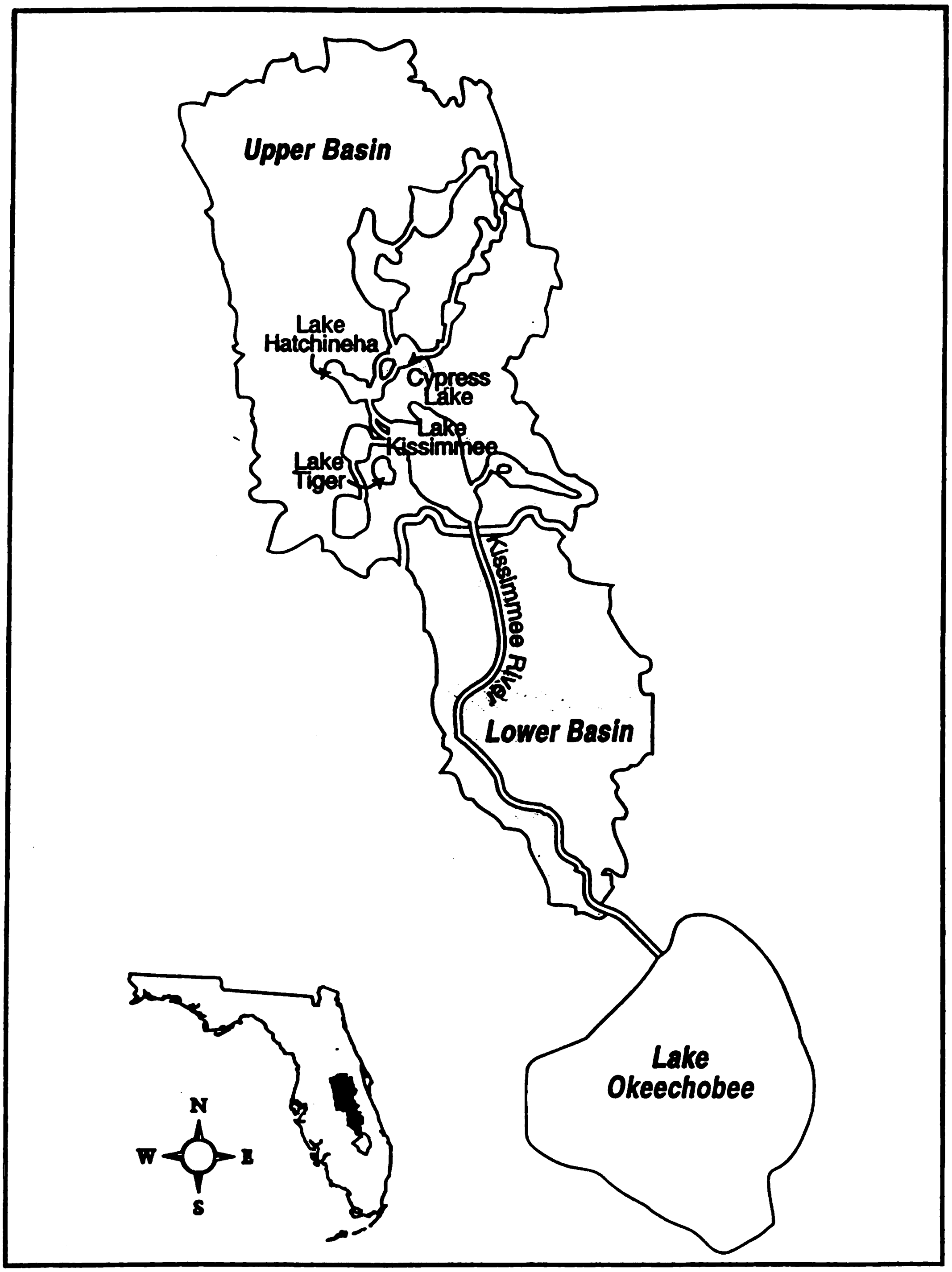

Figure 1. The Kissimmee River basin from the 4229 km^2 upper basin headwaters in the Kissimmee Lakes through the 1200 km^2 lower basin and into Lake Okeechobee. Location of the basin in south-central Florida is indicated in the inset. From Merritt et al 1996.

In addition, the Kissimmee River supported as many as 35 species of fish, including a world class largemouth bass fishery (Trexler 1995), 16 species of wading birds, 16 species of waterfowl, and six other water bird species (Weller 1995).

Often, the life cycles of invertebrates, fish (Junk et al. 1989), and water birds (Weller 1995) are closely tied with seasonal flooding. Greater fish recruitment occurs in years with smooth increases in water levels and floods of high amplitude and long duration (Payne 1986). In other words, the natural fluctuations in water levels were necessary to sustain much of the Kissimmee River's fauna.

The Kissimmee River Channelization

In response to catastrophic flooding and settlement pressures in Central Florida, the U.S. Army Corps of Engineers began a project in 1962 that channelized the river. The once meandering river was converted to a straightened, 9 m deep by 100 m wide canal and impounded into a series of five relatively stagnant storage reservoirs, so that water levels no longer fluctuated on a seasonal basis. The project affected approximately 161 km of river and resulted in the conversion of 14,000 ha of floodplain wetland to pasture (Toth et al. 1995) (Figure 2). The elimination of the seasonal water level fluctuations and the extensive loss of wetland plant communities have had significant effects on both invertebrate and vertebrate communities (Merritt et al. 1996). Additionally, low flow through remnant channels resulted in a build up of senescent plant material that covered the sand substrate with large amounts of organic matter, greatly increasing the biological oxygen demand of the system (Toth 1990). Specific effects of channelization on the biological communities include a 90% decrease in the number of

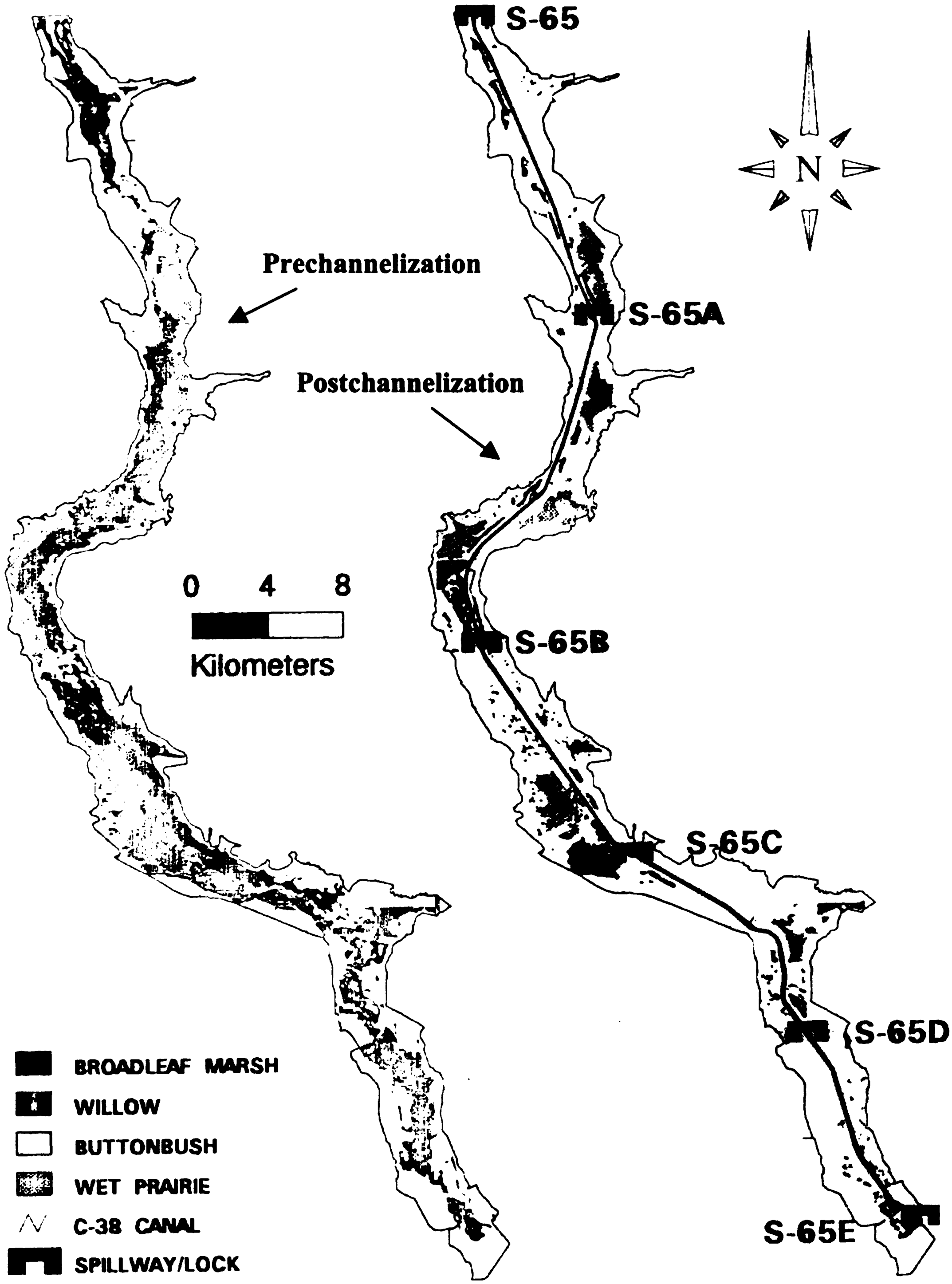

Figure 2. Pre and post-channelization distributions of dominant wetland plant communities on the Kissimmee River floodplain (modified from Toth et al. 1995).

waterfowl and wading birds (Weller 1995), a decline in the proportion of game fish captured in surveys (Trexler 1995), and a shift in invertebrates to those more common in lentic systems (Harris et al. 1995).

Soon after channelization was completed in the early 1970's, environmental concerns were raised, and this prompted the State of Florida and the U.S. Army Corps of Engineers to begin looking at options for restoration. Numerous structural and nonstructural plans were considered, including modification of upper basin lake regulation schedules, pool stage manipulations, earthen plugs, and backfilling (Koebel 1995). Analysis of these alternatives revealed that many of the plans were not feasible or did not meet restoration objectives. In late 1983, the U. S. Army Corps of Engineers narrowed its restoration focus down to two alternatives, including partial backfilling of the C-38 canal (the channelized river) and a combined wetlands approach that included pool stage manipulation and impounded wetlands.

The Pool B Demonstration Project

In 1984, the South Florida Water Management District (SFWMD) initiated a demonstration project to evaluate the effects of increased flow and floodplain inundation within the channelized river. This was accomplished with a series of three weirs that directed additional flow through three remnant channels along the section of the river known as Pool B (Figure 3). The results of the Demonstration Project was to reestablish prechannelization floodplain inundation patterns through small portions of three remnant channels in Pool B, resulting in the prolonged flooding of nearly 20% and periodic flooding of approximately 75% of the historical floodplain in this area.

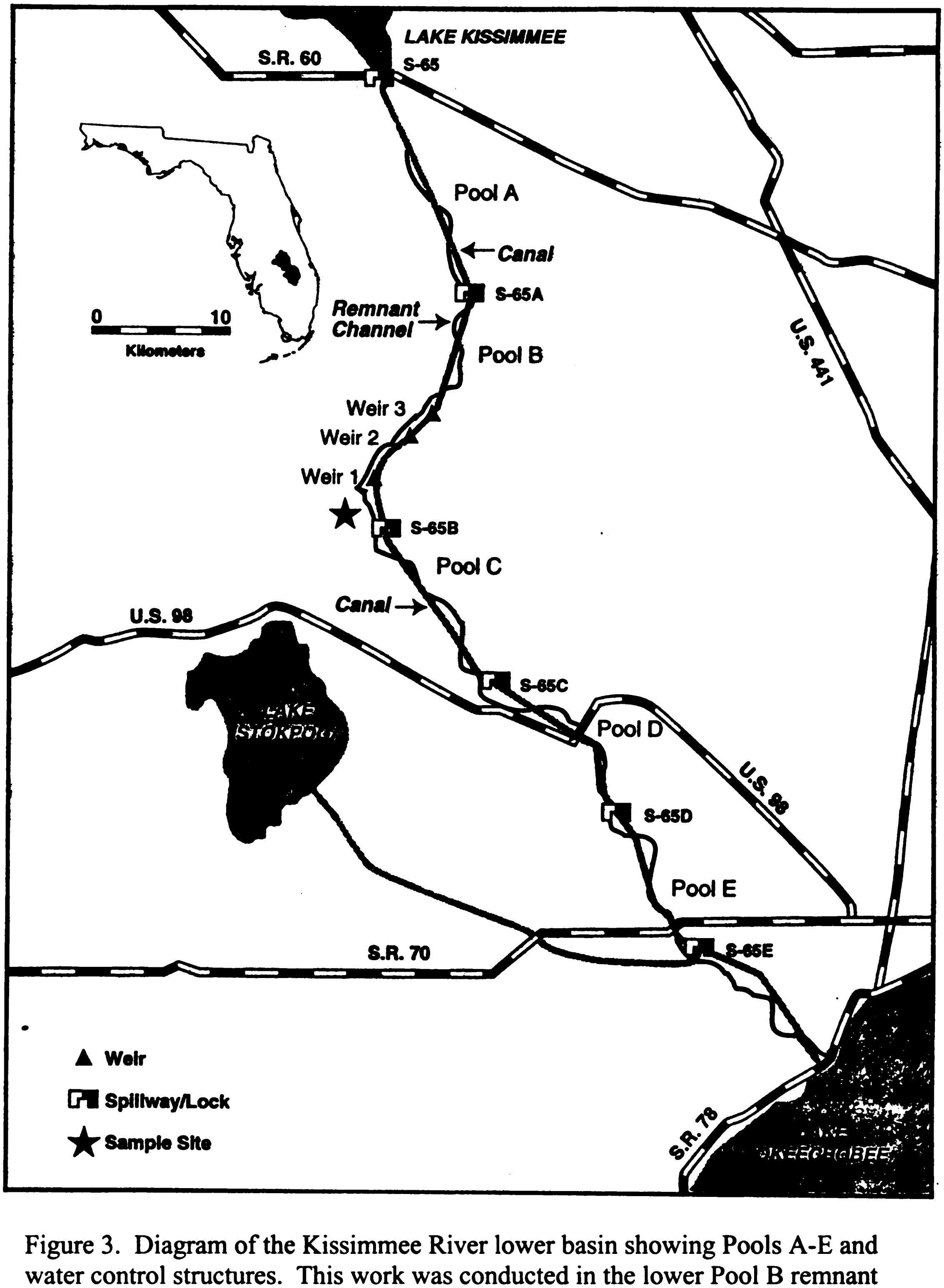

Figure 3. Diagram of the Kissimmee River lower basin showing Pools A-E and water control structures. This work was conducted in the lower Pool B remnant channel, the area affected by the Pool B Demonstration Project, denoted by the star.

Almost immediately upon completion of the Demonstration Project, wetland plant communities began to revert to those more characteristic of the historical system (Figure 2). Additionally, accumulations of dead organic matter were washed from the remnant channel into the C-38, restoring the natural sand substrate and reducing the biological oxygen demand (Koebel 1995). Reintroduction of flow through this area also has resulted in the colonization of invertebrate taxa more characteristic of lotic systems (Toth 1993) and increases in game fish (Wullschleger et al. 1990) and waterfowl (Toland 1990) relative to the unrestored portions of the river. The success of the demonstration project prompted the State of Florida to approve the SFWMD plan to backfill approximately 35 km of channelized river, eventually resulting in the restoration of about 11,000 ha of the historical floodplain wetland.

The Kissimmee River Restoration Project

The restoration of the Kissimmee River-floodplain ecosystem in central Florida is the largest project of its kind ever attempted. Major objectives of the restoration are to return the system to its historical condition in which it supported large populations of wading birds and waterfowl along with an outstanding sport fishery. This will be accomplished by returning the river to a state in which its flow, seasonal discharge patterns, floodplain inundation frequencies, and stage recession rates are comparable to the prechannelization conditions (Koebel 1995). As the floodplain and remnant channels are inundated with flowing water, the system is expected to shift from one dominated by pasture to one of riparian marsh habitat (Figure 4) (Merritt et al. 1999).

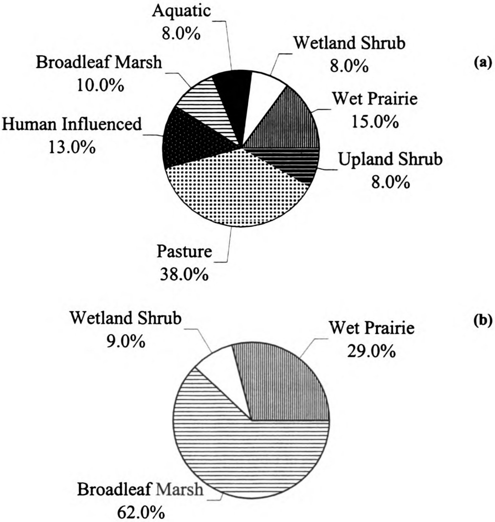

Figure 4. Current (a) and predicted post-restoration (b) vegetation in the Kissimmee River-floodplain ecosystem (Pools B, C, and D) (Modified from Toth et al. 1995).

During the restoration process, ecological conditions will be monitored to evaluate the project's success at restoring the habitats and populations of river and floodplain species. Invertebrates are an integral part of aquatic ecosystems and can serve as a useful indication of the extent to which this system is responding to restoration efforts. In the primarily lentic environment of the channelized Kissimmee River, invertebrate production has been restricted to the littoral zone with little floodplain habitat available. Since most productivity in large, undisturbed rivers occurs in the floodplain (Harris et al. 1995; Junk et al. 1989), the increase in floodplain habitat and reestablishment of the natural hydrological regime will undoubtedly have significant impacts on invertebrate communities, and these changes can help predict the effects of restoration on higher trophic levels.

Harris et al. (1995) suggested several key elements of the Kissimmee's invertebrate community for study prior to and during the Kissimmee River restoration. Secondary productivity must be studied in order to get an idea of overall community structure and the availability of food to higher trophic levels. Examining drift dynamics and determining the movement of organisms and organic matter in and out of the floodplain would aid in understanding the functional linkages between the river and its floodplain. They also suggested that diet studies of waterfowl, wading birds, and fish would clarify the specific trophic linkages between invertebrates and their potential predators and enable predictions to be made regarding the colonization of the restored habitat by higher trophic levels. In addition, special attention should be paid to invertebrate indicator groups and keystone species such as the grass shrimp, *Palaemonetes paludosus*.

A conceptual model has been developed by the SFWMD that identifies two key littoral fringe plant communities: *Nuphar luteum* and *Polygonum densiflorum* (Figure 5). The grass shrimp *Palaemonetes paludosus* (Gibbes) is particularly abundant in each of these plant communities (Figure 6) (Merritt et al. 1996, 1999). Because of its relative abundance and large size, *P. paludosus* is a significant link between primary producers and higher trophic levels in the Kissimmee River-floodplain system (Merritt et al. 1999), including vertebrate predators that detect their prey visually, such as many large fish, wading birds, and waterfowl (Figure 5).

GRASS SHRIMP ECOLOGY

The North American species of *Palaemonetes* represent what are probably the most poorly known of our freshwater decapoda. This is partly due to their limited commercial value and lack of extensive fieldwork (Strenth 1976). The existing knowledge of the group consists of work done on primarily marine and estuarine species such as *P. pugio* Holthuis (Welsh 1975; Kneib 1985; Gregg and Fleeger 1995, 1996; Eggleston et al. 1998; Vernberg and Piyatiratitivorakul 1998; Cross et al. 1996) and *P. vulgaris* (Miller et al. 1995; Sogard and Able 1994; Coen et al. 1981), with a relatively scant ecological knowledge base of freshwater species such as *P. paludosus*.

Data from studies of marine and estuarine *Palaemonetes* suggest that interactions among grass shrimp, benthic predators, and nektonic omnivores have strong direct and indirect effects upon benthic faunal densities and community composition (Posey and Hines 1991). Additionally, Pringle and others (1993) have determined that omnivorous shrimp are important organizers of lotic community structure and play a key role in

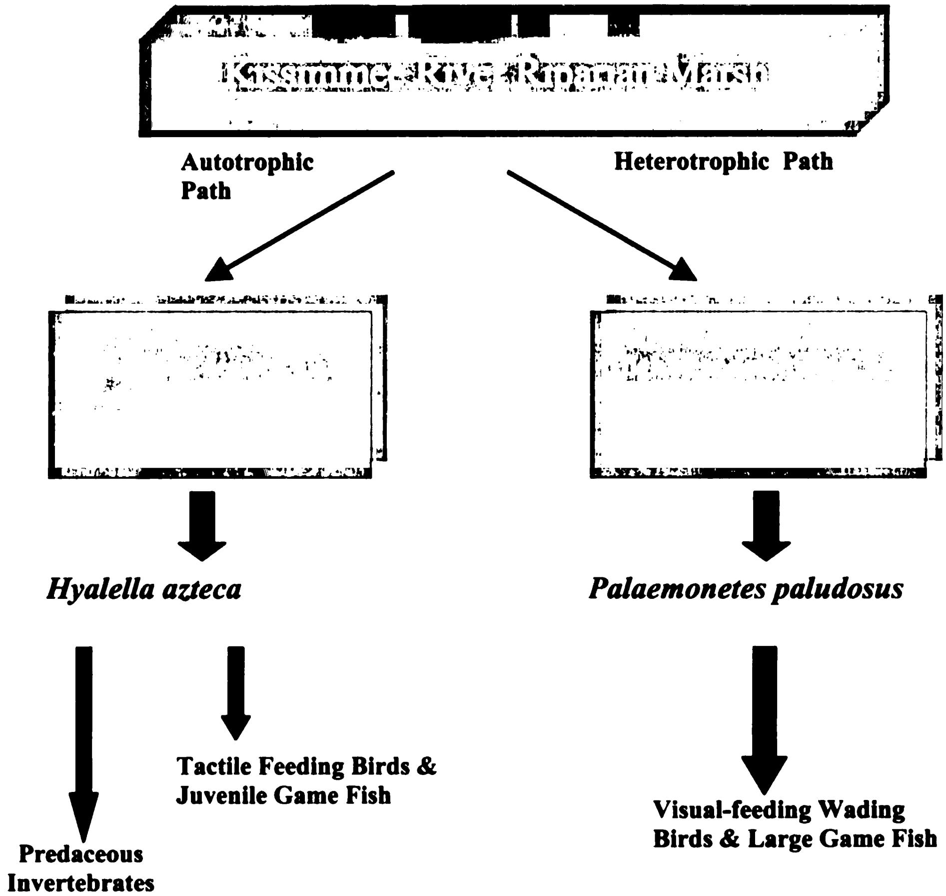

Figure 5. Conceptual model relating the autotrophic and heterotrophic pathways, the associated keystone invertebrates, and suggested links to higher trophic levels in the Kissimmee River riparian marsh ecosystem (modified from Merritt et al. 1999)

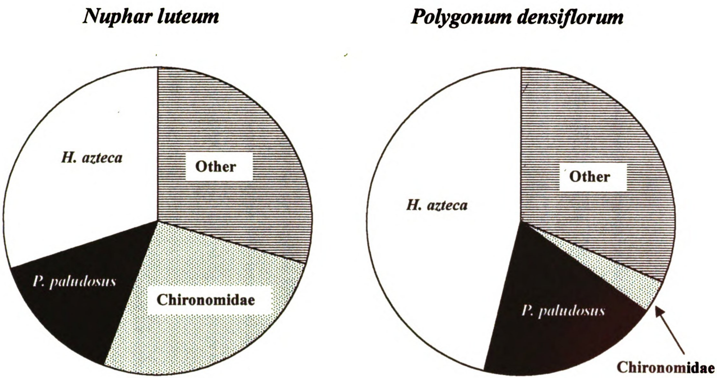

Figure 6. Relative abundance of selected invertebrate taxa (percentages based on numbers of animals) in the two dominant littoral fringe habitats of the Kissimmee River riparian marsh: *Nuphar luteum* and *Polygonum densiflorum*. Data from Merritt et al. 1999.

reducing sediment cover on rock substrata and enhancing algal populations. Grass shrimp have also been shown to be important predators of phytoplankton grazers such as cladocerans, and indirectly contribute to higher turbidity and eutrophication (Samuels and Mason 1998).

Palaemonetes paludosus is widespread in the eastern United States, and is found as far west as eastern Texas (Strenth 1976). This grass shrimp species is especially abundant in the extensive marshes and swamps of Southern Florida (Kushlan and Kushlan 1980), and can be found among emergent vegetation, snags, or clinging to the undersides of vegetation mats. Its body is transparent and ranges in size from 3-25 mm long (Meehean 1936). Although algae are its major food, *P. paludosus* is omnivorous and may feed on dead leaves, insects and other benthic coarse particulate organic matter (CPOM) (Beck and Cowell 1976). Some authors (e.g., Meehan 1936) describe *P. paludosus* as an intolerant species that is usually found in clean water with high dissolved oxygen. Other investigators (Kushlan and Kushlan 1980) maintain that they are extremely tolerant to low dissolved oxygen (DO) levels and have noticed them swimming at the surface in areas of low DO, presumably taking advantage of the oxygen diffusing across the surface layer.

In Florida, ovigorous females have been collected throughout the year (Dobkin 1963). However, the percentage of ovigorous females peaks when the water levels rise in the summer, and during early fall, when water levels are usually the highest (Kushlan and Kushlan 1980). This suggests that restoration of the natural hydrological regime in the Kissimmee River-floodplain ecosystem could have a positive effect on grass shrimp production.

Females typically produce broods of 8-85 eggs during their one year life cycle and carry eggs and zoeae for up to 2 months (Beck and Cowell 1976). Larval shrimp (zoeae) hatch from eggs after an incubation period of approximately 12-14 days at 26-28°C (Beck and Cowell 1976). The larvae molt three times before they reach sexual maturity. Hatching to maturity takes 2-3 months when water temperatures exceed 26°C, though cooler temperatures delay maturation (Beck and Cowell 1976). The frequency of molting and duration of larval life varies with the quantity and quality of food available (Broad 1957).

Study Objectives

I studied the distribution, diel migration, and growth of *Palaemonetes paludosus* to gain a better understanding of the functional linkage between the river and its floodplain for this species. This was aimed at providing information to predict how the restoration process and the resulting increase in floodplain habitat might affect the distribution and abundance of this species in the Kissimmee River-floodplain ecosystem. Four specific aspects of grass shrimp ecology in the restored Kissimmee River-floodplain were examined to evaluate the importance and success of this species. These include: 1) A comparison of its seasonal distribution and abundance in the riparian marsh as a function macrophyte type; 2) A comparison of its total biomass in the Kissimmee River riparian marsh in relation to the other keystone invertebrate, *H. azteca*; 3) Determining its diel migration patterns between the river and floodplain; and 4) Determining its growth rate as a function of the type of food consumed.

Methods and Materials

Study Site

The study site is located in the lower Pool B remnant channel of the Kissimmee River near Lorida, Florida in the partially restored area affected by the Demonstration Project (Figure 3). Flow through this remnant channel is generally low compared to historical conditions. During 1988, this remnant channel had discharges between 0-11 m^3/sec approximately 56% of the time and exceeded 26 m^3/sec 31% of the time (Toth 1991). Water temperature ranged from about 25°C in the winter to 35°C in the summer. Generally, dissolved oxygen levels are considered poor and were highest during the spring and lowest during the late summer and early fall (Wullschleger et al. 1990).

The two most dominant littoral fringe plant communities in this area are *Nuphar luteum* and *Polygonum densiflorum*, and are structured very differently from each other. *Nuphar* communities are characterized by relatively low stem densities (15/ m^2) (Cummins et al. 1999), high light penetration, and are generally autotrophic (Merritt et al. 1999). Much of the primary productivity is due to the dense periphyton communities that colonize *Nuphar* stems, and this is potentially a rich food source for invertebrates (Cummins and Klug 1979). *Polygonum* beds, on the other hand, are characterized by very high stem densities (46/m^2), with very little subsurface light penetration (Cummins et al. 1999). Because of this, *Polygonum* communities are generally heterotrophic. Dissolved oxygen levels are relatively low in both plant bed types, but tend to be slightly higher in the *Nuphar* beds than in the *Polygonum* beds, differing by between 1-2 mg/L (Figure 7). Water depth in both macrophyte beds ranged between 45 cm and 110 cm during the study period.

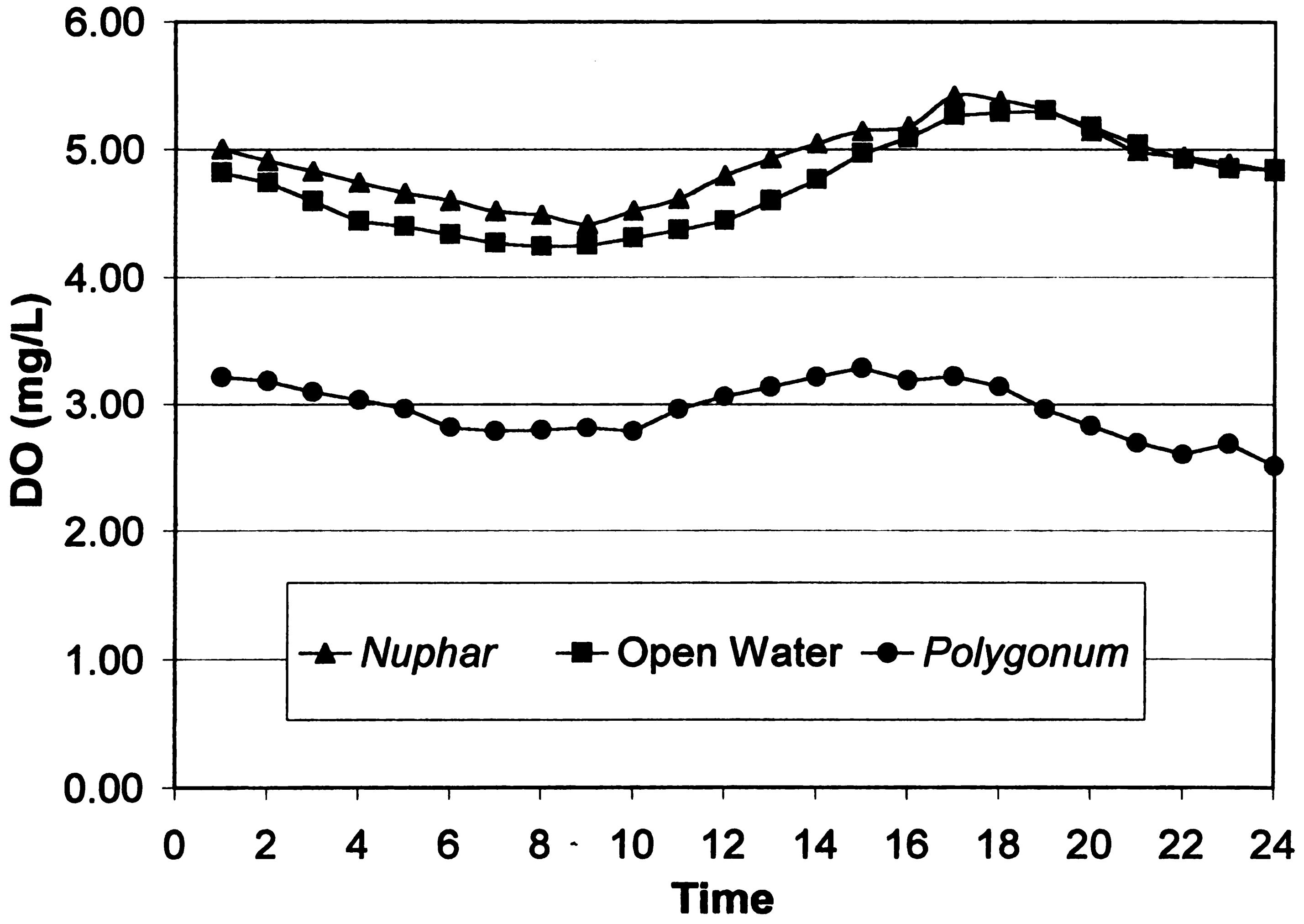

Figure 7. Diel dissolved oxygen curve comparing 2 riparian marsh habitats (*Nuphar* and *Polygonum*) and open water. (From sonde data collected on 5-6 May 1998)

Distribution and Abundance

The two dominant littoral fringe habitats (*Nuphar luteum* and *Polygonum densiflorum*) of the Kissimmee River riparian marsh along the lower remnant channel of Pool B were sampled twice a year under different flow and water level conditions for two years. Vegetation was sampled by positioning a D-frame aquatic dip net (0.8 mm mesh) several centimeters into the sediments and vigorously moving it along the stems of the plants for 30 seconds. I moved the net from side to side and front to back and brought it through the plant bed to the surface to insure dislodgment of the associated invertebrates. On each sampling date, 18 samples were taken from both *Nuphar* and *Polygonum* beds. For each sample, the net and its contents were washed into an enamel tray and the coarse material was washed off by hand into a whirlpac bag and preserved with 70% EtOH. Samples were returned to the lab for sorting and measuring of invertebrates under a dissecting microscope. The number of *P. paludosus* and *H. azteca* were recorded for each sample and biomass was determined from a length-biomass regression.

Data from both summer samples (Aug 97 and June 98) were pooled and compared to data from pooled winter samples (Feb 98 and Feb 99). Mean number of individuals per sample by plant type and season were calculated before log-transforming data in order to adhere to the ANOVA assumptions of normality and homogeneity of variance. Differences in grass shrimp distribution by plant type and season were analyzed with log-transformed data (log(y+1)) in a 2-way analysis of variance with season as the first factor (2 levels: summer and winter) and plant type as the second factor (2 levels: *Nuphar* and *Polygonum*) (SAS Institute 1996). Interactions were further dissected with Fisher's LSD tests.

To determine the seasonal differences in average shrimp size, mean biomass per individual was calculated for each sample, and a 2-way ANOVA tested the effect of season and plant type on average shrimp size (SAS Institute 1996). In this analysis, the mean individual shrimp size was calculated only from samples containing at least one individual. Zero values were not included, and values were left untransformed.

In order to evaluate the relative importance of the two keystone species in the two different macrophyte habitats of the Kissimmee River riparian marsh and test the SFWMD's conceptual model (Figure 5), a two-way ANOVA was conducted with species (2 levels: *P. paludosus* and *H. azteca*) and plant (2 levels: *Nuphar* and *Polygonum*) as the treatment factors. In order to take into account the extreme differences in these two species' sizes, mean biomass values per sample were used in the analysis.

For all tests performed, effects were considered significant when $p<0.05$. Although analyses were done on log-transformed values, figures display the more biologically significant untransformed values.

DIEL MIGRATION

Diel migration was examined by placing Breder traps at the margins of both *Polygonum* and *Nuphar* beds. Traps were placed in such a way as to capture grass shrimp as they move between the river channel and the floodplain and vertically within the water column (Figure 8). Traps were emptied just after sunrise and just before sunset to determine when shrimp were most likely to move between the floodplain and channel. The traps were set up in such a way as to preclude larger fish from gaining entry to

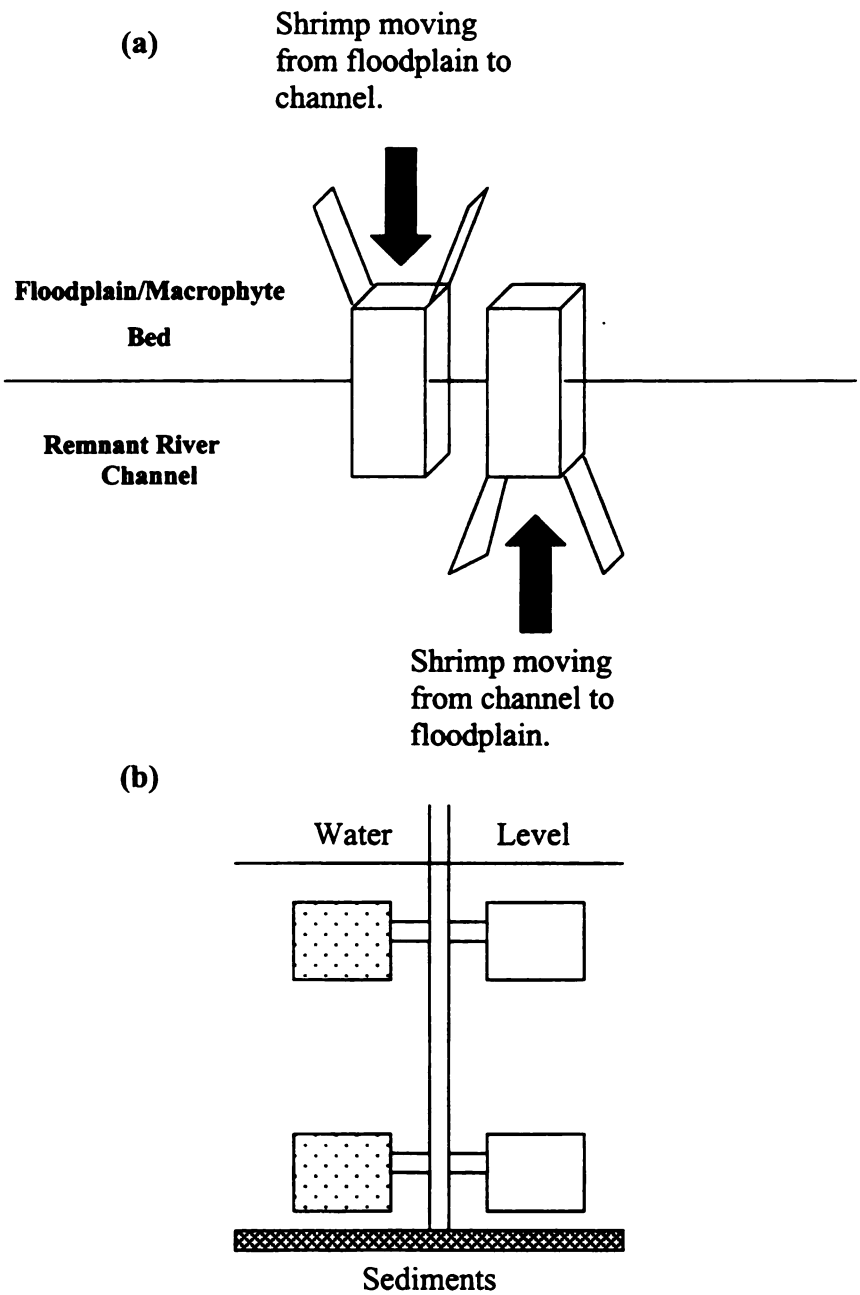

Figure 8. Diagram showing Breder trap placement in the Kissimmee River riparian littoral fringe macrophyte habitats. (a) Top view; (b) Side view (Shaded to show traps opening in opposite directions.)

minimize predation on captured shrimp. Previous studies show that Breder traps are an efficient means of capturing small fishes, and that the variety of invertebrates caught in these traps was equivalent to that of the fishes (Breder 1960).

Data were pooled according to whether they came from day or night runs, and mean numbers of grass shrimp caught in top versus bottom traps and traps opening toward the floodplain versus traps opening toward the channel were calculated. Differences in both vertical and horizontal grass shrimp movement were inferred from a Kruskal-Wallis non-parametric analysis of variance (SAS Institute 1996).

Growth Studies

To determine grass shrimp growth on different food types, I started with 180 shrimp of similar size. A subsample of 30 shrimp were dried and weighed to get an estimate of the initial dry weight. The remainder of the shrimp were used in the food treatments.

I examined 3 different food types commonly available to *P. paludosus* in the dominant macrophyte communities in the lower Pool B remnant channel:

1) *Nuphar* stems coated with dense periphyton
2) Conditioned *Polygonum* leaves
3) Fine detritus <1mm in diameter

The food was placed in Tupperware® growth containers (30 x 16 x 9 cm) (2 replications/food treatment). These containers were fitted with 500µm mesh panels on all sides and in the removable lid to allow circulation of stream water. Twenty-five shrimp were added to each container before it was placed in the remnant river channel adjacent to Riverwoods Field Laboratory near Lorida, FL. Growth containers remained in the channel for approximately 150 degree days (6 days at 25°C). After this period, shrimp were dried at 50°C for 24 hrs and then weighed to obtain gross dry weight to the nearest mg. The mean initial dry weight was then subtracted from each individual gross dry weight to obtain a measure of net dry weight for each grass shrimp that survived the experiment. Statistical analysis was conducted on the values for net dry weight.

The above experimental design is appropriate for a one-way ANOVA with subsampling providing that at least some shrimp survive in each container. However, in one *Nuphar* replication and one fine detritus replication, all shrimp died during the experimental period. Because of this, only one replication of *Nuphar* (n=6), and one replication of Fines (n=15), in addition to the two *Polygonum* reps (n=19; n=21) could be used in the analysis. The lack of independence of shrimp within each growth container prevents a legitimate ANOVA using individual shrimp as true replications because of the possibility of competition or cannibalism between shrimp living in the same container. The only choice, then, is to proceed with the original model and run the ANOVA with an error term based solely on the variation in the two *Polygonum* replicates.

Results and Discussion

Distribution and Abundance

Numbers of Grass Shrimp

A significantly higher proportion of grass shrimp were found in *Polygonum* beds as compared to *Nuphar* beds (Tables 1 and 2). When all sampling periods were combined and log values were analyzed, the mean number of *P. paludosus* per sample in the *Polygonum* beds was significantly higher (df=1; F=18.47; p<0.0001) than the number found in *Nuphar* beds (Table 1), with an average of 47.1 grass shrimp captured in *Polygonum* samples and only 5.0 shrimp captured in *Nuphar* samples (Table 2). There also appeared to be a seasonal effect on grass shrimp abundance. On average, 49.8 grass shrimp were caught in each summer sample and only 2.2 grass shrimp were caught in each winter sample (df=1; F=42.25; p<0.0001) (Table 2; Figure 9a). There were also significant season by plant interactions (df=1; F=5.16; p=0.0247) (Table 1). Results of Fisher's LSD tests (Table 3) indicated that the mean number of shrimp per sample was significantly higher in *Polygonum* beds than in *Nuphar* beds in the summer. However, there was no significant difference between *Nuphar* and *Polygonum* samples in the winter when numbers of grass shrimp per sample were low from both habitats (Table 3; Figure 9a).

Biomass of Grass Shrimp

When looking at biomass, the results were similar to those based on numerical data (Table 4; Figure 9b). *Polygonum* beds supported much more grass shrimp biomass on average than *Nuphar* beds, with an average of 298.5 mg per *Polygonum* sample and

Table 1. ANOVA table for distribution data. Dependant variable: Log(# *P. paludosus*+1).

Source	Df	SS	MS	F Value	Pr>F
Season	1	15.5454	15.5454	42.25	0.0001
Plant	1	6.7974	6.7974	18.47	0.0001
Season*Plant	1	1.8979	1.8979	5.16	0.0247
Error	140	51.5095	0.3679		
Total	143	75.7502			

Table 2. Number of grass shrimp per sample calculated by season and plant type. Log-transformed values were used in the statistical analysis.

Marginal Mean	Mean # Grass Shrimp/Sample (SE)	Log(Mean+1) (SE)
Summer	49.8 (10.4)	0.97 (0.10)
Winter	2.2 (0.5)	0.32 (0.04)
Nuphar	5.0 (1.2)	0.43 (0.06)
Polygonum	47.1 (10.5)	0.88 (0.10)

Table 3. Results from Fisher's LSD tests on season*plant combinations when considering average number of shrimp per sample. Tests were done on log-transformed values. Comparisons were not done between seasons.

Season*Plant Combination	Mean # Grass Shrimp/Sample (SE)	Log(Mean+1) (SE)	LSD
Summer**Nuphar*	8.1 (2.2)	0.65 (0.09)	B
Summer**Polygonum*	91.6 (18.3)	1.31 (0.16)	A
Winter**Nuphar*	1.9 (0.8)	0.21 (0.06)	A
Winter**Polygonum*	2.6 (0.5)	0.42 (0.06)	A

Table 4. ANOVA table for distribution data. Dependant variable: Log(*P. paludosus* biomass+1).

Source	Df	SS	MS	F Value	Pr>F
Season	1	24.5759	24.5759	25.50	0.0001
Plant	1	12.2978	12.2978	12.76	0.0005
Season*Plant	1	0.5271	0.5271	0.55	0.4608
Error	140	134.9361	0.9638		
Total	143	172.3368			

Table 5. Mean grass shrimp biomass (mg) per sample calculated by season and plant type. Log-transformed values were used in the statistical analysis.

Marginal Mean	Mean Biomass/Sample (SE) (mg)	Log(Mean+1) (SE)
Summer	313.6 (64.3)	1.58 (0.13)
Winter	42.1 (11.4)	0.75 (0.12)
Nuphar	57.2 (13.8)	0.88 (0.11)
Polygonum	298.5 (64.7)	1.46 (0.14)

Table 6. Results from Fisher's LSD tests on season*plant combinations when considering average shrimp biomass per sample. Tests were done on log-transformed values. Comparisons were not done between seasons.

Season*Plant Combination	Mean Biomass/Sample (SE) (mg)	Log(Mean+1) (SE)	LSD
Summer**Nuphar*	75.1 (19.3)	1.22 (0.15)	B
Summer**Polygonum*	552.1 (114.8)	1.93 (0.20)	A
Winter**Nuphar*	39.3 (19.5)	0.52 (0.15)	B
Winter**Polygonum*	44.9 (12.0)	0.98 (0.15)	A

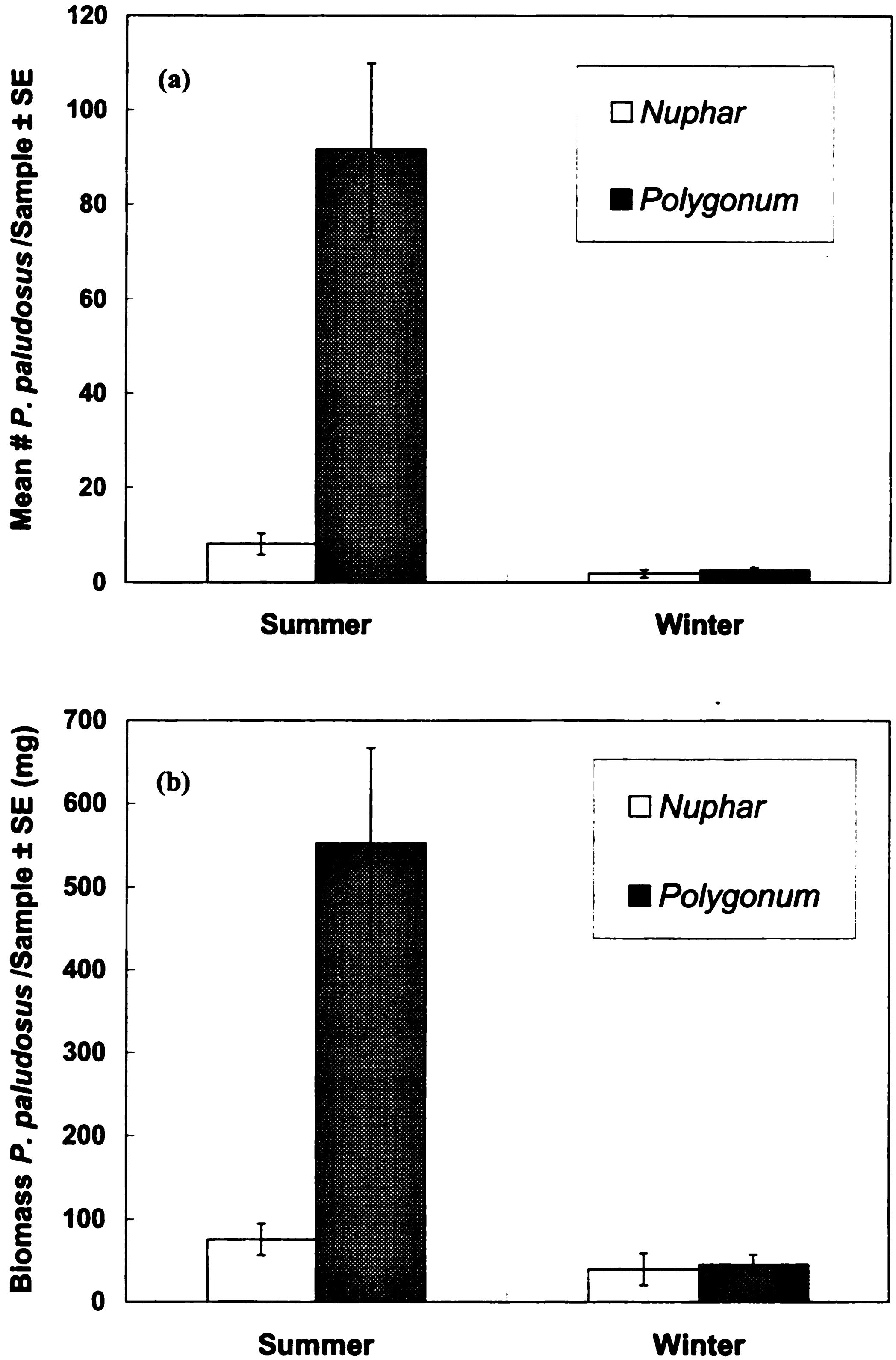

Figure 9. Mean number (a) and mean biomass (b) (±SE) of *P. paludosus* in the dominant macrophyte habitats of the Kissimmee River riparian marsh.

only 57.2 mg per *Nuphar* sample (df=1; F=12.76; p<0.0001) (Table 4). There was also a significant seasonal effect, with mean biomass per sample equal to 313.6 mg in the summer and only 42.1 mg in the winter (df=1; F=25.50; p=0.0005) (Table 5; Figure 9b). However, there was no significant season by plant interaction when considering mean biomass instead of numbers (df=1; F=0.55; p=0.4608) (Table 4). Results from Fisher's LSD test confirmed the ANOVA results and indicated that the plant effect was consistent throughout the year when considering log-transformed values for biomass instead of numbers (Table 6; Figure 9b).

Seasonal Differences in Average Grass Shrimp Size

There was no significant difference in size of shrimp between *Polygonum* and *Nuphar* plant communities (df=1; F=0.24; p=0.6241) (Table 7). However, shrimp sampled in the winter were significantly larger than those sampled in the summer (df=1; F=16.16; p<0.0001) (Table 7). The average grass shrimp captured in the summer samples weighted 7.97 mg, while the average shrimp captured in winter weighed 18.63 mg (Table 8). Higher numbers of grass shrimp were found in the summer samples as opposed to the winter samples (Table 8). These differences in average shrimp size help explain the disagreement between the tests looking at numbers and the tests looking at biomass. The increase in average shrimp biomass in the winter samples makes up for the lower numbers of shrimp per sample and results in an insignificant interaction term when considering log-transformed values for biomass instead of numbers.

Since summer samples contained a relatively large number of small shrimp while winter samples contained a smaller number of large shrimp, a reasonable inference is that

Table 7. ANOVA table for the test comparing average shrimp biomass across seasons and plant types. Dependent variable: Mean Individual *P. paludosus* biomass sample^{-1}. Data points with biomass=0 were removed for this analysis and biomass values were left untransformed.

Source	Df	SS	MS	F Value	Pr>F
Season	1	2484.54	2484.54	16.16	0.0001
Plant	1	37.20	37.20	0.24	0.6241
Error	90	13840.80	153.79		
Total	92	16326.08			

Table 8. Seasonal effect on grass shrimp density (number per sample) and average biomass (mg).

Marginal Mean	Mean # Shrimp per Sample	Mean Biomass per Individual (mg)
Summer	49.8	7.97
Winter	2.2	18.63

P. paludosus reproduces in early Spring. Additional sampling in early March confirmed that extremely high densities of larval shrimp (150-500 shrimp/sample) were being recruited into the populations. Summer samples contained shrimp in their early adult life, and winter samples appeared to be composed of this same cohort near the end of their life cycle.

Comparison of P. paludosus *and* H. azteca

P. paludosus made up a much higher proportion of overall biomass than *H. azteca* in the two dominant macrophyte communities of the Kissimmee River riparian marsh ($p=0.0001$) (Table 9; Figure 10). Even when biomass values for both species were combined, *Polygonum* still supported more biomass than *Nuphar* ($p=0.0001$) (Table 9; Figure 10). Comparing values for mean biomass of grass shrimp and amphipods separately for each macrophyte habitat, *P. paludosus* had significantly higher biomass per sample in both habitats than *H. azteca* did (*Nuphar*: $p=0.0005$; *Polygonum*: $p=0.0302$) (Figure10).

This is contrary to the SFWMD's conceptual model, which predicts that *H. azteca* is more abundant in *Nuphar* beds than in *Polygonum* because it is a scraper and can more efficiently harvest periphyton growing on *Nuphar* stems (Figure 5). These results emphasize the importance of *P. paludosus* in this system. Considering its relative abundance and large size compared to the other common macroinvertebrates in the Kissimmee River littoral fringe habitat, it is apparent that this species overwhelmingly dominates the macroinvertebrate fauna in the Pool B remnant channel of the Kissimmee

Table 9. ANOVA table comparing *P. paludosus* and *H. azteca* log transformed biomass values. Dependent variable: Log(Mass+1).

Source	Df	SS	MS	F Value	Pr>F
Plant	1	33.02	33.02	47.95	0.0001
Species	1	11.17	11.17	16.23	0.0001
Plant*Species	1	0.62	0.62	0.90	0.3439
Error	284	195.57	0.69		
Total	287	240.39			

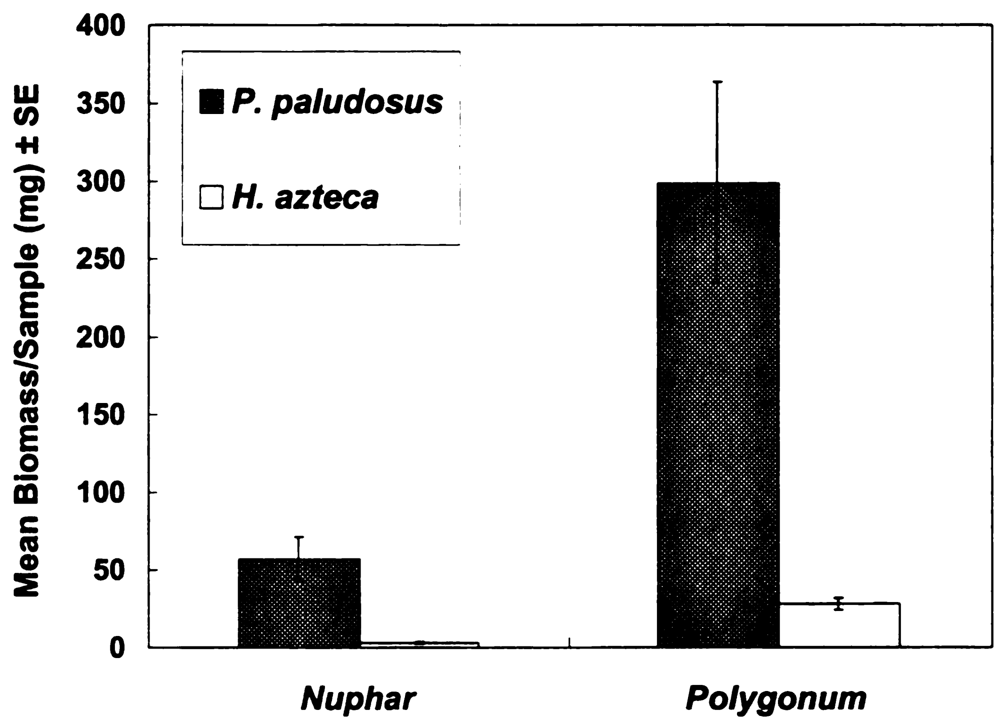

Figure 10. Comparison of mean *P. paludosus* vs *H. azteca* biomass per sample in the two dominant littoral fringe macrophyte habitats of the Kissimmee River riparian marsh.

River, and so must be a very important food source for higher trophic levels such as large fish, waterfowl, and wading birds.

Diel Migration

Results of the migration trials suggested that there were no significant diel horizontal movement patterns into or out of the floodplain of *P. paludosus* in the Kissimmee River riparian marsh (Table 10; Figure 11). However, in one case, there was a significant difference in grass shrimp captured in top versus bottom traps (Table 11; Figure 12).

Horizontal Movement

In *Polygonum* beds, shrimp capture rates were low, suggesting little shrimp movement overall. An average of 0.6 shrimp were captured moving from the channel into the floodplain, and the same number was captured moving out of the floodplain into the channel during the day. At night, these numbers differed only slightly, with an average of 0.9 shrimp moving from the channel into the floodplain and 1.0 shrimp moving in the opposite direction (Figure 11). In *Nuphar* beds, an average of 1.0 shrimp per trap was caught moving from the channel to the floodplain, while 3.0 shrimp on average were captured moving into channel during the day. However, these numbers are not significantly different ($p=0.1147$) (Table 10). At night, differences in horizontal movement were similar to the daytime trials and were not significant ($p=0.1941$) (Table 10). An average of 1.7 shrimp per trap were captured moving from the channel to the

Table 10. Results from the Kruskal-Wallis ANOVA testing differences in grass shrimp movement in and out of the floodplain during the day and at night.

Tests for Horizontal Movement		P Value
Day	*Nuphar*	0.1147
	Polygonum	0.1683
Night	*Nuphar*	0.1941
	Polygonum	0.5722

Table 11. Results form the Kruskal-Wallis ANOVA testing differences in grass shrimp vertical movement during the day and at night.

Tests for Vertical Movement		P Value
Day	*Nuphar*	0.0343
	Polygonum	0.5343
Night	*Nuphar*	0.1239
	Polygonum	0.1219

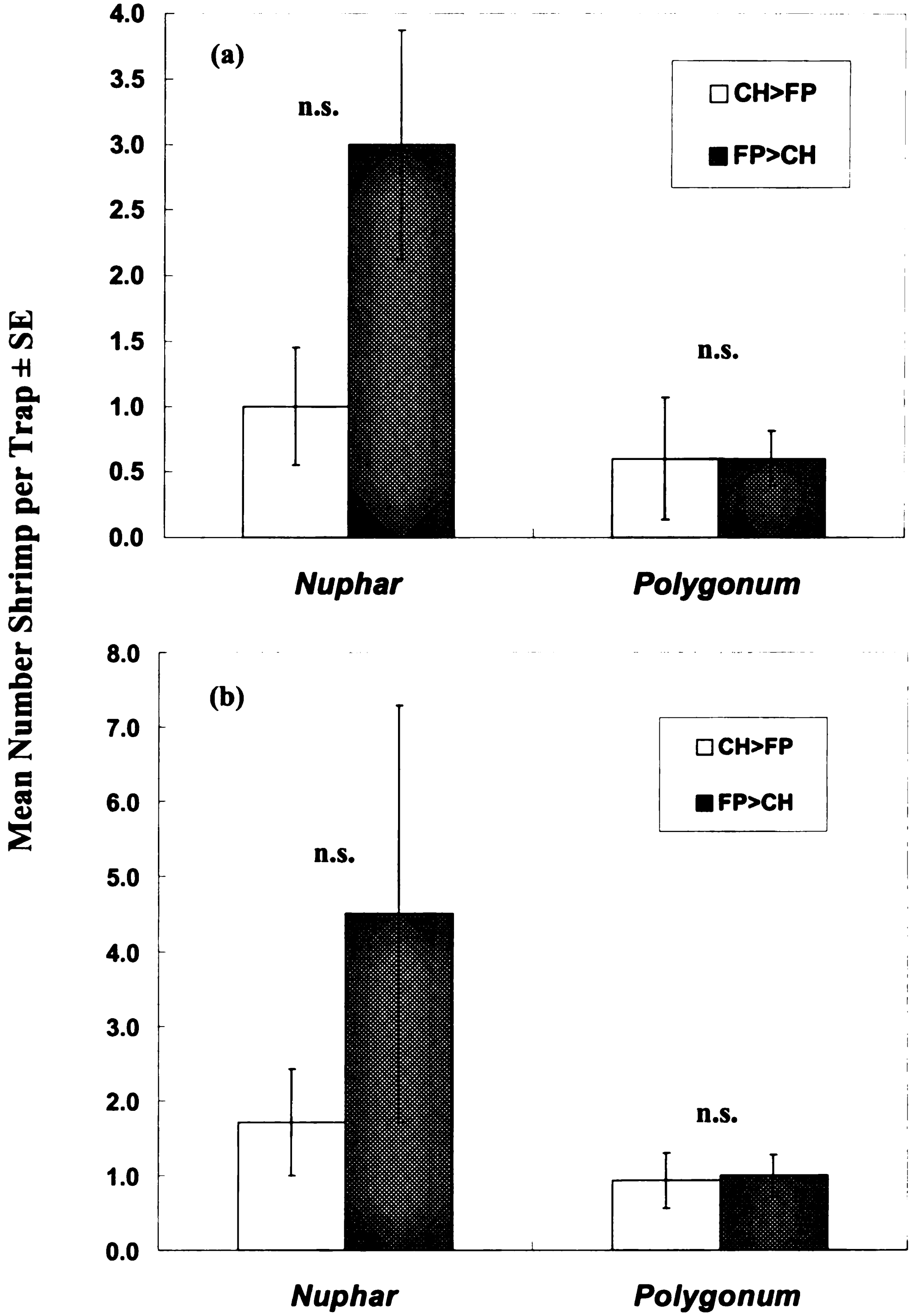

Figure 11. Mean number ± SE of *P. paludosus* captured moving from the channel to the floodplain (CH>FP) and from the floodplain to the channel (FP>CH) during the day (a) and at night (b).

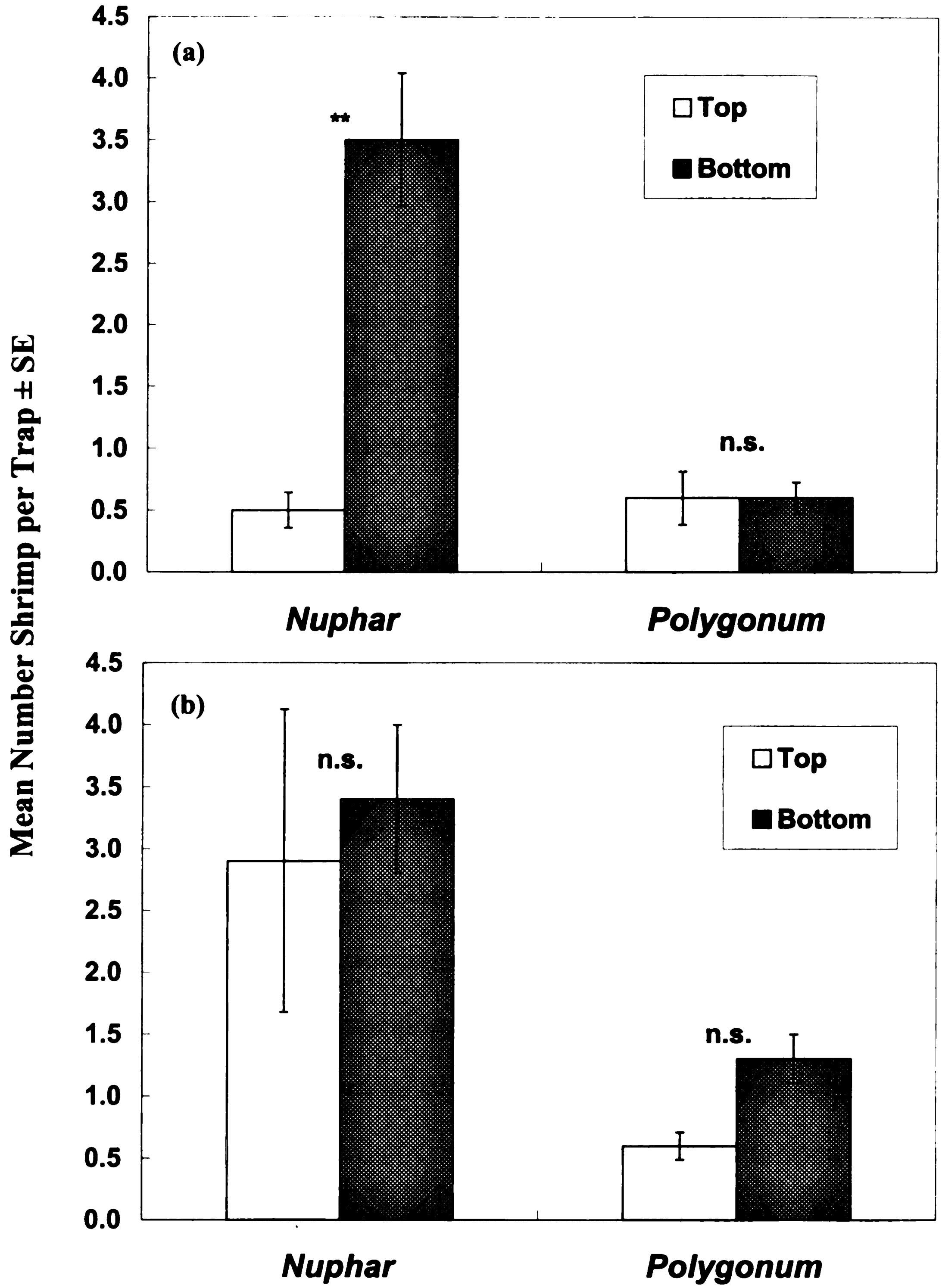

Figure 12. Mean number ± SE of *P. paludosus* captured in top and bottom Breder traps (a) during the day and (b) at night. Significant differences at $p<0.05$ denoted by double asterisks.

floodplain, while 4.5 shrimp per trap were captured on average moving in the opposite direction.

This section of the Kissimmee River, although partially restored, was still subject to stage management regimes, and this would confound any inherent diel horizontal pattern. When water is being drawn down, shrimp will be more likely to move out of the floodplain. Conversely, when water levels are increasing, shrimp will have a greater opportunity to use the riparian marsh habitat. These experiments should be repeated after the removal of the dam and lock structures when stage will be allowed to fluctuate more naturally.

Vertical Movement

An average of 0.6 shrimp were caught in both top and bottom traps in *Polygonum* beds during the day. At night, slightly more shrimp were captured in bottom versus top traps in *Polygonum*, with an average of 1.3 shrimp per trap caught moving along the bottom, and only 0.6 shrimp per trap were caught in the top traps (Figure 12). The results of the Kruskal-Wallis test indicated no significant difference in these numbers ($p=0.2246$) (Table 11). In *Nuphar* beds, an interesting pattern emerges. The difference in mean number of shrimp caught in top versus bottom traps is significant during the day ($p=0.0162$) (Table 11). On average, 3.5 shrimp were captured moving along the bottom, while only 0.5 were captured in top traps (Figure 12). At night, however, 3.4 shrimp were caught in bottom traps and 2.9 were caught in top traps, which were not statistically significant ($p=0.1299$) (Table 11; Figure 12).

The difference in numbers of shrimp captured in top vs. bottom traps in *Nuphar* beds during the day could reflect the lack of habitat complexity inherent in this habitat. Shrimp may be sticking close to the bottom during the day as a means of avoiding predation from visual predators such as wading birds and waterfowl. This is not necessary in *Polygonum* beds since they offer a much denser, more complex habitat.

The difference in diurnal versus nocturnal vertical distribution patterns suggests that generally, more shrimp were captured during the night than during the day (Figures 11 and 12). Other grass shrimp species show similar behavior. Sogard and Able (1994) observed higher nocturnal movement in *P. vulgaris*, and attribute this to diel variability to predation risk. Grass shrimp are relatively large, and it would be to their advantage to restrict daytime movement in order to avoid being spotted by visual predators. However, at night, this becomes less of an issue. Grass shrimp are transparent, and any movement associated with foraging would be much less likely to result in predator attacks at night.

Growth Studies

Results from the growth studies show at least some growth in all food treatments (Figure 13). However, no significant net growth occurred in the fine detritus treatment ($p=0.3072$), with a mean increase of only 1.99 ± 1.90 mg per shrimp after 150 degree days. *Polygonum* leaves resulted in significant net growth after 150 degree days ($p=0.0012$), with a mean increase of 4.03 ± 1.18 mg per shrimp. Periphyton on *Nuphar* stems resulted in the highest net growth overall, with a mean increase of 6.69 ± 3.04 mg per shrimp. However, there was no significant difference in net growth between shrimp

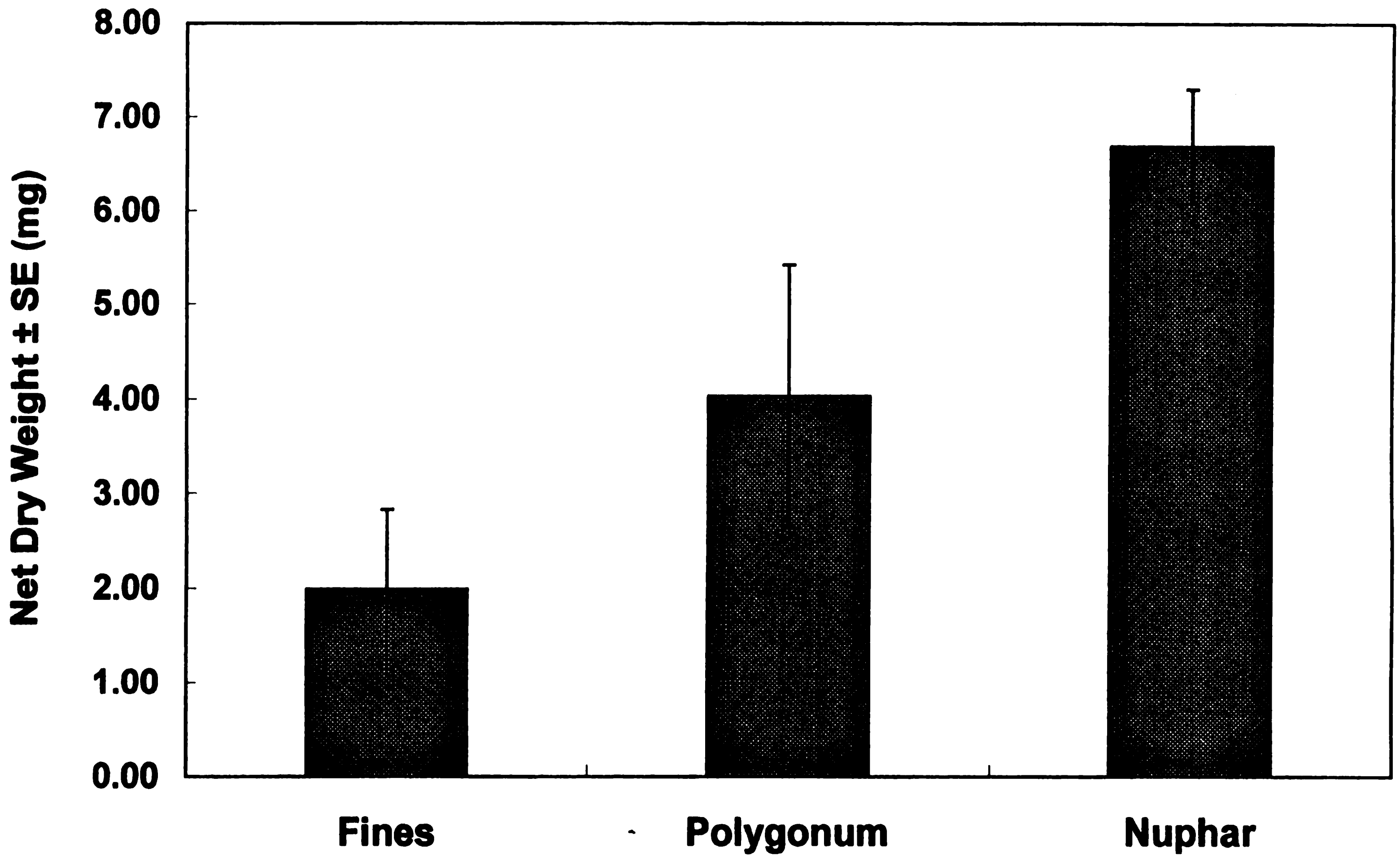

Figure 13. Net dry weight of *P. paludosus* in each of the three food treatments. Data derived by subtracting the mean initial weight from each dried shrimp that survived the growth experiment.

grown on *Polygonum* leaves and shrimp grown on periphyton from *Nuphar* stems (Figure 13).

From the data on distribution and abundance, it was shown that *P. paludosus* overwhelmingly preferred *Polygonum* beds, and the available food in these beds is senescent *Polygonum* leaves or fine detritus that collects on the bottom. There is little or no periphyton growth in these habitats due to *Polygonum*'s high stem density and low subsurface light. *P. paludosus* is a benthic species that very seldomly ventures into the water column. The structure of the two macrophyte beds is such that the most available food for a benthic species living in *Nuphar* beds is fine detritus. Only by moving up into the water column would periphyton become available to such a species. In *Polygonum* beds, a benthic species would have plenty of fine detritus in addition to the steady supply of decaying *Polygonum* leaves. Despite the fact that grass shrimp are physically able to harvest periphyton from *Nuphar* stems, their preference for *Polygonum* beds could be a response to the food type available given the fact that they are primarily benthic and spend most of their time foraging along the bottom.

General Discussion

P. paludosus was much more abundant in *Polygonum* beds according to data based on both numbers and biomass. Given these data, the question arises, "Why do grass shrimp prefer *Polygonum* habitat over *Nuphar*?" *P. paludosus* showed significant growth on both *Polygonum* leaves and periphyton associated with *Nuphar* stems (Figure 13). Their preference for *Polygonum* habitat, as mentioned above, could be a result of their benthic nature and the food type available to benthic species in each macrophyte community, but overall, food availability is probably not an important factor in grass shrimp habitat selection in the Pool B remnant channel of the Kissimmee River.

In the summer, dissolved oxygen sometimes dropped to near-zero levels in *Polygonum* beds, while the drop was not nearly as severe in *Nuphar* beds (Figure 7). Thus, dissolved oxygen levels are also probably not significant in driving grass shrimp habitat selection. Indeed, shrimp were more abundant in habitat with lower DO than is usually available in *Nuphar* (Figure 7). Thus, there must be some sort of trade-off for *P. paludosus* in choosing *Polygonum* habitat over *Nuphar*.

Trap data suggested that *P. paludosus* moved considerably less in *Polygonum* beds than they did in *Nuphar* beds with no well-defined horizontal or vertical diel migration pattern (Tables 10, 11; Figures 11, 12). In *Nuphar* beds, while overall density was less, movement seemed to be more pronounced, with a significant diel vertical distributional pattern (Figure 12). Shrimp appeared to remain close to the bottom during the day, while they move around in the water column more at night. Why do we see a vertical migration pattern in *Nuphar*, but not in *Polygonum*?

One explanation is that the higher habitat complexity inherent in *Polygonum* as opposed to *Nuphar* communities provides better refuge areas for *P. paludosus*. Several studies looking at the relationship between habitat complexity and macroinvertebrate habitat choice confirm this hypothesis (Crowder and Cooper 1982; Stoner and Lewis 1985). Vulnerability to predators is often inversely related to habitat complexity (Coen et al. 1981), and this is well documented for the decapoda. Crayfish density in lakes increased with the degree of macrophyte cover, and this relationship was modified by decreased vulnerability (i.e., increased size) to predators (Stein and Magnuson 1976).

The distribution of some marine species of *Palaemonetes* has been positively correlated with increased habitat complexity (Khan et al. 1997), and habitat complexity also has been shown to reduce predatory efficiency by reducing prey capture rates (Crowder and Cooper 1982). Khan et al. (1997) suggested that characteristics of the macrophytes (physical complexity) and the shrimp (residual predator conditioning) were important factors in observed grass shrimp distributions. It seems reasonable that *P. paludosus* capitalizes on this increased protection from predators provided by the complex habitat of *Polygonum* communities.

Another possible explanation for this is that the relatively low DO in *Polygonum* confers an advantage to grass shrimp by reducing the number of fish predators present in these beds, thereby increasing its survival. Furse et al. (1996) found that changes in DO, particularly declines below stressful levels, were the primary influence in largemouth bass habitat use and overall movement patterns. They found that largemouth bass use both *Nuphar* and *Polygonum* macrophyte communities almost equally overall, but were more likely to be found in areas where DO>2 mg/L throughout the year. Whitmore et al. (1960) showed that largemouth bass showed strong avoidance of habitats with DO levels <1.5 mg/L, while Petit (1973) reported that largemouth bass stopped feeding at DO of 2 mg/L, and at 1 mg/L, all died within 11 hours. Each of these studies found increasing avoidance in vegetation as temperatures increased, suggesting that the high temperatures in the Kissimmee River Pool B remnant channel would contribute even more to fish stress related to low DO. As metabolic needs increase due to high temperatures, their tolerance to low DO would decrease even more. The fact that DO is often lower in *Polygonum* beds and sometimes falls below 2.5 mg/L, due to the low subsurface light and heterotrophic nature of these communities (Figure 7), suggests that largemouth bass are more likely to choose *Nuphar* beds over *Polygonum*. Therefore, grass shrimp inhabiting *Polygonum* beds would be less likely to have contact with their fish predators than those living in *Nuphar*.

Whether grass shrimp inherently prefer denser, more complex habitats such as *Polygonum* because they are provided with more refuge areas, or the uneven distribution of grass shrimp in the Pool B remnant river channel of the Kissimmee River is a result of decreased predator efficiency in *Polygonum* beds, it seems reasonable that the innate complexity of *Polygonum* communities could help explain why grass shrimp are more abundant in these areas.

CONCLUSIONS

A goal of the Kissimmee River restoration project is to increase littoral fringe macrophyte communities such as *Nuphar* and *Polygonum*, which will increase the overall abundance of *P. paludosus*. Understanding the distribution of grass shrimp with respect to plant type enables predictions to be made regarding biological interactions within the Kissimmee River-floodplain ecosystem and how they will respond to restoration efforts. Since *P. paludosus* is a keystone invertebrate species in this system (Merritt et al. 1996) due to its relatively large size and abundance, knowledge of its distribution and abundance will help locate and quantify the potential food base for visual feeding bird predators and large game fish.

This information will be useful when evaluating the success of Kissimmee River Restoration Project. The expected increase in wetland plant communities, including *Polygonum* and *Nuphar*, combined with an overall increase in dissolved oxygen, will have significant effects on biological communities. By quantifying the distribution and abundance of *P. paludosus,* and using information obtained from the growth studies, it will be possible to calculate estimates of *P. paludosus* production in the Kissimmee River riparian marsh.

LITERATURE CITED

Beck, J.T. and B.C. Cowell. 1976. Life history and ecology of the freshwater caridean shrimp, *Palaemonetes paludosus* (Gibbes). American Midland Naturalist 96: 52-65.

Breder, C.M. 1960. Design for a fry trap. Zoologica 45: 155-160.

Broad, A.C. 1957. The relationship between diet and larval development of *Palaemonetes*. Biological Bulletin (Woods Hole, MA) 112: 162-170.

Coen, L.D., K.J. Heck, and L.G. Abele. 1981. Experiments on competition and predation among shrimps of seagrass meadows. Ecology 62: 1484-1493.

Cross, R. E., R.T. Kneib, and A.E. Stiven.1996 Size-dependent interactions in fish and shrimp. Twenty Fourth Annual Benthic Ecology Meeting, Columbia, SC. p. 94.

Crowder, L.B. and W.E. Cooper. 1982. Habitat structural complexity and the interaction between bluegills and their prey. Ecology 63: 1802-1813.

Cummins, K.W. and M.J. Klug. 1979. Feeding ecology of stream invertebrates. Ann. Rev. Ecol. Syst. 10: 147-172.

Dobkin, S. 1963. The larval development of *Palaemonetes paludosus* (Gibbes 1850) (Decapoda:Palaemonidae) reared in the laboratory. Crustaceana 6: 2-61.

Eggleston, D.B., L.L. Etherington, and W.E. Elis. 1998. Organism response to habitat patchiness: species and habitat-dependent recruitment of decapod crustaceans. Journal of Experimental Marine Biology and Ecology 223: 111-132.

Furse, J.B., L.J. Davis, and L.A. Bull. 1996. Habitat use and movements of largemouth bass associated with changes in dissolved oxygen and hydrology in Kissimmee River, Florida. Proceeding of the Annual Conference of the Southeastern Association of Fish and Wildlife Agencies 12-25.

Gregg, C. and J. Fleeger. 1995. Why are they called grass shrimp? Experimental tests of the effects *Palaemonetes pugio* has on benthic and phytal dwelling communities. Twenty-third Benthic Ecology Meeting, New Brunswick, NJ.

Gregg, C. and J. Fleeger.1996. Effects of the grass shrimp, *Palaemonetes pugio*, on sediment and stem-dwelling saltmarsh fauna. Twenty-fourth Annual Benthic Ecolgoy Meeting, Columbia, SC. p. 43.

Harris, S.C., T.H. Martin, and K.W. Cummins. 1995. A model for aquatic invertebrate response to Kissimmee River restoration. Restoration Ecology 3: 181-194.

Junk, W. J., Bayley, P. B., and Sparks, R. E.1989. The flood pulse concept in river-floodplain systems. Proceedings of the International Large River Symposium, Ottawa, Canada. Pp. 11-27.

Khan, R.N., H.C. Merchant, and R.E. Knowlton. 1997. Effects of macrophytic cover on the distribution of grass shrimps, *Palaemonetes pugio* and *P. vulgaris*. Invertebrate Biology 116: 243-247.

Kneib, R.T. 1985. Predation and disturbance by grass shrimp, *Palaemonetes pugio* Holthuis, in soft-substratum benthic invertebrate assemblages. Journal of Experimental Marine Biology and Ecology 93: 91-102.

Koebel, J.W. 1995. An Historical Perspective on the Kissimmee River Restoration Project. Restoration Ecology 3: 149-159.

Kushlan, J.A. and M.S. Kushlan. 1980. Population Fluctuations of the Prawn, *Palaemonetes paludosus*, in the Everglades. American Midland Naturalist 103: 401-403.

Meehean, O.L. 1936. Notes on the freshwater shrimp *Palaemonetes paludosa* (Gibbes). Trans. Am. Microsc. Soc. 55: 433-441.

Merritt, R.W., M.J. Higgins, K.W. Cummins, and B. Vandeneeden, 1999. Seasonal Differences in Invertebrate Functional Feeding Group Relationships of the Kissimmee River-floodplain Ecosystem, Florida. In: D. Batzer, R.B. Rader, and S.A. Wissinger (eds), Invertebrates in Freshwater Wetlands of North America, John Wiley & Sons, Inc., pp. 55-79.

Merritt, R.W., J.R. Wallace, M.J. Higgins, M.K. Alexander, M.B. Berg, W.T. Morgan, K.W. Cummins, and B. Vandeneeden. 1996. Procedures for the functional analysis of invertebrate communities of the Kissimmee River-floodplain ecosystem. Florida Scientist 59: 216-274.

Miller, D.C., S.L. Poucher, L. Coiro, S. Rego, and W. Munns. 1995. Effects of hypoxia on growth and survival of crustaceans and fishes of Long Island Sound. Proceedings of the Long Island Brook, NY (U. S. EPA) p. 92.

Payne, A.J., 1986. The ecology of tropical lakes and rivers, John Wiley and Sons, New York.

Petit, G.D. 1973. Effects of dissolved oxygen on survival and behavior of selected fishes of western Lake Erie. Ohio Biological Survey Bulletin 4: 1-76.

Posey, M.H. and A.H. Hines. 1991. Complex predator-prey interactions within an estuarine benthic community. Ecology 72: 2155-2169.

Pringle, C.M., G.A. Blake, A.P. Covich, K.M. Buzby, and A. Finley. 1993. Effects of omnivorous shrimp in a montane tropical stream: sediment removal, disturbance of sessile invertebrates and enhancement of understory algal biomass. Oecologia 93: 1-11.

Samuels, A.J. and C.F. Mason. 1998. Shrimps and eutrophication in the waterbodies of a coastal grazing marsh. Hydrobiologia 377: 195-199.

SAS Institute. 1996. SAS user's guide: statistics, version 6.12. SAS Institute, Cary, North Carolina, USA.

Shen, H.W., G. Tabios, and J.A. Harder. 1994. Kissimmee River Restoration Study. Journal of Water Resources Planning and Management 120: 330-349.

Sogard, S.M. and K.W. Able. 1994. Diel variation in immigration of fishes and decapod crustaceans to artificial seagrass habitat. Estuaries 17: 622-630.

Stein, R.A. and J.J. Magnuson, 1976. Behavioral response of crayfish to a fish predator. Ecology 57: 751-761.

Stoner, A.W. and F.I. Lewis. 1985. The influence of quantitative and qualitative aspects of habitat complexity in tropical sea-grass meadows. Journal of Experimental Marine Biology and Ecology 94: 19-40.

Strenth, N.E. 1976. A Review of the Systematics and Zoogeography of the Freshwater Species of *Palaemonetes* Heller of North America (Crustacea: Decapoda). Smithsonian Contributions to Zoology 228: 1-27.

Toland, B.R. 1990. Effects of the Kissimmee River Pool B Restoration Demonstration Project on Ciconiiformes and Aseriformes. Proceedings of the Kissimmee River Restoration Symposium pp. 83-91.

Toth, L.A. 1990. Impacts of channelization on the Kissimmee River ecosystem. Proceedings of the Kissimmee River Restoration Symposium pp. 47-56.

Toth, L.A. 1993. The ecolgical basis for the Kissimmee River restoration plan. Florida Scientist 56: 25-51.

Toth, L.A., D.A. Arrington, M.A. Brady, and D.A. Muszick. 1995. Conceptual evaluation of factors potentially affecting restoration of habitat structure within the channelized Kissimmee River ecosystem. Restoration Ecology 3: 160-180.

Trexler, J.C. 1995. Restoration of the Kissimmee River: A conceptual model of past and present fish communities and its consequences for evaluating restoration success. Restoration Ecology 3: 195-210.

Vernberg, F.J. and S. Piyatiratitivorakul. 1998. Effects of salinity and temperature on the bioenergetics of adult stages of the grass shrimp (Palaemonetes pugio Holthuis) from the North Inlet Estuary, South Carolina. Estuaries 21: 176-193.

Weller, M.W. 1995. Use of two waterbird guilds as evaluation tools for the Kissimmee River restoration. Restoration Ecology 3: 211-224.

Welsh, B.L. 1975. The role of grass shrimp, *Palaemonetes pugio*, in a tidal marsh ecosystem. Ecology 56: 513-530.

Whitmore, C.M., C.E. Warren, and P. Doudoroff. 1960. Avoidance reactions of salmonid and centrarchid fishes to low oxygen concentrations. Transactions of the American Fisheries Society 106: 323-330.

Wullschleger, J.G., S.J. Miller, and L.J. Davis. 1990. an evaluation of the effects of the restoration demonstration project on Kissimmee River fishes. Proceedings of the Kissimmee River Restoration Symposium pp. 67-81.