NSU Florida
NOVA SOUTHEASTERN UNIVERSITY

Nova Southeastern University
NSUWorks

HCNSO Student Theses and Dissertations

HCNSO Student Work

8-1-2009

Segregation of Palaemonid Shrimp Along the Shark River Estuary: Implications for Trophic Function

Lauren C. McCarthy
Nova Southeastern University, mccarthyl@ecu.edu

Follow this and additional works at: https://nsuworks.nova.edu/occ_stuetd

Part of the Marine Biology Commons, and the Oceanography and Atmospheric Sciences and Meteorology Commons

Share Feedback About This Item

NOVA SOUTHEASTERN UNIVERSITY
OCEANOGRAPHIC CENTER

**SEGREGATION OF PALAEMONID SHRIMP ALONG THE SHARK RIVER
ESTUARY: IMPLICATIONS FOR TROPHIC FUNCTION**

By

Lauren C. McCarthy

Submitted to the Faculty of
Nova Southeastern University Oceanographic Center
in partial fulfillment of the requirements for
the degree of Master of Science with a specialty in:

Marine Biology

Nova Southeastern University

August 2009

Masters of Science:

Marine Biology

Thesis of
Lauren C. McCarthy

Submitted in Partial Fulfillment of the Requirements for the Degree of

Nova Southeastern University
Oceanographic Center

August 2009

Approved:

Thesis Committee

Major Professor :_____
Jennifer S. Rehage, Ph.D.

Committee Member :_____
James D. Thomas, Ph.D.

Committee Member :_____
William F. Loftus, Ph.D

Table of Contents

List of Figures

List of Tables

Acknowledgements

I would like to dedicate this work to my family, especially my parents Joe and JoAnne McCarthy. I am thankful for all their love and support along the way and without them I would not have had this opportunity. They have introduced me to nature and the outdoors through hiking, visiting museums and traveling across America.

I thank Dr. Jennifer Rehage for giving me the opportunity to work in such an amazing place as the Everglades. Her invaluable knowledge and enthusiasm for wildlife and nature have greatly inspired me. She has helped me become a better scientist to which I am grateful. Jenn and her husband Paul always opened their home after long field days and even provided a few boat rescues that I am especially appreciative of.

I thank Dr. James Thomas for all of his helpful office chats and his love for amphipods has shown me it is ok to be obsessed with invertebrates. He is the type of quirky professor I would someday like to become. He has also given me the chance to visit some of the best places on earth, including Belize and Australia. Those memories will be with me for a lifetime.

I thank Dr. William Loftus for all of his insightful knowledge of the Everglades. His sense of humor got you through the long field days. He tried to teach me the proper technique of reaching into a muddy cooler full of slippery fish and sometimes eels, but as much fun as that was I think I'll stick with the invertebrates. His stable-isotope knowledge was also of great help with this project.

I am forever indebted to those who helped me with my field work in the sometimes brutal but always loving Everglades. They survived swarms of mosquitoes and no-see-ums, scary thunderstorms in the middle of nowhere, boat breakdowns and

In Loving Memory of Mary E. Stoltzfus

A wonderful Aunt

I love and miss you!

Abstract

This study examined the abundance, distribution, and spatiotemporal variation of palaemonid shrimp species in relation to season and salinity in the Shark River Estuary, Everglades National Park (ENP), Florida, USA. Five palaemonid species occurred in the samples: *Palaemonetes paludosus*, *P. pugio, P. intermedius*, *Palaemon floridanus,* and *Leander paulensis*; *L. paulensis* was collected only during the wet season. Overall, shrimp catches in traps doubled in the dry season. Catches in the upper estuary were dominated by *P. paludosus*, particularly in the wet season, while catch per unit effort (CPUE) at the most downstream, highest salinity sites were dominated by *Palaemon floridanus*. At mid-estuary, several species co-occurred. To investigate spatiotemporal shifts in trophic position of the shrimp, stable-isotope analysis was used. $\delta^{15}N$ analyses revealed most species filled similar roles in the community, with the exception of *P. paludosus*, which shifted from enrichment in the dry season to depletion in the wet season. Palaemonid $\delta^{13}C$ values varied between sites and seasons, with shrimp in upstream sites being more depleted than downstream sites. These data suggest that changes in salinity regimes resulting from restoration may result in species replacement, with potential implications for trophic dynamics.

Key Words: *Shark River estuary*, *Palaemonid shrimp, Distribution*, *Salinity*, *Stable-Isotopes*

Introduction

Estuaries link freshwater upstream sources with downstream marine systems, and are dominated by variability in climate, hydrology, and geomorphology (DeAngelis 1994, Attrill & Rundle 2002). Spatial and temporal shifts in these processes affect estuary function at a variety of scales, contributing to the complexity of these ecosystems (Wolanski et al. 2009). Spatial variation may be caused by elevational changes, spatial distribution of freshwater flow and nutrient inputs, proximity to oceans, and drying fronts (DeAngelis 1994, Sutula et al. 2003). Temporal variation results from seasonal cycles of freshwater inputs and tidal cycles. Both spatial and temporal variation can strongly influence the distribution and abundance of organisms (Attrill & Power 2000, Kupschus & Tremain 2001, Akin et al. 2003, Sheaves & Johnston 2009).

Fish and invertebrate populations in estuaries often vary seasonally in response to hydrological variation (Staples et al. 1995, Barletta et al. 2006). Organisms can also utilize spatiotemporal shifts in hydrology and tides to aid in migrations, instream movements, and larval dispersal (Roberston & Blaber 1992, Vance et al. 1996, Barletta et al. 2003). Not all changes in estuarine environments are useful, however; fluctuating salinities that interact with other environmental gradients can produce harsh environments that organisms must withstand to survive (Ley & McIvor 2002, Childers et al. 2005, Green et al. 2006). Therefore, organisms adapted to large fluctuations in physical and chemical conditions can reap the benefits offered by estuaries, such as food resources, protective cover, and nursery grounds (Nagelkerken et al. 2000, Katherisan & Bingham 2001, Sheridan & Hays 2003).

The Everglades ecosystem is characterized by a marked seasonality in rainfall that affects salinity regimes in the coastal areas (Duever et al. 1994, McIvor et al. 1994, Davis et al. 2005). As much as 60% of the rainfall occurs in the wet season months (June-September) and only 25% in the dry season months (November-April) (Duever et al. 1994). This seasonality results in temporal and spatial gradients in salinity and other factors, with flora and fauna distributed along the gradients produced (McIvor et al. 1994, Ley et al. 1999). How species respond to this variation is poorly understood in the vast Everglades mangrove estuaries. Furthermore, little is known about how distributional changes in response to hydrological variation may affect trophic structure and function, especially at the level of small decapod crustaceans, such as palaemonid shrimp.

Palaemonid shrimp are abundant in temperate and tropical estuaries throughout the world where they are important detritivores, predators of other small invertebrates, and prey for many fishes and birds (Bauer 2004). Thus, they play important ecological roles as they pass energy to higher trophic levels (Beck & Cowell 1975, Welsh 1975, Anderson 1985, Gallin 2002). Species in the genus *Palaemonetes* dominate brackish to freshwater habitats, and are often collected among submerged marsh grasses or other aquatic vegetation, while *Palaemon* species are found in shallow marine habitats but can tolerate the brackish water typical of estuaries (Bauer 2004). Most of what is known about palaemonid shrimp in the Everglades comes from studies of *P. paludosus* in freshwater habitats, where it is a dominant member of aquatic communities (Kushlan & Kushlan 1980, Jordan 1996, Turner et al. 1999, Rehage & Trexler 2006). Little is known about the ecology of the other palaemonid species in the Everglades, except for early descriptive studies by Tabb et al. (1962), McPherson (1970) and Odum and Heald (1972).

In this study, the spatial and seasonal variation of palaemonid shrimp was examined across the Shark River estuary in the southwest region of ENP. In particular the following questions were asked: (1) How do palaemonid shrimp species segregate spatially along the Shark River Estuary?; (2) How does species distribution relate to the spatial and seasonal variation in hydrological conditions?; and, (3) Does this spatiotemporal variation in distribution of species affect their trophic function? To address these questions, multiple sites were sampled throughout the estuary in the wet and dry seasons and shrimp tissues were analyzed for stable-isotope signatures. Stable carbon isotope ratios (δ^{13}C) provide insights into the dietary carbon sources, whereas stable nitrogen isotope ratios (δ^{15}N) may reveal relative trophic positions of the consumers (DeNiro & Epstein 1978, Haines & Montague 1979, DeNiro & Epstein 1981, Peterson & Fry 1987, Vander Zanden & Resmussen 1999, Post 2002). Spatially, stable-isotopes are useful for detecting organism movements in estuaries, tracing offshore migrations, and investigating the fate of mangrove carbon (Newell et al. 1995, Deegan & Garritt 1997, Connolly et al 2005, Dittmar et al. 2006, Guest et al. 2006, Bouillon et al. 2008). Temporally, stable isotopes can show shifts in diet and trophic position within a species or community in response to seasonal changes (Loneragan et al. 1997, Wissel & Fry 2005).

Materials and Methods

Study system

The Shark River estuary (25˚28'N, 80˚51'W to 25˚21'N, 81˚04'W), is composed of one of the largest coastal rivers within the greater Everglades ecosystem, approximately

32.1 km in length (Fig. 1). The estuary's headwaters consist of the Shark River Slough,

which is the main freshwater drainage in the southern Everglades (McIvor et al. 1994).

At the marsh-mangrove ecotone, mangrove-lined creeks in an area known as Rookery

Branch connect upstream freshwater marshes to mangrove-dominated estuarine habitats

(Odum & Heald 1972, McIvor et al. 2007, Rehage & Loftus 2007). The freshwater

marsh of Shark River Slough contains stands of sawgrass (*Cladium jamaicense*) and

spikerush (*Eleocharis cellulosa*) in the deeper prairies (Gunderson & Loftus 1993, Busch

et al. 1998, Jaffe et al. 2007). Freshwater inflow from the marsh into the mangrove

creeks delivers nutrients to primary producers and creates salinity gradients (McIvor et al,

1994), although nutrient inputs are higher from the marine environment than the

freshwater (Jaffe et al. 2007). The Shark River estuary is less oligotrophic compared to

other drainages (i.e., Taylor Slough) (Green et al. 2006). It is also well mixed, with

moderate fluctuations during tidal cycles and diurnal tidal flow increasing downstream

(Levesque 2001). In 2005-2006 annual wet season discharge from the Shark River was

approximately 280,000 acre-feet compared to approximately 75,000 acre-feet in the dry

season (Woods & Zucker 2008). Water depth ranges from approximately 1.5 to 4.6 m

throughout the estuary (McPherson 1970). Bare limestone, shell, and organic debris

comprise the bottom of the estuary, with peat and marl forming the banks (McPherson

1970, Smith et al. 1994). The plant community is largely dominated by red mangrove

(*Rhizophora mangle*), with a lower abundance of both black (*Avicennia germinans*) and

white mangroves (*Laguncularia racemosa*) (Smith et al. 1994). The mangrove canopy

may extend to 25 m in height, with the largest mangroves of ENP found along the

downstream portions of the Shark River (Smith et al. 1994, Smith & Whelan 2006).

Fig. 1. Map of southwestern Everglades National Park showing the location of red study sites (⊙) along the Shark River estuary. Black stars (★) denote approximate locations of NPS and USGS hydrostations along the estuary including: SH1 in the Shark River Slough just upstream of study site RB10 and CN near study site RB8 which correspond to the upper estuary. SH2 is located near mid-estuary study site SRS4 in Tarpon Bay. GI and SR represent the lower estuary, with GI near study site SRS5 and SR near study site PDLB1

9

Field Collections

To capture seasonal variation, palaemonid shrimp were sampled along the estuary in April-May and September-October, 2008, which corresponded to peak dry and wet seasons, respectively. Eight sites were sampled along the river course from the marsh-mangrove ecotone to Ponce de Leon Bay, where the river empties into the Gulf of Mexico. Sites were equally spaced (approximately 4 km apart): three in the upper estuary area of Rookery Branch (RB 10, 9 and 8), two sites were in Tarpon Bay (SRS 4 and TB 1), and 3 sites in the lower estuary (SRS 5, SRS 6 and PDLB 1) (Fig. 1). At each site, 10 unbaited Gee® minnow traps (3-mm metal mesh, 2.5-cm opening) were randomly set within a 100-m stretch of mangrove shoreline. This passive sampling method has been effective at capturing bottom-dwelling fishes and invertebrates (Everhart & Youngs 1981, Kneib & Craig 2001), including within Shark River mangrove creeks (Rehage and Loftus 2007). Trapping was conducted overnight for two days within each sampling month (8 sites x 10 traps x 2 days x 2 months x 2 seasons = 640 traps). Traps were tied to mangrove prop roots, with trap depths averaging $0.82m \pm 0.02$. At most sites, traps rested on the benthos, except at SRS 5 and 6, where due to deeper water (approximately 2.5 m), traps were suspended in the water column. Traps were set on Day 1, emptied and reset at the same location on Day 2, and then emptied again on Day 3. Daily catches were kept separate for analysis. All trap contents were either frozen or preserved in 10% formalin and brought back to the lab for processing. Palaemonid shrimp were identified and counted using a dissecting microscope, the carapace length of individuals were measured with dial calipers, and they were weighed wet after blotting (Williams 1984, Abele & Kim 1986).

Using a YSI 85 unit, salinity, dissolved oxygen, and water temperature were measured at each trap during deployment (days 1 and 2 of each sample). Tide height (low, mid or high) and direction (incoming or outgoing) were qualitatively assessed. To further characterize the salinity regime of this estuary, daily salinity readings were obtained from three Everglades National Park (NPS) and two United States Geological Survey (USGS) hydrological stations located near our study sites (Fig. 1).

To compare trophic roles among the palaemonid shrimp species, a sub-sample of the collections were analyzed for stable isotopes. In the dry season only, stable-isotope sampling was conducted separately from the sampling described above (20 days prior to April sample), using the same trapping methods, but with one exception. Dry-season isotope samples were collected from seven sites instead of eight. A site located intermediate between RB 9 and RB 8 was used (RB 13 in Fig. 1). RB 9 and RB 8 were later added, replacing RB 13, to capture more spatial variability (Fig. 1).

In the laboratory, muscle tissue was extracted from individual shrimp and dried at 60˚C for 48 h in a drying oven. Once dried, tissue was ground into a fine powder, weighed, and packed into a tin capsule for isotopic analysis in a mass spectrometer (Fry 2006). Mass spectrometric analyses of C and N stable-isotope ratios were performed at Southeast Environmental Research Center Stable Isotope Laboratory at Florida International University, Miami, FL. Individuals of each species collected at each site were analyzed, for a total of 91 dry-season samples and 147 wet-season samples. Adequate sample sizes from the literature averaged 5-15 individuals per site; an average of 16 individuals were used when possible, with a maximum of 17 individuals to as few

as one individual per site, depending on catch availability (Fry & Smith 2002, Bouillon et al. 2004).

Isotope values are signified by the delta (δ) notation and calculated relative to an accepted standard by:

$$\delta X (‰) = [(R_{SAMPLE} / R_{STANDARD} - 1)] * 1000,$$

where X is either ^{13}C or ^{15}N, and R is the ratio of the heavy isotope to the light isotope (e.g., ^{13}C: ^{12}C, and ^{15}N:^{14}N). The standard for carbon is Vienna Pee Dee Belemnite (VPDB) and the standard for nitrogen is atmospheric nitrogen. Negative δ values indicate depletion relative to the standard, whereas positive δ values indicate enrichment (Fry 2006, Michener & Lajtha 2007).

Data Analyses

A model selection procedure (Burnham & Anderson 2002) was used to examine variation in palaemonid CPUE (# of shrimp collected per trap night). A partially nested analysis of covariance (ANCOVA) model was fitted to the total CPUE and the CPUE of each species with the following terms: season, site, site x season, month(season), site x month(season). Month was nested within season to account for the hierarchy in replication (Underwood 1997). The following abiotic variables were also included: salinity, water temperature, dissolved oxygen, trap depth, tide, and tidal direction. Model selection was conducted using the SAS® PROC GLMSELECT procedure, which uses Akaike's Information Criterion (AIC) to estimate the distance between the fitted model of

predicted outcomes and true model that produced the observed data. The sequential term option in the model was used, where each term in the model that minimized AIC values was kept, in particular those that reduced AIC values by > 2 units indicating the most support for the model (Richards 2005). Simple linear regressions were used to examine the relationship between any covariates deemed important by model selection and CPUE.

Two-way nested analysis of variance (ANOVA) models were used to examine seasonal and spatial variation in salinity, water temperature, and dissolved-oxygen levels. All CPUE were ln (observed value + 1) transformed prior to analysis to meet the assumptions of normality and homogeneity of variance. Variations in $\delta^{13}C$ and $\delta^{15}N$ shrimp values were analyzed with a three-way ANOVA examining variation among sites, seasons, species, and all interactions. Post-hoc comparisons were performed using Tukey's (HSD) pairwise comparisons. All analyses were performed in SAS® Version 9.1.3.

Results

Variation in abiotic conditions

The salinity regime of the Shark River estuary was strongly influenced by freshwater input from upstream marshes, but this input varied spatially and temporally (Fig. 2). Upper- and mid-estuary sites showed higher variation in salinity during the dry season months, whereas lower estuary sites were more variable in the wetter months. The greatest variation in salinity occurred in the lower parts of the estuary (SRS5, Hydrostation GI) where salinity varied from approximately 0-20ppt in daily and monthly cycles.
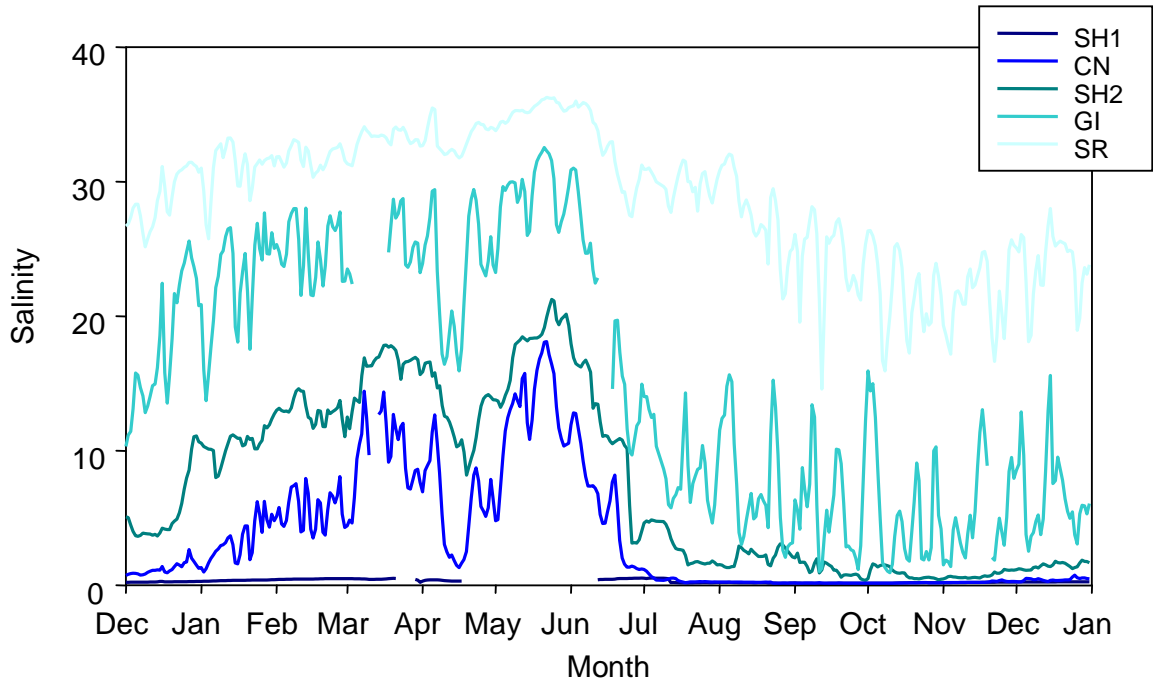
Fig. 2. Mean daily salinity from NPS and USGS hydrostations in the proximity of our study sites for 2008 (See Fig. 1) (Data provided by G. Anderson & T. Smith, 2009 and K. Kotun, 2009)

Environmental conditions at our sampling sites showed spatiotemporal patterns similar to the long-term data collected at the hydrostations. Salinity varied across sites, months, and seasons (significant site by month(within season) interaction, $F_{14, 607} = 362.4$, $p = 0.0001$). In the dry season, salinity gradually increased across sites, but in the wet season the pattern was different. Average salinity was minimal at upper- and mid-estuary sites, sharply increasing only at lower estuary sites influenced by tides (Fig. 3A). Average salinity was highest in May and lowest in October. Temperature was not as variable as salinity but did vary significantly across sites and seasons ($F_{7, 607} = 23.9$, $p = 0.0001$), with higher temperatures in the wet season, in particular at PDLB 1. Dissolved oxygen also varied significantly by site and season ($F_{7, 607} = 70.7$, $p = 0.0001$). Dry-season levels were higher for most sites, with the most drastic increases at upper-estuary sites, RB 10 and RB 9, and mid-estuary site, SRS 4 (Fig 3B).
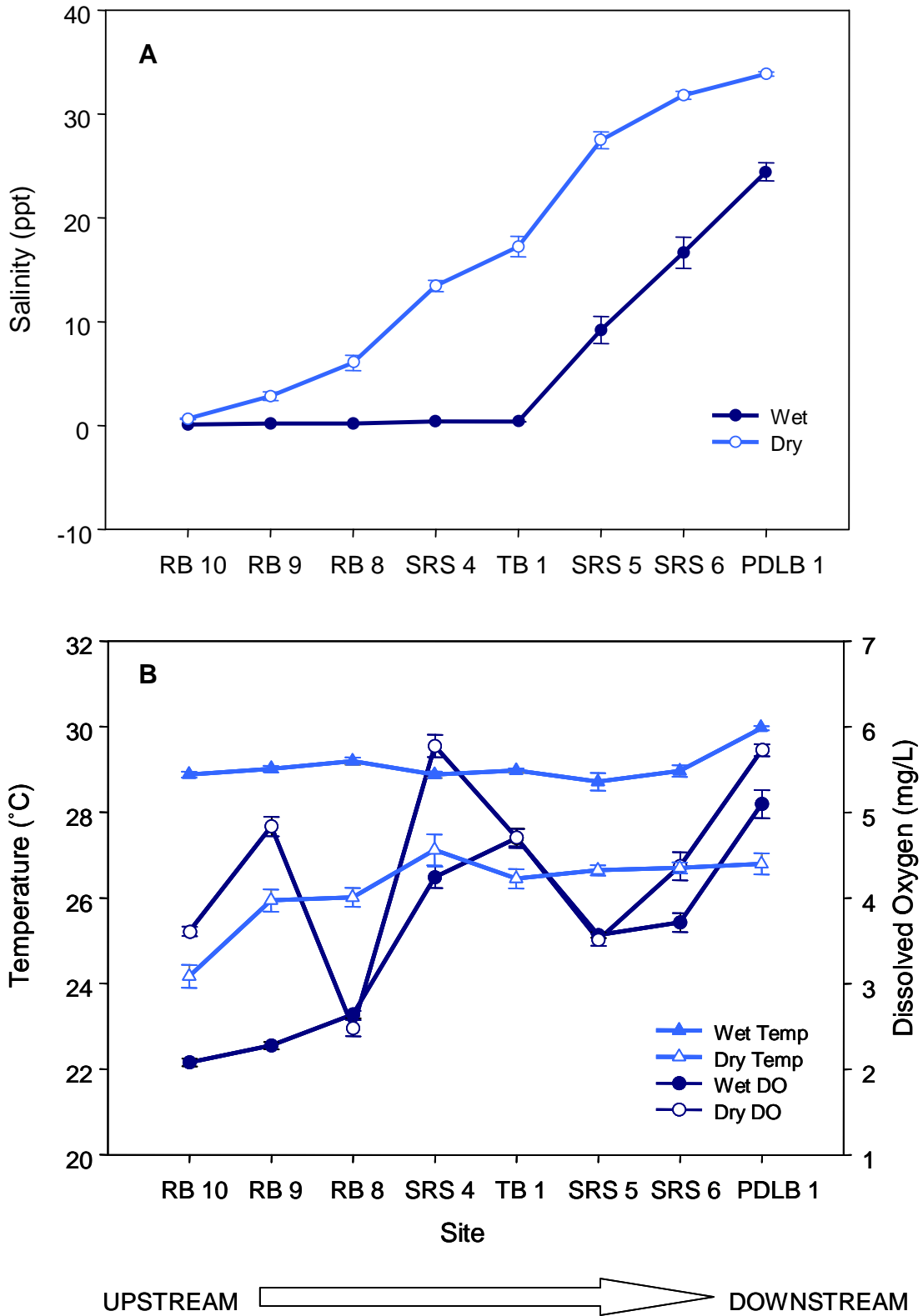
Fig. 3. (A) Mean salinity (± 1 SE) across study sites and seasons (B) Mean temperature and dissolved oxygen (± 1 SE) across study sites and seasons

16

Variation in CPUE

Total CPUE of palaemonid shrimp differed significantly among sites and seasons. In the dry season, shrimp were more abundant at the most upstream site (RB 10), in closest proximity to freshwater marshes. Catches decreased downstream, with the lowest collections at SRS 5 (Fig. 4). In the wet season, shrimp catches were more evenly distributed across sites, with the highest catches occurring downstream at SRS 6. CPUE also differed in shorter temporal scales. Average catches differed strongly between dry season months April (1.0 ± 0.15) and May (5.9 ± 1.6), with less variation between wet season months September (1.4 ± 0.2) and October (2.0 ± 0.2).

Five species of palaemonid shrimp were caught in traps: *P. paludosus* (riverine grass shrimp), *P. intermedius* (brackish grass shrimp), *P. pugio* (daggerblade grass shrimp), *Palaemon floridanus* (Florida grass shrimp) (hereafter abbreviated *Pal. floridanus* to distinguish from *Palaemonetes*), and *Leander paulensis* (red-algae shrimp) (See Appendix A). Despite this, occurrence of multiple species at any one site was rather limited. At most, three species were caught at one site, TB 1. In both the dry and wet seasons, *P. paludosus* comprised 100% of CPUE at RB 10 (Fig. 5A), but they were more dispersed downstream in the wet season, reaching sites approximately 24 km from the headwaters (Fig. 5B). *P. pugio* also appeared to disperse downstream in the wet season, with higher abundance in the mid- versus upper-estuary in the dry season. *P. intermedius* was abundant in the mid-estuary during the dry season, but comprised only a small portion of the catch there in the wet season. Lower estuary sites also shifted from purely *Pal. floridanus* in the dry season to multiple species in the wet season. *L. paulensis* was collected only in the wet season when it dominated catches at the most downstream site,

17
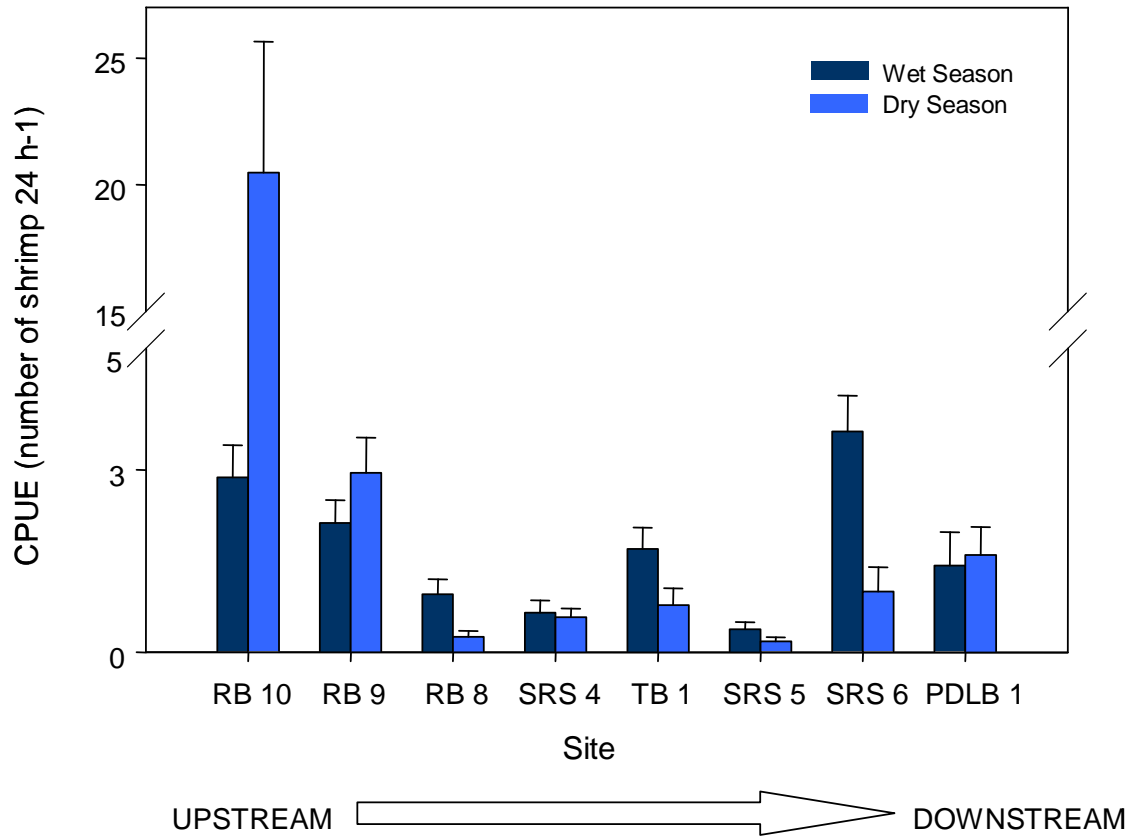
Fig. 4. Mean minnow-trap CPUE (± 1 SE) over two seasons and at 8 study sites. Other fauna was collected in traps but not analyzed
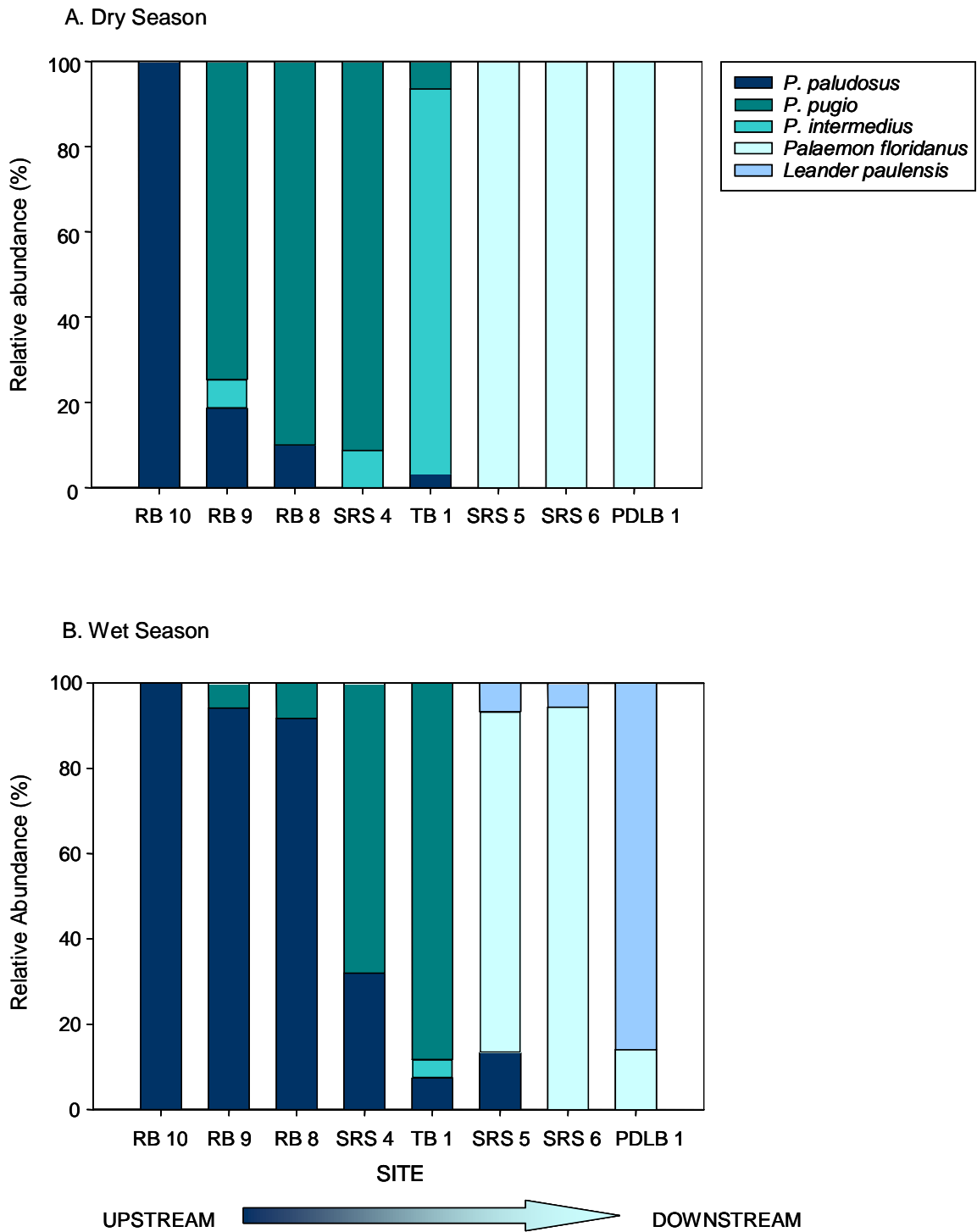
Fig. 5. (A) Dry season and (B) Wet season estimates of palaemonid shrimp abundance from minnow-trap CPUE across sites

PDLB 1.

The inclusion of abiotic variables, including salinity, in the statistical models did not improve model fit significantly (Table 1). Only water temperature and dissolved oxygen were important in explaining the distribution of two species collected, but these were not significant and only improved model fit slightly. Dissolved oxygen appeared to play a role in explaining the distribution of *Pal. floridanus*, while temperature helped explain variability in *L. paulensis*. The largest catches of *L. paulensis* and *Pal. floridanus* occurred in the wet season, coincident with warmer temperatures and lower dissolved oxygen, although dissolved oxygen levels were high when compared to the remaining estuary. Linear regression analyses revealed significant but very low fit relationships between temperature and *L. paulensis* (F = 10.4, p = 0.001, R^2 = 0.016), and between dissolved oxygen and *Pal. floridanus* (F=15.3, p = 0.0001, R^2 = 0.023), so that these relationships appear tenuous.

Table 1. Summary of stepwise model selection procedure used to examine variation in total CPUE, and palaemonid shrimp species CPUE across sites, seasons and the following covariates: salinity, water temperature, dissolved oxygen, trap depth, tide and tidal direction. For each model, Akaike's Information Criteria (AIC) are shown for the terms that increased model fit significantly, along with F, p and R^2 values generated by the model

Palaemonid Shrimp	Source of Variation			
	Site x Season	Site x Month(Season)	Temperature	Dissolved Oxygen
P. paludosus				
F, p	-	31.27, <.0001	-	-
AIC		-680.52		
R^2		0.5937		
P. pugio				
F, p	-	20.32, <.0001	-	-
AIC		-1181.77		
R^2		0.4825		
P. intermedius				
F, p	4.79, <.0001	-	-	-
AIC	-1906.56			
R^2	0.0929			
Pal. foridanus				
F, p	-	24.40, <.0001	2.30, 0.1300	1.98, 0.1601
AIC		-1205.02	-1205.44	-1205.53
R^2		0.5303	0.5316	0.5325
L. paulensis				
F, p	-	9.89, <.0001	3.24, 0.0723	-
AIC		-1612.42	-1613.83	
R^2		0.3003	0.3035	
Total CPUE				
F, p	-	14.79, <.0001	-	-
AIC		-351.1		
R^2		0.3996		

Variation in stable isotopes signatures

^{13}C and ^{15}N values varied significantly among the five palaemonid species collected (Table 2, Fig. 6). The three-way interaction of site x season x species was a significant effect for δ^{15}N, but two-way interactions revealed that seasonal differences had more of an effect than site on shrimp δ^{15}N variation. Shrimp δ^{13}C values were significantly different across site, species, and seasons.

In the dry season, δ^{13}C values in shrimp tissues from upper- and mid-estuary sites were depleted, while lower-estuary shrimp showed enriched values (Fig 6A). This pattern, which closely followed the salinity gradient from fresh to marine waters, was not as evident in the wet season (Fig. 6B). Furthermore, shrimp δ^{13}C values had a wider range during the dry versus wet season, with more species falling within the range of -30‰ to -27‰ in the wet season. During the dry season, *P. paludosus* δ^{13}C values were the most depleted of all species (Table 3). In the wet season, *P. paludosus* δ^{13}C values from all sites except RB 10 were tightly grouped despite being from different sites (Fig. 6b). *P. intermedius* δ^{13}C values were more depleted than those of *P. pugio* at TB 1 during both seasons. *L. paulensis* values were more depleted than *Pal. floridanus* values when they co-occurred at lower estuary sites.

Seasonal comparisons of shrimp species δ^{15}N values revealed that most remained the same and ranged from 9-10‰ (Fig. 6, Table 3). However, many *P. paludosus* showed a dramatic shift from enrichment (13‰) in the dry season to depletion (7‰) during the wet season. The exception was *P. paludosus* collected from RB 10, which did not exhibit this seasonal shift. *P. pugio* δ^{15}N values from RB 9 and RB 8 did not show the depletion pattern evident for *P. paludosus* collected at the same sites.

Table 2. Summary of results of a 3-way ANOVA testing the effects of site, season and palaemonid shrimp species on $\delta^{13}C$ and $\delta^{15}N$ stable-isotope ratios

Source of Variation	$\delta^{13}C$				$\delta^{15}N$		
	df	*F*	*p*		*df*	*F*	*p*
Site	8, 214	15.56	<.0001		8, 214	16.07	<.0001
Season	1, 213	1.64	0.2013		1, 213	1.17	0.2800
Species	4, 213	6.45	<.0001		4, 213	26.68	<.0001
Site x Species	5, 213	5.69	<.0001		5, 213	2.26	0.0498
Season x Species	3, 213	4.39	0.0051		3, 213	6.89	0.0002
Site x Season x Species	3, 213	6.43	0.0003		3, 213	2.29	0.0796
R^2			0.829				0.792
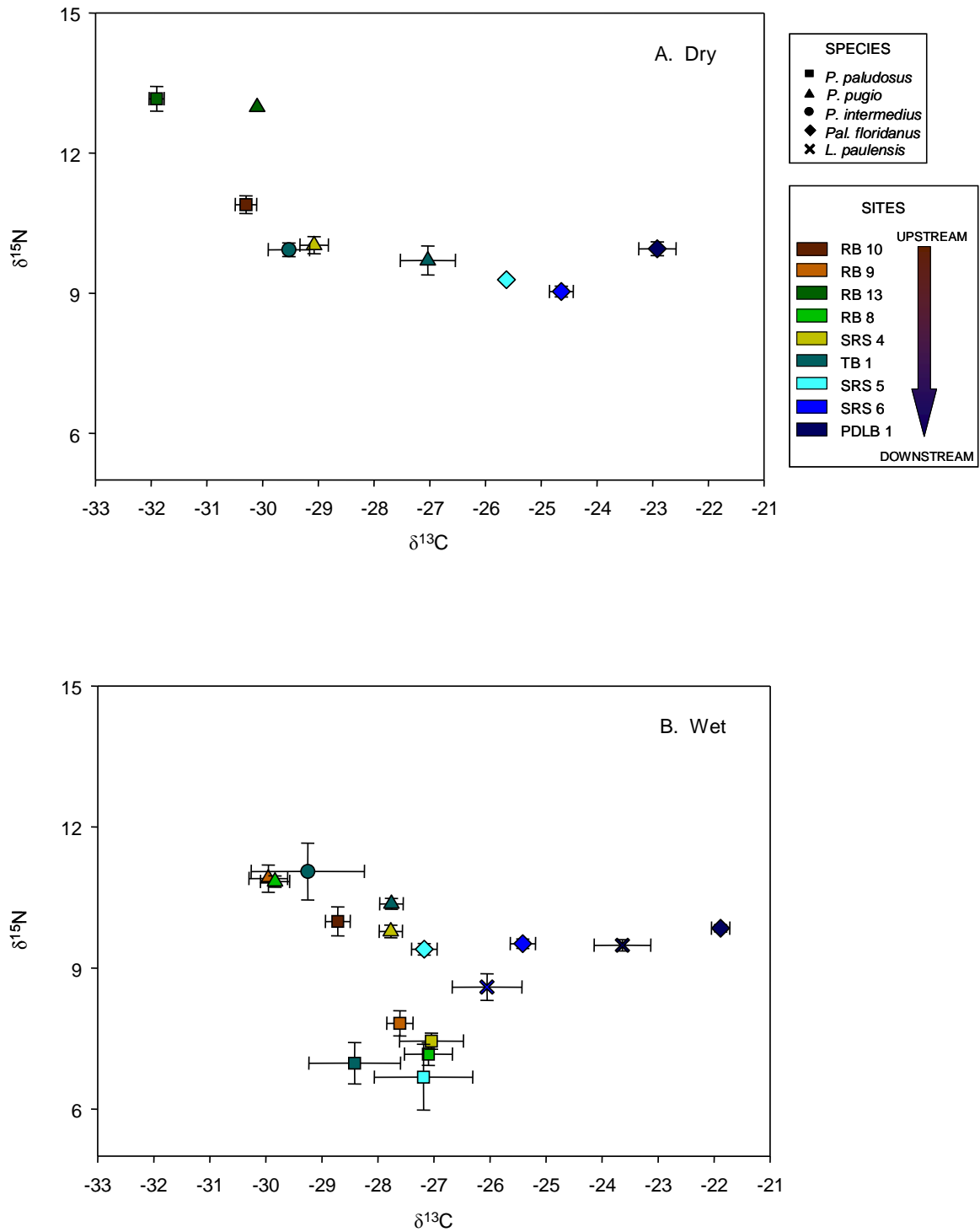
Fig. 6. (A) Dry season and (B) Wet season mean $\delta^{13}C$ and $\delta^{15}N$ ratios for stable-isotopes (± 1 SE) for palaemonid shrimp across sites. Site RB 13 was only used in the dry season, sites RB 8 and RB 9 replace it during the wet season sample

Table 3. Mean stable-isotope ratios (± 1 SE) for $\delta^{13}C$ and $\delta^{15}N$ for palaemonid shrimp by sites and seasons (Values in parentheses are sample sizes, - no data)

Species and site	$\delta^{13}C$		$\delta^{15}N$	
	dry	wet	dry	wet
P. paludosus				
RB 10	-30.3 ± 0.19 (16)	-28.7 ± 0.22 (16)	10.9 ± 0.19 (16)	10.0 ± 0.31 (16)
RB 13	-31.9 ± 0.13 (8)	-	13.2 ± 0.27 (8)	-
RB 9	-	-27.6 ± 0.23 (13)	-	7.8 ± 0.27 (13)
RB 8	-	-27.1 ± 0.43 (8)	-	7.2 ± 0.24 (8)
SRS 4	-	-27.0 ± 0.57 (6)	-	7.4 ± 0.17 (6)
TB 1	-	-28.4 ± 0.82 (5)	-	7.0 ± 0.44 (5)
SRS 5	-	-27.2 ± 0.88 (2)	-	6.7 ± 0.70 (2)
P. pugio				
RB 13	-30.1 (1)	-	13.0 (1)	-
RB 9	-	-30.0 ± 0.35 (5)	-	10.9 ± 0.29 (5)
RB 8	-	-29.8 ± 0.26 (3)	-	10.8 ± 0.12 (3)
SRS 4	-29.1 ± 0.26 (16)	-27.8 ± 0.21 (17)	10.0 ± 0.18 (16)	9.8 ± 0.13 (17)
TB 1	-27.0 ± 0.49 (5)	-27.8 ± 0.21 (16)	9.7 ± 0.31 (5)	10.4 ± 0.17 (16)
P. intermedius				
TB 1	-29.5 ± 0.37 (17)	-29.3 ± 1.01 (2)	9.9 ± 0.14 (17)	11.1 ± 0.61 (2)
Pal. floridanus				
SRS 5	-25.6 (1)	-27.2 ± 0.23 (12)	9.3 (1)	9.4 ± 0.12 (12)
SRS 6	-24.6 ± 0.21 (17)	-25.4 ± 0.23 (15)	9.0 ± 0.12 (17)	9.5 ± 0.10 (15)
PDLB 1	-22.9 ± 0.34 (13)	-21.9 ± 0.16 (8)	10.0 ± 0.15 (13)	9.8 ± 0.08 (8)
L. paulensis				
SRS 5	-	-	-	8.46 (1)
SRS 6	-	-26.1 ± 0.62 (9)	-	8.6 ± 0.28 (9)
PDLB 1	-	-23.6 ± 0.51 (14)	-	9.5 ± 0.12 (14)

Discussion

While palaemonid shrimp are found in fresh, brackish, and marine waters throughout the world, little is known about their abundance and distribution, and the factors governing these patterns in coastal systems such as the Everglades. The data from this study provide insights into shrimp species composition and trophic dynamics in relation to spatiotemporal variation in freshwater inflow and salinity. Five palaemonid shrimp species were found within the Shark River Estuary, and their distribution segregated significantly by site. McPherson (1970) collected palaemonid shrimp from the Shark River estuary and some similarities were found. Like in this study, his most abundant shrimp were *P. paludosus*, *P. intermedius*, and *P. pugio*. Specimens of *P. paludosus* were found only in the upper estuary, in contrast to this study in which *P. paludosus* was collected as far downstream as the Shark River (SRS 5) in the wet season. McPherson (1970) found *P. pugio* and *P. intermedius* only in the mid- to lower estuary, with *P. intermedius* collected as far downstream as Ponce de Leon Bay; but it was not collected there in this study. *P. intermedius* may have been responding to the lower salinity levels at lower estuary sites prevalent during the time of McPherson's collections.

Environmental variables did not significantly explain variation in catches, except in two species. The distribution of lower-estuary inhabitants, *Pal. floridanus* and *L. paulensis*, was slightly influenced by temperature and dissolved oxygen. Unfortunately, there is little information on how temperature and dissolved oxygen affect these species. Coen et al. (1981) collected *Pal. floridanus* from Apalachee Bay, FL at temperatures from 14-30˚C, and Sheridan (1992) also collected *Pal. floridanus* from Rookery Bay, FL

from 19-32˚C. They made no mention of how those temperature ranges affected shrimp distributions.

Abiotic variables recorded at trap deployment only offer a snapshot of the conditions in time and did not account for larger time scales which could possibly better explain catch variations. Salinity was not an important factor in any of the statistical models. Rozas et al. (2005) found that salinity failed to explain density distributions of penaeid shrimp even though there was a strong salinity gradient present at their study sites. Despite this, others have shown that increased freshwater flow reduced salinity and affected estuarine animal distributions (Alber 2002, Barletta et al. 2006, Gonzalez-Ortegon et al. 2006, Greenwood et al. 2007); therefore, salinity may have played a role in variation palaemonid abundance as it shifted spatially across the estuary and temporally according to the seasonal effects of rainfall, tide, and freshwater flow (Davis et al. 2005).

The fact that palaemonid species distributions matched their individual salinity tolerances during both seasons is further evidence for the important role of salinity. *P. paludosus* is the least salinity-tolerant species, usually found within salinities of 0-10ppt (Anderson 1985). *P. pugio* and *P. intermedius* are typically more salinity tolerant with ranges from 2-36ppt and 5-39ppt, respectively, although *P. intermedius* is usually found in higher salinities than *P. pugio* (Dobkin & Manning 1964, Anderson 1985, Gallin 2002). *Pal. floridanus* and *L. paulensis* are the most salinity-tolerant species, found in salinities of 17-36ppt and 16-37ppt, respectively (Tabb et al. 1962, McPherson 1970, Coen et al. 1981, Sheridan 1992). During the dry season, high salinities most likely prevented large-scale movements along the river by shrimp, but during the wet season, *P. paludosus* and *P. pugio* could have expanded downstream when salinities were much

lower and closer to their optima. Cartaxana (1994) found this with *Palaemon longirostris* which migrated downstream when freshwater inputs lowered salinity.

Another reason for changes in distribution with shifting salinity may relate to life-history requirements. Knowlton and Kirby (1984) performed laboratory studies on *P. pugio* larvae and found they could not survive as wide a salinity range as adults, and also had optimum survival rates in higher salinities. *P. pugio* may move with the freshwater pulses downstream to release eggs there in order to increase larval survival. *P. paludosus* larvae can survive surprisingly large salinity ranges; larvae incubated in fresh water were able to metamorphose in salinities up to 30ppt (Lowe & Provenzano 1990). This implies *P. paludosus* larvae could survive if salinities increased after being flushed downstream during the wet season.

There was significant seasonal variation in the distribution of palaemonid species across the estuary, but certain species appeared to be more affected than others. Seasonal variation in the distribution of palaemonid shrimp has been previously documented (Gray 1991, Peterson & Turner 1994, Matheson et al 1999, Turner et al. 1999, Jordan et al. 2000, Goodfriend 2004, Liston et al. 2007). In this study, *P. paludosus*, the common freshwater-marsh inhabitant, seemed to be affected strongly by drying in the marsh, which had been documented by others (Kushlan & Kushlan 1980, Jordan et al. 2000). *P. paludosus* is a dominant member of Everglades marshes comprising 61% of invertebrate biomass with average collections of 23-34 individuals per m^2 (Turner et al. 1999, Jordan et al. 2000). Catches of *P. paludosus* at our uppermost site were very high in the dry season relative to the wet season. During the dry season, Everglades marshes can dry completely forcing aquatic organisms to take refuge in remaining ponds, alligator holes

and deeper pools (Kushlan & Kushlan 1980, Loftus & Eklund 1994, Chick et al. 2004). Marsh dry downs are more pronounced in the Everglades because of decreases in historic freshwater flows (Fennema et al. 1994). Therefore, the high catches of *P. paludosus* at RB 10 most likely resulted from an influx of marsh residents escaping the drying marsh. McPherson (1970) found a similar pattern; he collected *P. paludosus* at the end of March and early April in 1969 from Rookery Branch (corresponding to our upper-estuary sites RB 10 and 9) in high numbers of 1,790 individuals per 1000 cubic meter. More recently, Rehage and Loftus (2007) also found freshwater fish abundances increased in the upper estuary during periodic marsh drying. Similarly, Rehage and Trexler (2006) found higher numbers of shrimp in the vicinity of deep water canals in the dry season. Jordan et al. (2000) also found high densities of *P. paludosus* (425 individuals $\cdot$m^{-2}) in deeper slough habitat during a severe marsh dry down in the northern Everglades.

Average catches were more evenly distributed in the wet season, perhaps because of increased freshwater flow that would allow shrimp to move more freely throughout the estuary. Pulses from heavy rains can result in long-distance biotic movement as the estuary is flushed (Katherisan & Bingham 2001). This may explain how *P. paludosus* traveled long distances downstream in the wet season. Many species utilize increased flow from rainfall for larval and juvenile dispersal (Dittel & Epifanio, 1990). For instance, Vance et al. (1998) found emigration rates of *Penaeus merguiensis* juveniles were significantly correlated with increased rainfall.

Palaemonid shrimp movement through the Shark River estuary may also be aided by mangrove leaves. In Costa Rica, penaeid and palaemonid shrimp were found associated with floating mangrove leaves, most likely to reduce predation threat and

minimize energy costs during movement (Wehrtmann & Dittel 1990). It is possible that palaemonid shrimp in the Shark River estuary hitchhike on floating mangrove leaves to aid their movements downstream in the wet season. Tides may also contribute to palaemonid movement in the lower estuary as documented with other species (Roberston & Blaber 1992, Ronnback et al. 1999, Barletta et al. 2003). During high tide, juvenile *Penaeus merguiensis* and small fishes moved 43 m into mangrove forest (Vance et al. 1996). The appearance of *L. paulensis* in the wet season may have been due to movement from the Gulf into the estuary with tides, as it was most abundant at PDLB 1.

Although not investigated in this study, biotic variables, such as predation, could have affected patterns of abundance and distribution of palaemonid shrimp. *P. pugio* moved to shallower habitat when placed in the same tank as multiple predatory taxa (Bretsch & Allen 2006). Davis et al. (2003) also found *P. pugio* altered habitat choice when with predators, but more specifically moved to areas opposite of fish foraging styles. In the Everglades, palaemonid shrimp are a food source for many fishes, such as Florida gar, largemouth bass, warmouth, gray snapper and juvenile snook (Odum et al. 1982). It is possible that as freshwater, estuarine, and marine fish move in response to abiotic and biotic variables in the estuary, they also disrupt patterns of palaemonid abundance and distribution as they prey on them.

Stable-isotope analysis helped elucidate palaemonid shrimp spatiotemporal patterns. Values for ^{13}C fit the expected spatial pattern for organisms living along a gradient from fresh to marine waters. Overall, the most depletion in palaemonid ^{13}C values happened in the upper estuary. ^{13}C depletion upstream versus ^{13}C enrichment downstream occurs as carbon sources shift from diluted terrestrial organic matter

(dissolved organic carbon, DOC) in the upper estuary to seagrasses towards the coast (Coffin & Cifuentes 1999). Abrantes and Sheaves (2008) found epiphytes, microphytobenthos, and epilithic algae were more depleted in ^{13}C at mangrove sites, due to mangroves releasing depleted ^{13}C. The released DOC becomes further decomposed into dissolved inorganic carbon (DIC) and dissolved CO_2, which leaves highly depleted sources of carbon for benthic producers, epiphytes, and suspended primary producers, such as phytoplankton (Coffin & Cifuentes 1999, Abrantes & Sheaves 2008). Producers in typical estuarine headwaters have $\delta^{13}C$ values from -30 to -26‰, while $\delta^{13}C$ values at the river mouth range from -22 to -18‰ (Fry & Sherr 1984, Peterson & Fry 1987). In this study, this pattern was well defined in the dry season, but less so in the wet season. During the wet season, increased freshwater flow would bring more terrestrial and freshwater organic matter to the system, which may explain the clumping of palaemonid shrimp $\delta^{13}C$ values near those of terrestrial organic matter. Seasonal variation in stable isotopes can result from variation in available nutritional sources and may be useful in tracking organism movements (Simenstad & Wissmar 1985, Conkright & Sackett 1986, Boullion et al. 2000, Dittmar et al. 2001, Wissel & Fry 2005). For example, Loneragan et al. (1997) found that *Penaeus merguiensis* in seagrass had low $\delta^{13}C$ values in the wet season indicative of mangrove $\delta^{13}C$ values, suggesting the shrimp had moved there recently from mangrove creeks.

In pristine estuaries, ^{15}N should change slightly from fresh to marine waters; however, increased anthropogenic inputs upstream of estuaries often result in higher freshwater ^{15}N signatures (Fry 2002). In the Everglades, the freshwater Shark River Slough has high levels of dissolved organic matter rich in nitrogen, but this dissolved

31

organic nitrogen may be consumed or transformed before reaching the estuarine ecotone (Childers 2006). Yet, Fry & Smith (2002) documented high isotopic N compositions in the upper Shark River estuary and cited possible enrichment from the upstream Everglades watershed. Cornett (2006) also found higher mean total nitrogen levels at the upper estuary versus Ponce de Leon Bay. We found that δ^{15}N values for palaemonid shrimp did not shift appreciably across the estuary, or during the two seasons, with the exception of *P. paludosus.*

P. paludosus showed the most dramatic spatiotemporal shifts in both δ^{13}C and δ^{15}N, while other palaemonid shrimp showed little shifts. *P. paludosus* in the upper estuary (RB 13) in the dry season had markedly different values from those in the wet season (RB 9, 8). Interestingly, wet-season δ^{13}C and δ^{15}N values for *P. paludosus* showed little variation despite the shrimp having been collected at a number of sites from upper-, mid- and lower-estuary sites (RB 9, 8, SRS 4, TB 1, and SRS 5). This pattern suggests *P. paludosus* inhabited the upper estuary in the dry season where they consumed similar prey, and were then flushed downstream with large freshwater outflows that occurred during the wet season. Palaemonid shrimp turnover rates are not known, but penaeids exhibit muscle tissue turnover rates in the range of 3-15 days (Parker et al. 1991, Fry et al. 2003). Assuming similar palaemonid shrimp tissue-turnover rates, shrimp collected far downstream of their original upstream habitat could still exhibit an upstream signal even when collected days after their movement. In contrast to this wet-season clustering of δ^{15}N and δ^{13}C values, *P. paludosus* from the uppermost site (RB 10) showed less seasonal variation than those collected downstream. Those shrimp were probably not flushed downstream, because the uppermost portions of the estuary are

small, winding, densely vegetated creeks that likely impede movement, versus other

upper-estuary sites situated along the wider main-stem.

The interpretation of spatiotemporal shifts in ^{13}C and ^{15}N is however rather

limited because data on the ^{13}C and ^{15}N ratios of potential shrimp dietary items and basal

resource pools were not collected. Thus, it was not possible to make inferences about

absolute trophic placement of these species based on their ^{15}N values. Mangrove δ^{15}N

can vary over short distances in estuaries by as much as 10‰, likely due to variation in N

pools and fractionation processes (Fry et al. 2000, Bouillon et al. 2008). The timing and

rates of nitrogen cycling may also affect δ^{15}N values, leading to misleading

interpretations of trophic-level variation (Hart & Lovvorn 2002). Increases in δ^{15}N can

be attributed to a number of mechanisms beyond the consumption of animal material.

Anthropogenic nitrogen inputs, the presence of mangrove-derived material after

microbial processing, and the presence of microphytobenthos may all contribute to

nitrogen enrichment in producers that would affect consumer values (Bouillon et al.

2004, 2008). Rozas et al. (2005) found high ^{15}N values in organisms at inflow sites

versus reference sites, probably from enrichment in the Mississippi River source.

Palaemonid shrimp at the same study had enriched ^{15}N values thought to be derived from

the consumption of epiphytes that utilized recycled ammonium.

Although direct inferences about the trophic placement of the shrimp species

cannot be made, previous work indicates *P. paludosus* may function at a higher trophic

level than most invertebrates. Isotope research in Everglades freshwater marshes has

found *P. paludosus* to be a secondary benthic consumer with δ^{13}C and δ^{15}N values

similar to those of fishes, and approximately a full trophic level higher than crayfish

(Loftus 2000, Williams & Trexler 2006, Liston et al. 2007). A study in the mid to lower

Shark River Estuary found palaemonid shrimp had the highest $\delta^{15}N$ values compared to

other mangrove invertebrates and small fishes (e.g., snails, crabs, mosquitofish, and

gobies) (McIvor et al. 2007), indicative of a diet rich in animal material. In contrast,

other palaemonid shrimp are thought to be more omnivorous. For instance, *P. pugio* has

been described as a detritivore, efficiently breaking down detritus by plucking at the

cellular matrix of detrital fragments (Odum & Heald 1972, Welsh 1975). In Florida's

Indian River Lagoon, stomach-content analyses of *P. intermedius* revealed the most

commonly ingested food item was the shoal seagrass, *Halodule wrightii* (Zupo & Nelson

1999). Everglades research points to *P. intermedius* feeding on algae, vascular plant

detritus, and microcrustaceans (Odum & Heald 1972). There is no known dietary

information for *Pal. floridanus* or *L. paulensis,* although both are noted as being found in

red algae where they could potentially consume epiphytes (Manning 1961, Tabb et al.

1962, Coen et al. 1981).

An interesting pattern in our data was the relatively limited co-occurrence of

palaemonid species at any one site. This might result from competition being an

important factor limiting their distribution. Studies have shown that palaemonid shrimp

species compete for preferred substrate, but it is not well understood if they compete for

food (Thorp 1976, Coen et al. 1981, Khan et al. 1997, Rowe 2002). Palaemonid shrimp

$\delta^{13}C$ values overlapped less during the dry season than the wet season. In the dry season,

P. intermedius and *P. pugio* $\delta^{13}C$ values from the mid-estuary were similar, whereas

multiple species $\delta^{13}C$ values overlapped in the wet season. This suggests competition for

food resources between shrimp species is possible in the Shark River estuary, especially

since prior gut content analyses and laboratory experiments indicate use of similar resources (Beck & Cowell 1976, Kneib 1985, Gregg & Fleeger 1998).

In the wet season, *L. paulensis* and *Pal. floridanus* showed similar $\delta^{13}C$ values at lower-estuary site SRS 6. Both species have been found inhabiting red algae mats, but the larger *Pal. floridanus* should be able to exclude the smaller *L. paulensis* competitively as it was capable of excluding another palaemonid, *Palaemonetes vulgaris*, from red algae in an earlier study (Tabb et al. 1962, Coen et al. 1981). This may explain the small collections of *L. paulensis* at SRS 5 and 6 where *Pal. floridanus* dominated. Their $\delta^{13}C$ values did not overlap at PDLB 1, and more *L. paulensis* were collected there, indicating they were possibly utilizing a substrate other than red algae.

In the estuarine environment, it is difficult to distinguish between terrestrial and mangrove $\delta^{13}C$ values because they are often very similar (Bouillon et al. 2008). This is evident along the Shark River estuary, making exact dietary inferences for palaemonid shrimp difficult. Previous work in the Shark River shows that $\delta^{13}C$ values for the producers in the system are indistinguishable (mangroves: -28.4‰ ± 0.29, mid-estuary algae: -28.9‰ ± 1.3, freshwater vascular plants: -27.1‰ ± 0.98, and other terrestrial plants: -28.2 ± 0.31 (Loftus 2000, Fry & Smith 2002, Cornett 2006, Reich & Worthy 2006, McIvor unpub. data). Distinct $\delta^{13}C$ values, however, were found for upper-estuary algae: -33.3‰ ± 0.89 and lower-estuary seagrasses: -16.4‰ ± 2.0 (Loftus 2000, Cornett 2006). Dry-season palaemonid $\delta^{13}C$ values from the upper estuary matched upper-estuary algal signatures, with mid-estuary values resembling mangrove, algal, and terrestrial carbon sources. Lower-estuary palaemonid shrimp $\delta^{13}C$ was more enriched than mangrove or terrestrial material, but not as enriched as seagrass, likely indicating a

mixture of carbon sources. Palaemonid δ^{13}C values for the wet season were shifted toward the mid-estuary where mangrove material was determined as the dominant source in a previous study (Fry & Smith 2002). The role of phytoplankton was not taken into consideration, which could an important missing source.

Even though exact food-web dynamics were not determined in this study, insights into palaemonid movement, diet, and trophic level were found using stable isotopes, which can serve as a basis for future isotopic studies in the area. Five palaemonid shrimp species were collected in the Shark River estuary and their abundance and distribution varied significantly by site and season. Although salinity was insignificant, the seasonal pattern suggests increased freshwater flow played a strong role in seasonal distributions. Knowledge of spatiotemporal patterns in distribution and abundance of these palaemonid shrimp species along the Shark River estuary could provide critical pre-restoration data. If proposed Everglades restoration occurs, more freshwater would be delivered to the Shark River estuary, reducing salinities and extending the oligohaline zone (Davis et al. 2005). This would affect palaemonid distributions and trophic function, since *P. paludosus* could increase in importance as a component of the estuarine community, while other brackish and marine shrimp would be forced farther downstream. As vital mangrove habitat continues to be destroyed and altered by human activities, information on organisms inhabiting this area also becomes critical since palaemonid shrimp are an integral part of the Everglades food web, serving as food for wading birds and gamefish predators (Roonback et al. 1999, Wessell et al. 2001).

LITERATURE CITED

Abele LG, Kim W (1986) An illustrated guide to the marine decapod crustaceans of Florida. State of Florida, Department of Environmental Protection, Tallahassee, Florida. 760 p

Abrantes K, Sheaves M (2008) Incorporation of terrestrial wetland material into aquatic food webs in a tropical estuarine wetland. Est Coast Shelf Sci 80: 401-412

Akin S, Winemiller KO, Gelwick FP (2003) Seasonal and spatial variations in fish and macrocrustacean assemblage structure in Mad Island Marsh estuary, Texas. Est Coast Shelf Sci 57: 269-282

Alber M (2002) A conceptual model of estuarine freshwater inflow management. Estuaries 25: 1246-1261

Anderson G (1985) Species profiles: life histories and environmental requirements of coastal fishes and invertebrates (Gulf of Mexico). Biological Report 82, U.S. Fish and Wildlife Service.

Attrill MJ, Rundle SD (2002) Ecotone or ecocline: ecological boundaries in estuaries. Est Coast Shelf Sci 55: 929-936

Attrill MJ, Power M (2000) Effects on invertebrate populations of drought-induced changes in estuarine water quality. Mar Ecol Prog Ser 203: 133-143

Barletta M, Amaral CS, Correa MFM, Guebert F, Dantas DV, Lorenzi L, Saint-Paul U (2008) Factors affecting seasonal variations in demersal fish assemgblages at an ecocline in a tropical-subtropical estuary. J Fish Biol 73: 1314-1336

Barletta M, Barletta-Bergan A, Saint-Paul U, Hubold G (2005) The role of salinity in structuring the fish assemblages in a tropical estuary. J Fish Biol 66: 45-72

Barletta M, Barletta-Bergan A, Saint-Paul U, Hubold G (2003) Seasonal changes in density, biomass, and diversity of estuarine fishes in tidal mangrove creeks of the lower Caete estuary (northern Brazilian coast, east Amazon). Mar Ecol Prog Ser 256: 217-228

Bauer RT (2004) Remarkable shrimps: adaptations and natural history of the carideans. University of Oklahoma Press, Norman

Beck JT, Cowell BC (1976) Life history and ecology of the freshwater caridean shrimp, *Palaemonetes paludosus* (Gibbes). Am Mid Nat 96:52-65

Bouillon S, Connolly RM, Lee SY (2008) Organic matter exchange and cycling in mangrove ecosystems: recent insights from stable isotope studies. J Sea Res 59: 44-58

Bouillon S, Moens T, Overmeer I, Koedam N, Dehairs F (2004) Resource utilization patterns of epifauna from mangrove forests with contrasting inputs of local versus imported organic matter. Mar Ecol Prog Ser 278: 77-88

Bouillon S, Mohan PC, Sreenivas N, Dehairs F (2000) Sources of suspended organic matter and selective feeding by zooplankton in an estuarine mangrove ecosystem as traced by stable isotopes. Mar Ecol Prog Ser 208: 79-92

Bretsch K, Allen DM (2006) Effects of biotic factors on depth selection by salt marsh nekton. J Exp Mar Bio Ecol 334: 130-138

Burnham KP, Anderson DR (2002) Model selection and multi-model inference. A practical information-theoretic approach, 2nd edn. Springer, Berlin

Busch DE, Loftus WF, Bass OL (1998) Long-term hydrological effects on marsh plant community structure in the Southern Everglades. Wetlands 18: 230-241

Cartaxana A (1994) Distribution andmigrations of the prawn *Palaemon longirostris* in the Mira River Estuary (southwest Portugal). Estuaries 17: 685-694

Chick JH, Ruetz CR, Trexler JC (2004) Spatial scale and abundance patterns of large fish communities in freshwater marshes of the Florida Everglades. Wetlands 24: 652-664

Childers DL (2006) A synthesis of long-term research by the Florida Coastal Everglades LTER program. Hydrobiologia 569:531-544

Childers DL, Iwaniec D, Rondeau D, Rubio GA, Verdon E, Madden CJ (2006) Responses of sawgrass and spikerush to variation in hydrologic drivers and salinity in southern Everglades marshes. Hydrobiologia 569: 273-292

Coen LD, Heck KL, Abele LG (1981) Experiments on competition and predation among shrimps of seagrass meadows. Ecology 62:1484-1493

Coffin RB, Cifuentes LA (1999) Stable isotope analysis of carbon cycling in the Perdido Estuary, Florida. Estuaries 22: 917-926

Conkright ME, Sackett WM (1986) A stable carbon isotope evaluation of the contribution of terriginous carbon to the marine food web in Bayboro Harbor, Tampa Bay, Florida. Cont Mar Sci 29: 131-139

Connolly RM, Gorman D, Guest MA (2005) Movement of carbon among estuarine habitats and its assimilation by invertebrates Oecologia 144: 684-691

Cornett VC (2006) Spatial distribution of submerged aquatic vegetation in the Shark River estuary and implications for understanding movement and feeding patterns of manatees (*Trichechus manatus latirostris*). MS thesis, Florida International University, Miami, Florida

Davis JLD, Metcalfe WJ, Hines AH (2003) Implications of a fluctuating fish predator guild on behavior, distribution, and abundance of a shared prey species: the grass shrimp *Palaemonetes pugio*. J Exp Mar Bio Ecol 293: 23-40

Davis SM, Childers DL, Lorenz JJ, Wanless HR, Hopkins TE (2005) A conceptual model of ecological interactions in the mangrove estuaries of the Florida Everglades. Wetlands 25: 832-842

DeAngelis DL (1994) Synthesis: spatial and temporal characteristics of the environment. In: Davis SM, Ogden JC (eds) Everglades: The ecosystem and its restoration. St. Lucie Press, Boca Raton, p 307-320

Deegan LA, Garritt RH (1997) Evidence for spatial variability in estuarine food webs. Mar Ecol Prog Ser 147: 31-47

DeNiro MJ, Epstein S (1978) Influence of diet on the distribution of carbon isotopes in animals. Geo et Cosm Acta 42: 495-506

DeNiro MJ, Epstein S (1981) Influence of diet on the distribution of nitrogen isotopes in animals. Geo et Cosm Acta 45: 341-351

Dittel AI, Epifanio CE (1990) Seasonal and tidal abundance of crab larvae in a troical mangrove system, Gulf of Nicoya, Costa Rica. Mar Ecol Prog Ser 65: 25-34

Dittmar T, Lara RJ, Kattner G (2001) River or mangrove? Tracing major organic matter sources in tropical Brazilian coastal waters. Mar Chem 73: 253-271

Dobkin S, Manning RB (1964) Osmoregulation in two species of *Palaemonetes* (Crustacea: Decopoda) from Florida. Bull Mar Sci Gulf Car 14: 149-157

Duever MJ, Meeder JF, Meeder LC, McCollom JM (1994) The climate of south Florida and its role in shaping the Everglades ecosystem. In: Davis SM, Ogden JC (eds) Everglades: The ecosystem and its restoration. St. Lucie Press, Boca Raton, p 225-248

Everhart WH, Youngs WD (1981) Principles of fisheries science, 2nd edition. Comstock, Ithaca

Fennema RJ Neidrauer CJ, Johnson RA, MacVicar TK, Perkins WA (1994) A computer model to simulate natural everglades hydrology. In: Davis SM, Ogden JC (eds) Everglades: The ecosystem and its restoration. St. Lucie Press, Boca Raton, p 225-248

Fry B (2006) Stable isotope ecology. Springer, New York

Fry B, Baltz DM, Benfield MC, Fleeger JW, Gace A, Haas HL, Quinones-Rivera ZJ (2003) Stable isotope indicators of movement and residency for brown shrimp (*Farfantepenaeus aztecus*) in coastal Louisiana marshscapes. Estuaries 26:82-97

Fry B (2002) Conservative mixing of stable isotopes across estuarine salinity gradients: A conceptual framework for monitoring watershed influences on downstream fisheries production. Estuaries 25:264-271

Fry B, Smith TJ (2002) Stable isotope studies of red mangroves and filter feeders from the Shark River estuary, Florida. Bull Mar Sci 70:871-890

Fry B, Bern AL, Ross MS, Meeder JF (2000) δ^{15}N studies of nitrogen use by the red mangrove, *Rhizophora mangle* L. in south Florida. Est Coast Shelf Sci 50:291-296

Fry B, Sherr E (1984) δ^{13}C measurements as indicators of carbon flow in marine freshwater ecosystems. Cont Mar Sci 27:13-47

Gallin RB (2002) Effects of salinity and temperature on survival and behavior of two sympatric species of grass shrimp, *Palaemonetes pugio* and *Palaemonetes vulgaris*, and implications of these effects on their distribution at Point Lookout State Park, Maryland. . PhD dissertation, George Washington University, Washington DC

Goodfriend DS (2004) The relative value of seagrass, marsh edge, and oyster habitats to the brackish grass shrimp, *Palaemonetes intermedius*, along the gulf coast of Florida. MS thesis, University of Florida, Gainesville, Florida

Gonazalez-Ortegon E, Pascual E, Cuesta JA, Drake P (2006) Field distribution and osmoregulartory capacity of shrimps in a temperate European estuary (SW Spain). Est Coast Shelf Sci 67: 293-302

Gray CA (1991) Demographic patterns of the palaemonid prawn *Macrobrachium intermedium* in southeastern Australia: spatial heterogeneity and the effects of species of seagrass. Mar Ecol Prog Ser 75: 239-249

Green D, Trexler JC, Lorenz JJ, McIvor CC, Philippi T (2006) Spatial patterns of fish communities along two estuarine gradients in southern Florida. Hydrobiologia 569: 387-399

Greenwood MFD, Matheson RE, McMichael RH, MacDonald TC (2007) Community structure of shoreline nekton in the estuarine portion of the Alafia River, Florida: Differences along a salinity gradient and inflow-related changes. Est Coast Shelf Sci 74: 223-238

Gregg CS, Fleeger JW (1998) Grass shrimp *Palaemonetes pugio* predation on sediment- and stem-dwelling meiofauna: field and laboratory experiments. Mar Ecol Prog Ser 175: 77-86

Guest MA, Connolly RM, Lee SY, Loneragan NR, Breitfuss MJ (2006) Mechanism for the small-scale movement of carbon among estuarine habitats: organic matter transfer not crab movement. Oecologia 148: 88-96

Gunderson LH, Loftus WF (1993) The Everglades. In: Martin WH, Boyce SG, Echternacht AC (eds) Biodiversity of the Southeastern United States. John Wiley and Sons, New York, p 199-255

Haines EB, Montague CL (1979) Food sources of estuarine invertebrates analyzed using $^{13}C/^{12}C$ ratios. Ecology 60: 48-56

Hart EA, Lovvorn JR (2002) Interpreting stable isotopes from macroinvertebrate foodwebs in saline wetlands. Limn Oceano 47: 580-584

Jaffe R, Childers DL, Boyer J, Fourqurean J, Trexler J (2007) Florida Coastal Everglades LTER. Final Report for NSF Award # 9910514.

Jordan F (1996) Spatial ecology of decapods and fishes in a northern Everglades wetland mosaic. PhD dissertation, University of Florida, Gainesville, Florida

Jordan F, Babbitt KJ, McIvor CC, Miller SJ (2000) Contrasting patterns of habitat use by prawns and crayfish in a headwater marsh of the St. Johns River, Florida. J Crust Biol 20: 769-776

Kathiresan K, Bingham BL (2001) Biology of mangroves and mangrove ecosystems. Advances in Mar Bio 40: 81-251

Khan RN, Merchant HC, Knowlton RE (1997) Effects of macrophytic cover on the distribution of grass shrimps, *Palaemonetes pugio* and *P. vulgaris*. Inv Biol 116: 243-247

Kneib RT, Craig AH (2001) Efficacy of minnow traps for sampling mummichogs in tidal marshes. Estuaries 24: 884-893

Kneib RT (1985) Predation and disturbance by grass shrimp, *Palaemonetes pugio* Holthuis, in soft-substratum benthic invertebrate assemblages. J Exp Mar Bio Ecol 93: 91-102

Knowlton RE, Kirby DF (1984) Salinity tolerance and sodium balance in the prawn *Palaemonetes pugio* Holthuis, in relation to other *Palaemonetes* spp. Comp Biochem Physiol 77A: 425-430

Knowlton RE, Vargo CK (2004) The larval morphology of *Palaemon floridanus* Chance, 1942 (Decapoda, Palaemonidae) compared with other species of *Palaemon* and *Palaemonetes*. Crustaceana 77: 683-715

Kupschus S, Tremain D (2001) Associations between fish assemblages and environmental factors in nearshore habitats of a subtropical estuary. J Fish Biol 58: 1383-1403

Kushlan JA, Kushlan MS (1980) Population fluctuations of the prawn, *Palaemonetes paludosus*, in the Everglades. Am Midl Nat 103: 401-403

Levesque VA (2004) Water flow and nutrient flux from five estuarine rivers along the south-west coast of the Everglades National Park, Florida, 1997-2001. United States Geological Survey Scientific Investigations Report 2004-5412

Ley JA, McIvor CC (2002) Linkages between estuarine and reef fish assemblages: enhancement by the presence of well-developed mangrove shorelines. In: Porter JW, Porter KG (eds) The Everglades, Florida Bay and Coral Reefs of the Florida Keys: an Ecosystem Sourcebook. CRC Press, Boca Raton, p 539-562

Ley JA, McIvor CC, Montague CL (1999) Fishes in mangrove prop-root habitats of northeastern Florida Bay: distinct assemblages across an estuarine gradient. Estuar Coast Shelf Sci 48: 701-723

Liston SE, Katin N, Lorenz JJ (2007) Sampling aquatic fauna in cypress forests, Big Cypress National Preserve. In: Liston SE, Lorenz JJ, McIvor CC, Loftus WF (eds) Development and Testing of Protocols for Sampling Fishes in Forested Wetlands of Southern Florida. Final Report to the U.S. Army Corps of Engineers, Everglades National Park, and the U.S. Geological Survey.

Loftus WF (2000) Accumulation and fate of mercury in an Everglades aquatic food web. PhD dissertation, Florida International University, Miami, Florida

Loftus WF, Eklund AM (1994) Long-term dynamics of an Everglades small-fish assemblage. In: Davis SM, Ogden JC (eds) Everglades: The ecosystem and its restoration. St. Lucie Press, Boca Raton, p 461-483

Lonergan NR, Bunn SE, Kellaway DM (1997) Are mangroves and seagrasses sources of organic carbon for panaeid prawns in a tropical Australian estuary? A multiple stable isotope study. Mar Biol 130: 289-300

Lowe BT, Provenzano AJ (1990) Survival and reproduction of *Palaemonetes paludosus* (Gibbes, 1850) (Decapoda: Palaemonidae) in saline water. J Crust Biol 10: 639-647

Manning RB (1961) A redescription of the palaemonid shrimp, *Leander paulensis* Ortmann, based on material from Florida. Bull Mar Sci Gulf Car 11: 525-536

Matheson RE, Camp DK, Sogard SM, Bjorgo KA (1999) Changes in seagrass-associated fish and crustacean communities on Florida Bay mud banks: The effects of recent ecosystem changes? Estuaries 22: 534-551

McCutchan JH, Lewis WM, Kendall C, McGrath CC (2003) Variation in trophic shift for stable isotope ratios of carbon, nitrogen, and sulfur. Oikos 102: 378-390

McIvor CC, Silverman N, Kuss K (2007) Sampling fishes in mangrove forests of Everglades National Park. In: Liston SE, Lorenz JJ, McIvor CC, Loftus WF (eds) Development and Testing of Protocols for Sampling Fishes in Forested Wetlands of Southern Florida. Final Report to the U.S. Army Corps of Engineers, Everglades National Park, and the U.S. Geological Survey.

McIvor CC, Ley JA, Bjork RD (1994) Changes in fresh-water inflow from the Everglades to Florida Bay including effects on biota and biotic processes: a review. In: Davis SM, Ogden JC (eds) Everglades: The ecosystem and its restoration. St. Lucie Press, Boca Raton, p 117–146

McPherson BF (1970) Hydrobiological characteristics of Shark River Estuary, ENP, FL. United States Geological Survey, Water Resources Division. Tallahassee, Florida. p 1-109

Nagelkerken I, Van der velde G, Gorissen MW, Meijer GJ, van't Hof T, den Hartog C (2000) Importance of mangroves, seagrass beds and the shallow coral reef as a nursery for important coral reef fishes, using a visual census technique. Est Coast Shelf Sci 51: 31-44

Newell RIE, Marshal N, Sasekumar A, Chong VC (1995) Relative importance of benthic microalgae, phytoplankton, and mangroves as sources of nutrition for penaeid prawns and other coastal invertebrates from Malaysia. Mar Biol 123: 595-606

Odum WE, McIvor CC, Smith TJ (1982) The ecology of the mangroves of south Florida: A community profile. US Fish and Wildlife Service, Office of Biological Services, Washington, DC FWS/OBS-81/24 p 144

Odum WE, Heald EJ (1972) Trophic analyses of an estuarine mangrove community. Bull Mar Sci 22: 671-738

Parker PL, Anderson RK, Lawrence AL (1991) Stable isotope methodology for evaluation of nutritional requirement of shrimp. In: DeLoach P, Dougherty WJ, Davidson MA (eds) Frontiers in shrimp research. Elsevier, Amsterdam, p 157-171

Peterson BJ, Fry B (1987) Stable isotopes in ecosystem studies. Ann Rev Ecol Sys 18: 293-320

Peterson GW, Turner RE (1994) The value of salt marsh edge vs interior as a habitat for fish and decapod crustaceans in a Louisiana tidal marsh. Estuaries 17: 235-262

Post DM (2002) Using stable isotopes to estimate trophic position: models, methods, and assumptions. Ecology 83: 703-718

Rehage JS, Trexler JC (2006) Assessing the net effect of anthropogenic disturbance on aquatic communities in wetlands: community structure relative to distance from canals. Hydrobiol 569: 359-373

Rehage JS, Loftus WF (2007) Seasonal fish community variation in headwater mangrove creeks in the southwestern Everglades: An examination of their role as dry-down refuges. Bull Mar Sci 80: 625-645

Reich KJ, Worthy GAJ (2006) An isotopic assessment of the feeding habits of free-ranging manatees. Mar Ecol Prog Ser 322: 303-309

Richards SA (2005) Testing ecological theory using the information-theoretic approach: examples and cautionary results. Ecology 86: 2805-2814

Roberston AI, Blaber SJM (1992) Plankton, epibenthos and fish communities. In: Roberston AI, Alongi DM (eds) Tropical mangrove ecosystems (Coastal and estuarine studies; 41) American Geophysical Union, Washington DC, p 173-224

Ronnback P, Troell M, Kautsky N, Primavera JH (1999) Distribution pattern of shrimps and fish among *Avicennia* and *Rhizophora* microhabitats in the Pagbilao mangroves, Philippines. Est Coast Shelf Sci 48: 223-234

Rowe CL (2002) Differences in maintenance energy expenditure by two estuarine shrimp (*Palaemonetes pugio* and *P. vulgaris*) that may permit partitioning of habitats by salinity. Comp Biochem Phys Part A 132: 341-351

Rozas LP, Minello TJ, Munuera-Fernandez I, Fry B, Wissel B (2005) Macrofaunal distributions and habitat change following winter-spring releases of freshwater in to the Breton Sound estuary, Louisiana (USA). Est Coast Shelf Sci 65: 319-336

Sheaves M, Johnston R (2009) Ecological drivers of spatial variability among fish fauna of 21 tropical Australian estuaries. Mar Ecol Prog Ser 385: 245-260

Sheridan P, Hays C (2003) Are mangroves nursery habitat for transient fishes and decapods? Wetlands 23: 449-458

Sheridan PF (1992) Comparative habitat utilization by estuarine macrofauna within the mangrove ecosystem of Rookery Bay, Florida. Bull Mar Sci 50: 21-39

Simenstad CA, Wissmar RC (1985) ^{13}C evidence of the origins and fates of organic carbon in estuarine and nearshore food webs. Mar Ecol Prog Ser 22: 141-152

Smith TJ, Whelan KT (2006) Development of allometric relations for three mangrove species in South Florida for use in the greater Everglades ecosystem restoration. Wetlands Ecol Man 14: 409-419

Smith TJ, Robblee MB, Wanless HR, Doyle TW (1994) Mangroves, hurricanes, and lightning strikes. Biosci 44: 256-262

Staples DJ, Vance DJ, Loneragan NR (1995) Penaeid prawn recruitment variability: effect of the environment. In: Courtney AJ, Cosgrove MG (eds) Proceedings of the workshop on spawning stock-recruitment relationships (SRRs) in Australian crustacean fisheries. Department of primary industries, Brisbane

Sulzman E (2007) Stable isotope chemistry and measurement: a primer. In: Michener R, Lajtha K (eds) Stable isotopes in ecology and environmental science. Blackwell Publishing, Cambridge

Sutula MA, Perez BC, Reyes E, Childers DL, Davis S, Day JW, Rudnick D, Sklar F (2003) Factors affecting spatial and temporal variability in material exchange between the southern Everglades wetlands and Florida Bay (USA). Est Coast Shelf Sci 57: 757-781

Tabb DC, Dubrow DL, Manning RB (1962) The ecology of northern Florida Bay and adjacent estuaries. Florida Board of Conservation, Tech Ser No. 39, p 1-81

Thorp JH (1976) Interference competition as a mechanism of coexistence between two sympatric species of the grass shrimp *Palaemonetes* (Decapoda: Palaemonidae). J Exp Mar Biol Ecol 25: 19-35

Turner AM, Trexler JC, Jordan CF, Slack SJ, Geddes P, Chick JH, Loftus WF (1999) Targeting ecosystem features for conservation: standing crops in the Florida Everglades. Cons Biol 13: 898-911

Underwood AJ (1997) Experiments in ecology. Cambridge University Press, Cambridge

Vance DJ, Haywood MDE, Heales DS, Kenyon RA, Loneragan NR (1998) Seasonal and annual variation in abundance of postlarval and juvenile banana prawns *Penaeus merguiensis* and environmental variation in two estuaries in tropical northeastern Australia: a six year study. Mar Ecol Prog Ser 163: 21-36

Vance DJ, Haywood MDE, Heales DS, Kenyon RA, Loneragan NR, Pendrey RC (1996) How far do prawns and fish move into mangroves? Distribution of juvenile banana prawns *Penaeus merguiensis* and fish in a tropical mangrove forest in northern Australia. Mar Ecol Prog Ser 131: 115-124

Vander Zanden MJ, Resmussen JB (2001) Variation in δ^{15}N and δ^{13}C and trophic fractionation: implications for aquatic food web studies. Limnol Oceanogr 46: 2061-2066

Vander Zanden MJ, Resmussen JB (1999) Primary consumer δ^{13}C and δ^{15}N and the trophic position of aquatic consumers. Ecology 80: 1395-1404

Wehrtmann IS, Dittel AI (1990) Utilization of floating mangrove leaves as a transport mechanism of estuarine organisms, with emphiasis on decapod crustacea. Mar Ecol Prog Ser 60: 67-73

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

Wessell KJ, Merritt RW, Cummins KW (2001) Distribution, diel movement, and growth of the grass shrimp *Palaemonetes paludosus* in the Kissimmee River-floodplain ecosystem, Florida. Ann Limnol 37: 85-95

Williams, AB (1984) Shrimps, lobsters, and crabs of the Atlantic coast of the Eastern United States, Maine to Florida. Washington D.C.: Smithsonian Institution Press

Williams AJ, Trexler JC (2006) A preliminary analysis of the correlation of food-web characteristics with hydrology and nutrient gradients in the southern Everglades. Hydrobiol 569: 493-504.

Wissel B, Fry B (2005) Tracing Mississippi River influences in estuarine food webs of coastal Louisiana. Oecologia 144: 659-672

Wolanski E, Brinson MM, Cahoon DR, Perillo GME (2009) Coastal wetlands: A synthesis. In: Perillo GME, Wolanski E, Cahoon DR, Brinson MM (eds) Coastal wetlands: An integrated ecosystem approach. Elsevier, Amsterdam

Woods J Zucker M (2008) Coastal gradients of flow, salinity and nutrients. Annual summary report to the U.S. Army Corps of Engineers, Everglades National Park, and the U.S. Geological Society

Zupo V, Nelson WG (1999) Factors influencing the association patterns of *Hippolyte zostericola* and *Palaemonetes intermeidus* (Decaopda: Natantia) with seagrasses of the Indian River Lagoon, Florida. Mar Biol 134: 181-190

Appendix A. Palaemonid shrimp collected at study sites throughout Shark River Estuary. Palaemonid shrimp have similar morphological characters making them difficult to identify to species.   Below are key characteristics used for identification of the five species collected, including the number of dorsal and ventral teeth on the rostrum (A), the length of the fused versus free part of the antennules (B), and the number of teeth present on the second pereopod (C) (Williams, 1984; Anderson, 1985; Abele and Kim, 1986). Images were taken with LEICA camera purchased by the SFWMD.

*Palaemonetes paludosus*

A

B

C

Common name: Riverine grass shrimp Natural range: NJ to FL, but also occurs in MS, LA, TX, and OK Salinity range: 0-10, but have been captured in salinities as high as 25

a) Rostrum: 6-8 dorsal teeth, 3-4 ventral teeth.
b) Antennules: Fused longer than free.
c) Second pereopod: No teeth present.

Palaemonetes intermedius

A

B

C
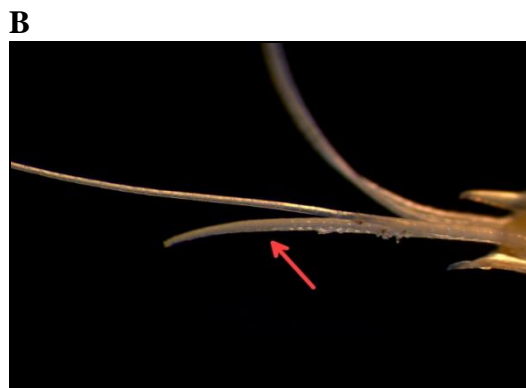
Common name: Brackish grass shrimp
Natural range: MA to TX and Mexico
Salinity range: 1-20.4

a) Rostrum: 7-10 dorsal teeth,
                    4-5 ventral teeth
b) Antennules: Fused shorter than free
c) Second pereopod: 1 tooth present

Palaemonetes pugio

A

B

C
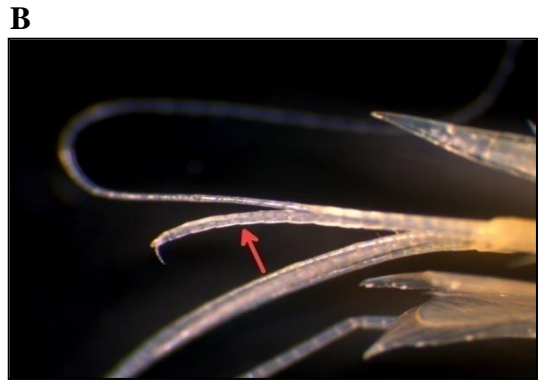
Common name: Daggerblade grass shrimp
Natural range: Nova Scotia to TX
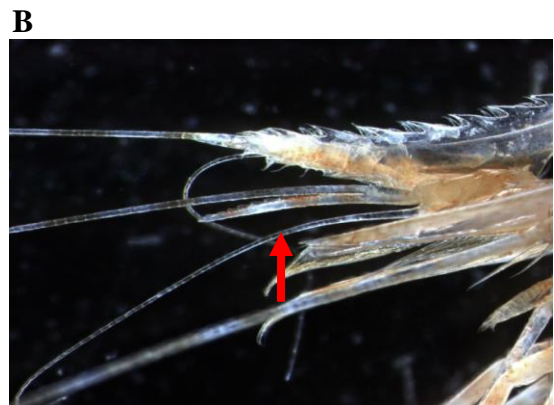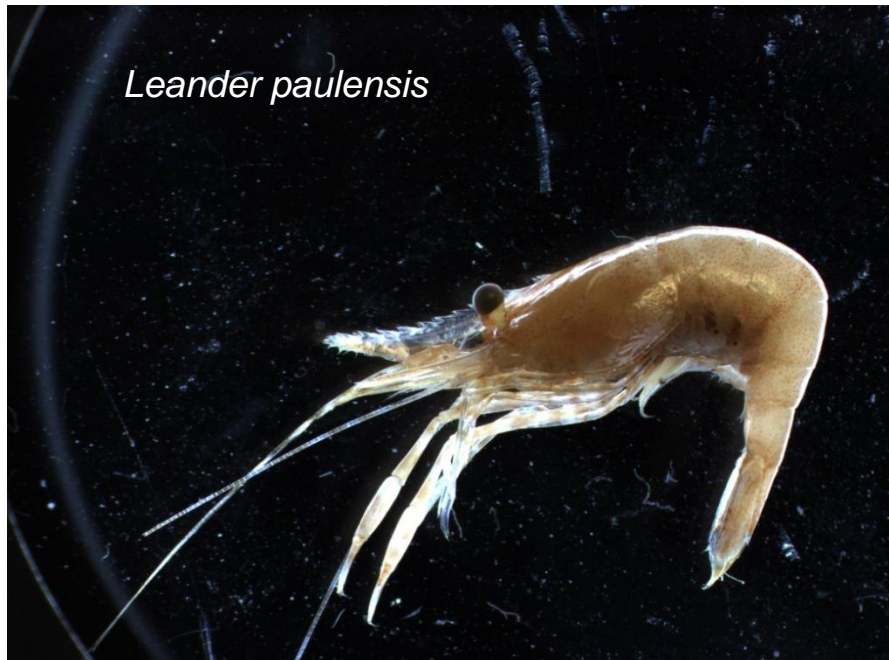Salinity range: 2-36

a) Rostrum: 5-7 dorsal teeth,
              2-4 ventral teeth
b) Antennules: Fused as long as free
c) Second pereopod: No teeth present

Palaemon floridanus

A

B

C

Common name: Florida grass shrimp
Natural range: Thought to be restricted
to southwestern FL, but recently has been
collected along the southern TX coast
(Knowlton and Vargo, 2004)
Salinity range: 22-31

a) Rostrum: 7-10 dorsal teeth
b) Antennules: Fused longer than free
c) Second pereopod: 2 teeth present

Leander paulensis

A

B

C

Common name: Red algae shrimp
Natural range: FL, Caribbean, Brazil
Salinity range: 16-36.5

a) Rostrum: 9-11 dorsal teeth, 5-6 ventral teeth
b) Antennules: Fused shorter than free
c) Second pereopod: 3 teeth present