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

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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

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Committee Member : __________________________
William F. Loftus, Ph.D.
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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. δ¹⁵N 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 δ¹³C 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 ($\delta^{13}$C) provide insights into the dietary carbon sources, whereas stable nitrogen isotope ratios ($\delta^{15}$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 cellulososa*) 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.
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 ± 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 (\(\delta\)) notation and calculated relative to an accepted standard by:

\[
\delta X \,(\%) = \left( \frac{R_{\text{SAMPLE}}}{R_{\text{STANDARD}}} - 1 \right) \times 1000,
\]

where \(X\) is either \(^{13}\text{C}\) or \(^{15}\text{N}\), and \(R\) is the ratio of the heavy isotope to the light isotope (e.g., \(^{13}\text{C} : ^{12}\text{C}\), and \(^{15}\text{N} : ^{14}\text{N}\)). The standard for carbon is Vienna Pee Dee Belemnite (VPDB) and the standard for nitrogen is atmospheric nitrogen. Negative \(\delta\) values indicate depletion relative to the standard, whereas positive \(\delta\) 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 δ¹³C and δ¹⁵N 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
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,
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.
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.

<table>
<thead>
<tr>
<th>Palaemonid Shrimp</th>
<th>Source of Variation</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Site x Season</td>
</tr>
<tr>
<td>P. paludosus</td>
<td>-</td>
</tr>
<tr>
<td>F, p</td>
<td>-</td>
</tr>
<tr>
<td>AIC</td>
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<tr>
<td>P. pugio</td>
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</tr>
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<td>F, p</td>
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</tr>
<tr>
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<td>F, p</td>
<td>-</td>
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<td>Pal. foridanus</td>
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<td>F, p</td>
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<tr>
<td>L. paulensis</td>
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<tr>
<td>F, p</td>
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</tr>
<tr>
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<td>Total CPUE</td>
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<tr>
<td>F, p</td>
<td>-</td>
</tr>
<tr>
<td>AIC</td>
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</table>
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 $\delta^{15}$N, but two-way interactions revealed that seasonal differences had more of an effect than site on shrimp $\delta^{15}$N variation. Shrimp $\delta^{13}$C values were significantly different across site, species, and seasons.

In the dry season, $\delta^{13}$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 $\delta^{13}$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* $\delta^{13}$C values were the most depleted of all species (Table 3). In the wet season, *P. paludosus* $\delta^{13}$C values from all sites except RB 10 were tightly grouped despite being from different sites (Fig. 6b). *P. intermedius* $\delta^{13}$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 $\delta^{15}$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* $\delta^{15}$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

<table>
<thead>
<tr>
<th>Source of Variation</th>
<th>$\delta^{13}$C</th>
<th></th>
<th></th>
<th>$\delta^{15}$N</th>
<th></th>
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<td>F</td>
<td>p</td>
<td>df</td>
<td>F</td>
<td>p</td>
</tr>
<tr>
<td>Site</td>
<td>8, 214</td>
<td>15.56</td>
<td>&lt;.0001</td>
<td>8, 214</td>
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<td>Season</td>
<td>1, 213</td>
<td>1.64</td>
<td>0.2013</td>
<td>1, 213</td>
<td>1.17</td>
<td>0.2800</td>
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<td>Site x Species</td>
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<td>&lt;.0001</td>
<td>5, 213</td>
<td>2.26</td>
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<tr>
<td>Season x Species</td>
<td>3, 213</td>
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<td>3, 213</td>
<td>6.89</td>
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</tr>
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<td>Site x Season x Species</td>
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<td>0.0003</td>
<td>3, 213</td>
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<td>$R^2$</td>
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<td>0.829</td>
<td></td>
<td></td>
<td>0.792</td>
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</tbody>
</table>
Fig. 6. (A) Dry season and (B) Wet season mean $\delta^{13}$C and $\delta^{15}$N ratios for stable-isotopes ($\pm$ 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 δ\textsuperscript{13}C and δ\textsuperscript{15}N for palaemonid shrimp by sites and seasons (Values in parentheses are sample sizes, - no data)

<table>
<thead>
<tr>
<th>Species and site</th>
<th>δ\textsuperscript{13}C dry</th>
<th>δ\textsuperscript{13}C wet</th>
<th>δ\textsuperscript{15}N dry</th>
<th>δ\textsuperscript{15}N wet</th>
</tr>
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<tbody>
<tr>
<td><strong>P. paludosus</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>RB 10</td>
<td>-30.3 ± 0.19 (16)</td>
<td>-28.7 ± 0.22 (16)</td>
<td>10.9 ± 0.19 (16)</td>
<td>10.0 ± 0.31 (16)</td>
</tr>
<tr>
<td>RB 13</td>
<td>-31.9 ± 0.13 (8)</td>
<td>-</td>
<td>13.2 ± 0.27 (8)</td>
<td>-</td>
</tr>
<tr>
<td>RB 9</td>
<td>-</td>
<td>-27.6 ± 0.23 (13)</td>
<td>-</td>
<td>7.8 ± 0.27 (13)</td>
</tr>
<tr>
<td>RB 8</td>
<td>-</td>
<td>-27.1 ± 0.43 (8)</td>
<td>-</td>
<td>7.2 ± 0.24 (8)</td>
</tr>
<tr>
<td>SRS 4</td>
<td>-</td>
<td>-27.0 ± 0.57 (6)</td>
<td>-</td>
<td>7.4 ± 0.17 (6)</td>
</tr>
<tr>
<td>TB 1</td>
<td>-</td>
<td>-28.4 ± 0.82 (5)</td>
<td>-</td>
<td>7.0 ± 0.44 (5)</td>
</tr>
<tr>
<td>SRS 5</td>
<td>-</td>
<td>-27.2 ± 0.88 (2)</td>
<td>-</td>
<td>6.7 ± 0.70 (2)</td>
</tr>
<tr>
<td><strong>P. pugio</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>RB 13</td>
<td>-30.1 (1)</td>
<td>-</td>
<td>13.0 (1)</td>
<td>-</td>
</tr>
<tr>
<td>RB 9</td>
<td>-</td>
<td>-30.0 ± 0.35 (5)</td>
<td>-</td>
<td>10.9 ± 0.29 (5)</td>
</tr>
<tr>
<td>RB 8</td>
<td>-</td>
<td>-29.8 ± 0.26 (3)</td>
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<td>10.8 ± 0.12 (3)</td>
</tr>
<tr>
<td>SRS 4</td>
<td>-29.1 ± 0.26 (16)</td>
<td>-27.8 ± 0.21 (17)</td>
<td>10.0 ± 0.18 (16)</td>
<td>9.8 ± 0.13 (17)</td>
</tr>
<tr>
<td>TB 1</td>
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<td>-27.8 ± 0.21 (16)</td>
<td>9.7 ± 0.31 (5)</td>
<td>10.4 ± 0.17 (16)</td>
</tr>
<tr>
<td><strong>P. intermedius</strong></td>
<td></td>
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<td></td>
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</tr>
<tr>
<td>TB 1</td>
<td>-29.5 ± 0.37 (17)</td>
<td>-29.3 ± 1.01 (2)</td>
<td>9.9 ± 0.14 (17)</td>
<td>11.1 ± 0.61 (2)</td>
</tr>
<tr>
<td><strong>Pal. floridanus</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>SRS 5</td>
<td>-25.6 (1)</td>
<td>-27.2 ± 0.23 (12)</td>
<td>9.3 (1)</td>
<td>9.4 ± 0.12 (12)</td>
</tr>
<tr>
<td>SRS 6</td>
<td>-24.6 ± 0.21 (17)</td>
<td>-25.4 ± 0.23 (15)</td>
<td>9.0 ± 0.12 (17)</td>
<td>9.5 ± 0.10 (15)</td>
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<tr>
<td>PDLB 1</td>
<td>-22.9 ± 0.34 (13)</td>
<td>-21.9 ± 0.16 (8)</td>
<td>10.0 ± 0.15 (13)</td>
<td>9.8 ± 0.08 (8)</td>
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<tr>
<td><strong>L. paulensis</strong></td>
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<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>SRS 5</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>8.46 (1)</td>
</tr>
<tr>
<td>SRS 6</td>
<td>-</td>
<td>-26.1 ± 0.62 (9)</td>
<td>-</td>
<td>8.6 ± 0.28 (9)</td>
</tr>
<tr>
<td>PDLB 1</td>
<td>-</td>
<td>-23.6 ± 0.51 (14)</td>
<td>-</td>
<td>9.5 ± 0.12 (14)</td>
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</tbody>
</table>
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
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 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 (Wehrmann & Dittel 1990). It is possible that palæamonid 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 palæamonid 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 palæamonid 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, palæamonid 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 palæamonid abundance and distribution as they prey on them.

Stable-isotope analysis helped elucidate palæamonid 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 palæamonid $^{13}$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
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 $\delta^{15}$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 $\delta^{13}$C and $\delta^{15}$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 $\delta^{13}$C and $\delta^{15}$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 $\delta^{15}$N and $\delta^{13}$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 $\delta^{15}$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 $\delta^{15}$N values, leading to misleading interpretations of trophic-level variation (Hart & Lovvorn 2002). Increases in $\delta^{15}$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 $\delta^{13}$C and $\delta^{15}$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 δ¹⁵N 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 (Thorpe 1976, Coen et al. 1981, Khan et al. 1997, Rowe 2002). Palaemonid shrimp δ¹³C values overlapped less during the dry season than the wet season. In the dry season, *P. intermedius* and *P. pugio* δ¹³C values from the mid-estuary were similar, whereas multiple species δ¹³C 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 δ\(^{13}\)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 δ\(^{13}\)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 δ\(^{13}\)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 δ\(^{13}\)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 δ\(^{13}\)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 δ\(^{13}\)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 δ\(^{13}\)C was more enriched than mangrove or terrestrial material, but not as enriched as seagrass, likely indicating a
mixture of carbon sources. Palaemonid $\delta^{13}$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
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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.

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.
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
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
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
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