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Distribution, diel movement, and growth of the grass shrimp *Palaemonetes paludosus* in the Kissimmee River-floodplain ecosystem, Florida

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Keywords : Crustacea, marsh, wetlands, aquatic macroinvertebrate, restoration.

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

Répartition, migration journalière et croissance de la crevette *Palaemonetes paludosus* dans la plaine humide inondable de la rivière Kissimmee, Floride

Mots clés : Crustacea, marais, plaine inondable, macroinvertébrés aquatiques, restauration.

Autrefois, la rivière Kissimmee effectuait des méandres dans une large plaine humide inondable. En réponse aux crues catastrophiques et aux impératifs de la réglementation en Floride Centrale, la rivière fut canalisée, transformant le réseau fluvial complexe en un canal rectiligne.

Le résultat fut une forte diminution des habitats riverains et des communautés associées. Sitôt après la fin des travaux de canalisation, par souci de l'environnement, l'Etat de Floride fut amené à examiner les options de restauration aptes à rétablir l'hydrologie naturelle de la rivière et à recréer les zones humides disparues.

La crevette *Palaemonetes paludosus* fut identifiée dans ce système comme une espèce clé d'invertébré. Cette étude avait pour objet d'examiner sa répartition, sa migration journalière et sa croissance dans les deux communautés dominantes de macrophytes des marais riverains de la rivière : *Nuphar* et *Polygonum*. Les résultats montrent que la crevette était plus abondante dans les herbiers de *Polygonum*. Cette espèce ne montrait également pas de migration journalière bien définie bien que nous ayons parfois observé un déplacement vertical significatif. La croissance de *Palaemonetes paludosus* était plus forte sur le périphyton et sur les feuilles de *Polygonum*. La répartition des crevettes peut s'expliquer par leur sensibilité moindre à la prédation à cause de la plus grande complexité des habitats dans les herbiers de *Polygonum*.

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1. Introduction

The Kissimmee River originates in the Kissimmee Lakes region of central Florida just south of Orlando and makes up the northern portion of the Kissimmee-Lake Okeechobee-Everglades watershed (Fig. 1a). Historically, the river was a complex braided channel that meandered approximately 166 km within a 1.5-3 km wide floodplain. In response to catastrophic flooding and settlement pressures in Central Florida, the U.S. Army Corps of Engineers began a project in 1962 that channelized the river. The once-meandering river was converted to a straightened, 9-m deep by 100-m wide canal and impounded into a series of five relatively stagnant storage reservoirs, so that water levels no longer fluctuated on a seasonal basis (Toth 1990). The project affected approximately 161 km of river and resulted in the conversion of 14,000 ha of floodplain wetland to pasture (Toth et al. 1995). The elimination of the seasonal water level fluctuations and the extensive loss of wetland plant communities have had significant effects on both invertebrate and vertebrate communities (Merritt et al. 1996). Specific effects of channelization on the biological communities include a 90 % decrease in the number of waterfowl and wading birds (Weller 1995), a decline in the proportion of game fish (Trexler 1995), and a shift in invertebrates to those more common in lentic systems (Harris et al. 1995).

In 1984, the South Florida Water Management District (SFWMD) initiated a demonstration project to evaluate effects of increasing flow and floodplain inundation within the channelized river. This was accomplished with a series of three weirs that directed additional flow through three remnant channels along the section of the river known as Pool B (Fig. 1b). Almost immediately upon completion of the demonstration project, wetland plant communities began to revert to those more characteristic of the historical system. Reintroduction of flow through this area also resulted in the colonization of invertebrate taxa more characteristic of lotic systems (Toth 1993) and increases in game fish (Wullschleger et al. 1990) and waterfowl (Toland 1990), relative to the unrestored portions of the river. The success of the demonstration project prompted the State of Florida to approve the SFWMD plan to backfill approximately 35 km of channelized river, which should eventually result in the restoration of about 11,000 ha of the historical floodplain wetland.

During the restoration process, ecological conditions have been monitored to evaluate the project's success at restoring the habitats and populations of river and floodplain species. Invertebrates are an integral part of aquatic ecosystems and can serve as a useful indication of the extent to which this system is responding to restoration efforts. The grass shrimp, *Palaemonetes paludosus* Gibbes, is particularly abundant in the remnant channels of the Kissimmee River floodplain ecosystem (Merritt et al. 1996, Merritt et al. 1999). Because of its high abundance and large size, it is a significant link between primary producers and detritus, and higher trophic levels in this ecosystem (Merritt et al. 1999).

Data from studies of marine and estuarine *Palaemonetes* suggest that interactions among grass shrimp, benthic predators, and nektonic omnivores have strong direct and indirect effects upon benthic faunal densities and community composition (Posey & Hines 1991). Additionally, Pringle et al. (1993) have determined that omnivorous shrimp are important organizers of lotic community structure and play a key role in reducing sediment cover on rock substrata and enhancing algal populations. Grass shrimp also have been shown to be important predators of phytoplankton grazers such as cladocerans. Also, they indirectly contribute to higher turbidity and eutrophication (Samuels & Mason 1998).

Palaemonetes paludosus is widespread in the eastern United States, and is found as far west as eastern Texas (Strenth 1976). This species is especially abundant in the extensive marshes and swamps of southern Florida (Kushlan & Kushlan 1980), and can be found among emergent vegetation, snags, or clinging to the undersides of vegetation mats. The body is transparent and ranges in size from 3-25 mm long (Meehean 1936). Although algae are the major food ingested, *P. paludosus* is omnivorous and may feed on dead leaves, insects and other benthic coarse particulate organic matter (Beck & Cowell 1976).

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

Females typically produce 8-85 eggs during their one-year life cycle and carry them for up to 2 months (Beck & Cowell 1976). Larval shrimp hatch from eggs after an incubation period of approximately 12-14 days at 26-28°C (Beck & Cowell 1976). Hatching to matu-

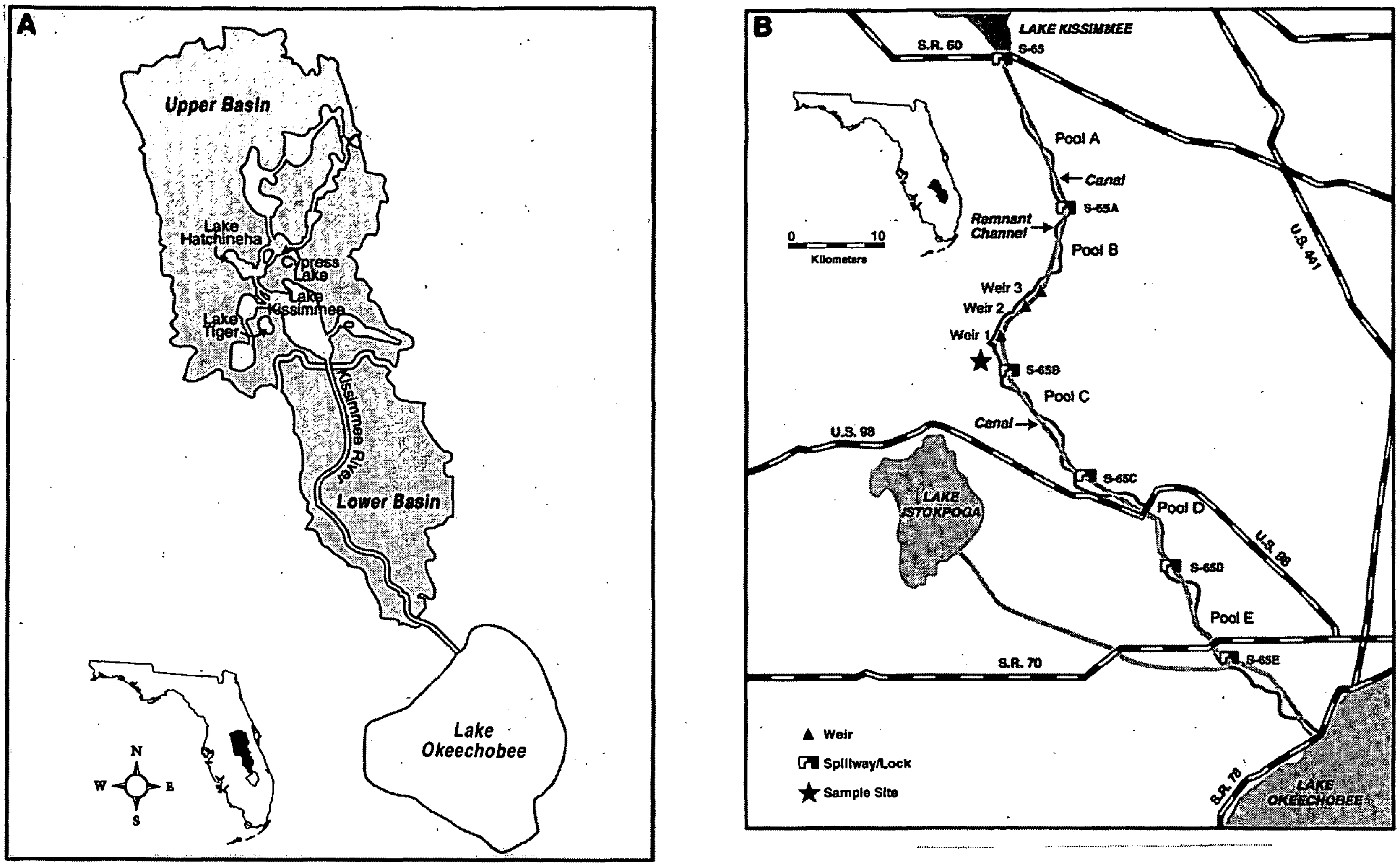

Fig. 1. a) The Kissimmee River basin from the 4229 km^2 upper basin headwaters in the Kissimmee Lakes through the 1200 km^2 lower basin and into Lake Okeechobee. Location of the basin in south-central Florida is indicated in the inset. b) Enlarged view showing Pools A-E and water control structures (Merritt et al. 1996).

Fig. 1. a) Bassin de la rivière Kissimee. Bassin supérieur (4229 km^2) jusqu'au Lac Kissimmee et bassin inférieur (120 km^2) jusqu'au Lac Okeechobee. La situation du bassin en Floride centro-méridionale est figurée en médaillon. b) Vue montrant les biefs A-E et les constructions hydrauliques pour la régularisation de l'eau (Merritt et al. 1996).

rity takes 2-3 months when water temperatures exceed 26°C, though cooler temperatures delay maturation (Beck & Cowell 1976).

Our goal was to gain a better understanding of how the restoration process and the resulting increase in floodplain habitat might affect the distribution and abundance of *P. paludosus* in the Kissimmee River-floodplain ecosystem. Three aspects of grass shrimp ecology in the restored Kissimmee River-floodplain were examined to evaluate the importance and success of this species. Specific objectives were to: 1) compare grass shrimp seasonal distribution and abundance with respect to macrophyte type; 2) determine grass shrimp diel movement patterns horizontally between the river and floodplain and vertically in the water column; and 3) determine grass shrimp growth rate as a function of the type of food consumed.

2. Methods and materials

2.1. Study site

The study site was located in the lower Pool B remnant channel of the Kissimmee River near Lorida, Florida, in the partially restored area affected by the demonstration project (Fig. 1b). Flow through this remnant channel was generally low compared to historical conditions. During the study period (1997-1999), water temperature ranged from about 25°C in the winter (February) to 35°C in the summer (August).

The two most dominant littoral fringe plant communities in this area are structurally very different. *Nuphar luteum* communities are characterized by relatively low mean stem densities (15/ m^2) (Cummins et al. 1999), high light penetration, and are generally considered autotrophic (Merritt et al. 1999). The majority of the primary productivity is due to the dense periphyton communities that colonize *Nuphar* stems, and this is potentially a rich food source for invertebrates (Cummins & Klug 1979). In contrast, *Polygonum densiflorum* beds are characterized by comparatively high mean stem densities (46/m^2), with very little subsurface light penetration (Cummins et al. 1999). Because of this, *Polygonum* communities are generally considered heterotrophic (Merritt et al. 1999). Dissolved oxygen levels were reported to be relatively low in both *Nuphar* and *Polygonum* beds (Wullschleger et al. 1990), but tended to be higher in the *Nuphar* beds than in the *Polygonum* beds, differing by between 1-2 mg/L (Fig. 2). Water depth in the macrophyte beds ranged between 45-110 cm during the study period.

2.2. Distribution and abundance

The two dominant littoral fringe habitats (*Nuphar luteum* and *Polygonum densiflorum*) of the Kissimmee River riparian marsh along the lower remnant channel of Pool B were sampled twice a year for two years under different flow and water level conditions. Vegetation was sampled by positioning a D-frame aquatic dip net (0.8 mm mesh) several centimeters into the sediments and vigorously moving it along the stems of the plants for 30 seconds. The net was moved from side to side and front to back through the plant bed to the surface to insure dislodgment of associated invertebrates (Merritt et al. 1996). On each sampling date, samples were taken from 18 randomly selected *Nuphar* beds and 18 randomly selected *Polygonum* beds. For each sample, the net and its contents were washed into an enamel tray. Coarse material was washed off by hand into a Whirlpac® bag and preserved with 70 % EtOH. Samples were returned to the lab for sorting and measuring of invertebrates under a dissecting microscope. The number of grass shrimp was recorded for each sample and biomass was calculated from measurements of the total length of each individual grass shrimp using INVERTCALC as described in Merritt et al. (1996).

Data from both summer samples (August 1997 and June 1998) were pooled and compared to data from pooled winter samples (February 1998 and Feb. 1999). Mean number of individuals and total biomass (mg) per sample by plant type and season were calculated

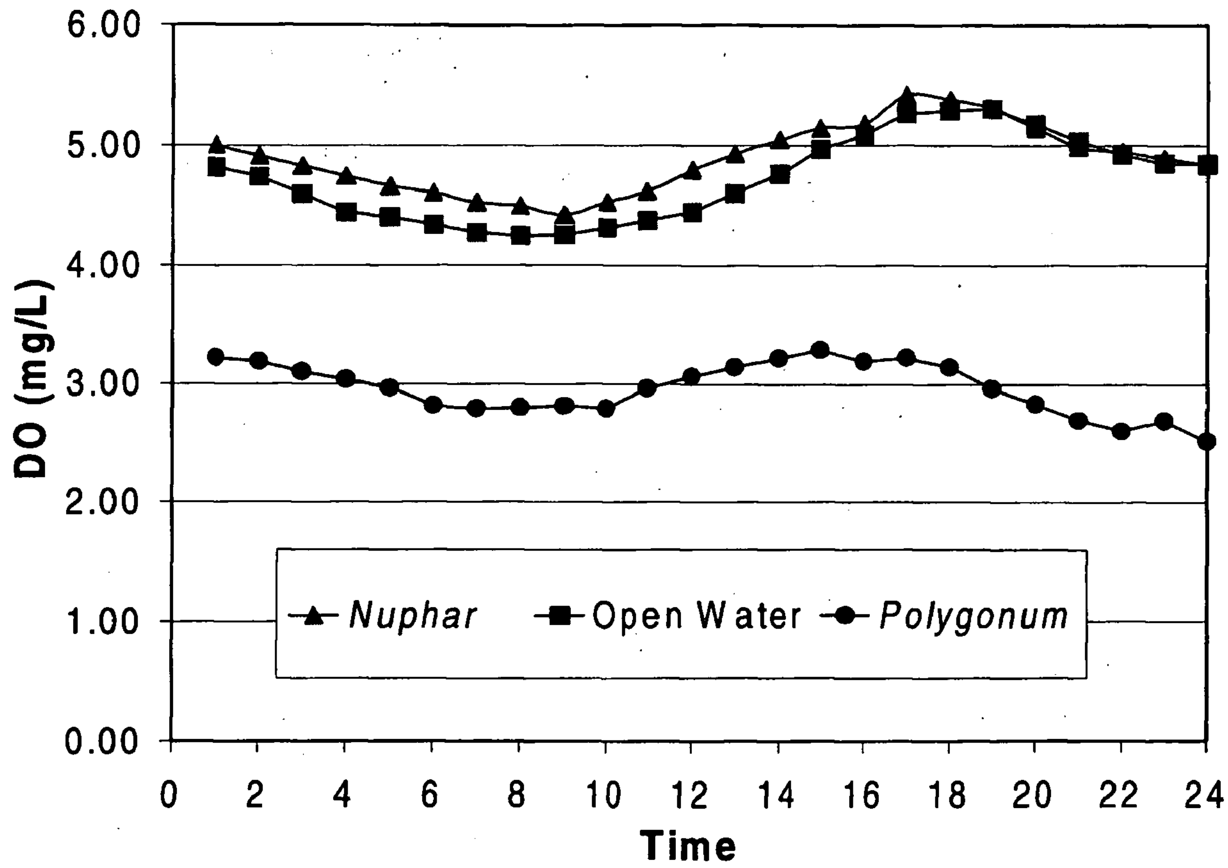

Fig. 2. Diel dissolved oxygen curve comparing two riparian marsh habitats (*Nuphar* and *Polygonum*) and open water (unpublished data collected in June 1998 by J. Brock, Rapid Creek Research).

Fig. 2. Comparaison des teneurs journalières en oxygène des deux marais riverains (*Nuphar* et *Polygonum*) et de l'eau libre. (Données non publiées récoltées en juin 1998 par J. Brock, Rapid Creek Research).

before log-transforming data in order to adhere to the ANOVA assumptions of normality and homogeneity of variance. Differences in grass shrimp distribution by plant type and season were analyzed with log-transformed data (log(y+1)) in a two-way ANOVA with season as the first factor (2 levels: summer and winter) and plant type as the second factor (2 levels: *Nuphar* and *Polygonum*) (SAS Institute 1996). Interactions were further dissected with Fisher's LSD tests (Fisher 1960).

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

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

2.3. Diel movement

Diel movement was examined by placing Breder traps (Breder 1960) at the margins of both *Polygonum* and *Nuphar* beds. Traps were placed in such a way as to capture grass shrimp as they moved between the river channel and the floodplain, and vertically within the water column. Traps were emptied just after sunrise and just before sunset to determine when shrimp movement was most pronounced. The opening of the traps fanned out to funnel invertebrates into a narrow opening to preclude larger fish from gaining entry, thus minimizing predation on captured shrimp. Previous studies showed that Breder traps are an efficient means of capturing small fish, and that the variety of invertebrates caught in these traps was equivalent to that of the fish (Breder 1960).

Data were pooled according to whether they came from day or night runs. Mean numbers of grass shrimp caught in top versus bottom traps, and traps opening toward the floodplain versus traps opening toward the channel were calculated. Significant differences in both vertical and horizontal grass shrimp movement were inferred from a Kruskal-Wallis non-parametric analysis of variance (SAS Institute 1996). Effects were considered significant when $p < 0.05$.

2.4. Growth studies

To determine grass shrimp growth on different food types, 180 shrimp of similar size were selected. A subsample of 30 shrimp was dried and weighed to obtain an estimate of initial dry mass. Remaining shrimp were used in the food treatments.

Grass shrimp growth was evaluated on three commonly available food sources in the dominant macrophyte communities in the lower Pool B remnant channel: 1) *Nuphar* stems coated with dense periphyton; 2) microbially-conditioned *Polygonum* leaves; and 3) fine detritus < 1mm in diameter (FPOM). The food was placed in Tupperware® growth containers (30 x 16 x 9 cm) (2 replications/food treatment). These containers were fitted with 500 µm-mesh panels on all sides and on the lid to allow circulation of stream water. Twenty-five shrimp were added to each container before it was tied down in the remnant river channel adjacent to Riverwoods Field Laboratory near Lorida, FL. Growth containers remained in the channel for approximately 150 degree days (6 days at 25°C). After this period, shrimp were removed from the growth containers, dried at 50°C for 24 h, and then weighed to obtain gross dry mass to the nearest mg. Mean initial dry mass was then subtracted from each individual's gross dry mass to obtain a measure of net dry mass gained for each grass shrimp that survived the experiment. Statistical analysis was conducted on the values for net dry mass.

3. Results

3.1. Distribution and abundance

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

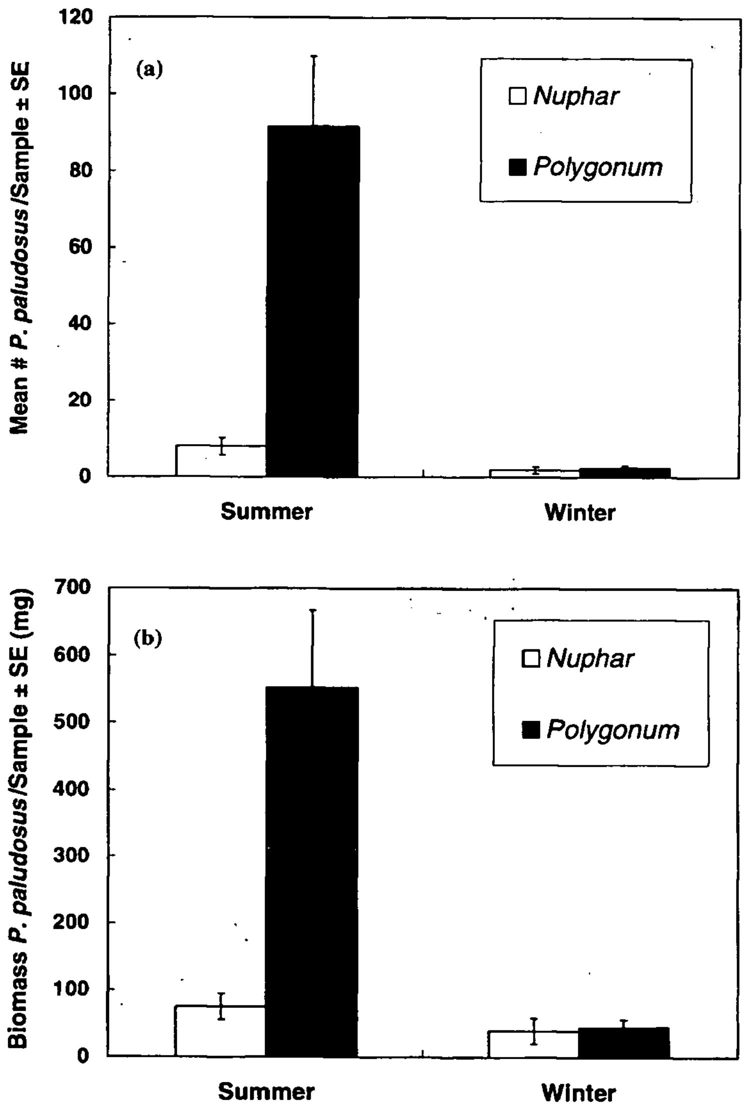

Fig. 3. a) Mean number and b) mean biomass (±SE) of *P. paludosus* in the dominant macrophyte habitats of the Kissimmee River riparian marsh.

Fig. 3. a) Nombre moyen et b) biomasse moyenne (± ES) par échantillon de *P. paludosus* dans les 2 herbiers dominants des marais riverains de la rivière Kissimmee.

Biomass results were similar to the numerical results. *Polygonum* beds supported significantly more grass shrimp biomass on average than *Nuphar* beds, with a mean of 298.5 mg per *Polygonum* sample and only 57.2 mg per *Nuphar* sample (df = 1; F = 12.76; p < 0.0001) (Fig. 3b). There also was a significant seasonal effect, with mean biomass per sample equal to 313.6 mg in the summer and only 42.1 mg in the winter (df = 1; F = 25.50; p = 0.0005) (Fig. 3b). However, there was no significant season by plant interaction when considering mean biomass instead of numbers (df = 1; F = 0.55; p = 0.4608). Results from Fisher's LSD test confirmed the ANOVA results and indicated that the plant effect was consistent throughout the year when considering values for biomass instead of numbers (Fig. 3b, Table 2).

There was no significant difference in mean size of shrimp between *Polygonum* and *Nuphar* plant communities (df = 1; F = 0.24; p = 0.6241). However, shrimp sampled in the winter were significantly larger than those sampled in the summer (df = 1; F = 16.16; p < 0.0001) (Fig. 4). The average grass shrimp captured in the summer samples weighed 8.06 mg, while the average shrimp captured in winter weighed 18.40 mg.

3.2. Diel movement

In *Polygonum* beds, shrimp capture rates were low, suggesting little shrimp movement overall. During the day, a mean of 0.6 shrimp per trap was captured moving from the channel into the floodplain, and the same number were captured moving out of the floodplain into the channel (p = 0.1683; Fig.5a). At night, these numbers differed only slightly: 0.9 and 1.0 shrimp respectively (Fig. 5b). In *Nuphar* beds, an average of 1.0 shrimp per

Table 1. Results from Fisher's LSD tests on season*plant combinations when considering average number of shrimp per sample. Log-transformed values were tested. Comparisons were not made between seasons.

Tableau 1. Résultats des tests LSD de Fisher sur les interactions saison*plante en considérant le nombre moyen de crevettes par échantillon. Les valeurs testées ont subi une transformation Log. Les comparaisons entre saisons n'ont pas été effectuées.

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

Table 2. Results from Fisher's LSD tests on season*plant combinations when considering average shrimp biomass per sample. Log-transformed values were tested. Comparisons were not made between seasons.

Tableau 2. Résultats des tests LSD de Fisher sur les interactions saison*plante en considérant la biomasse moyenne de crevettes par échantillon. Les valeurs testées ont subi une transformation Log. Les comparaisons entre saisons n'ont pas été effectuées.

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

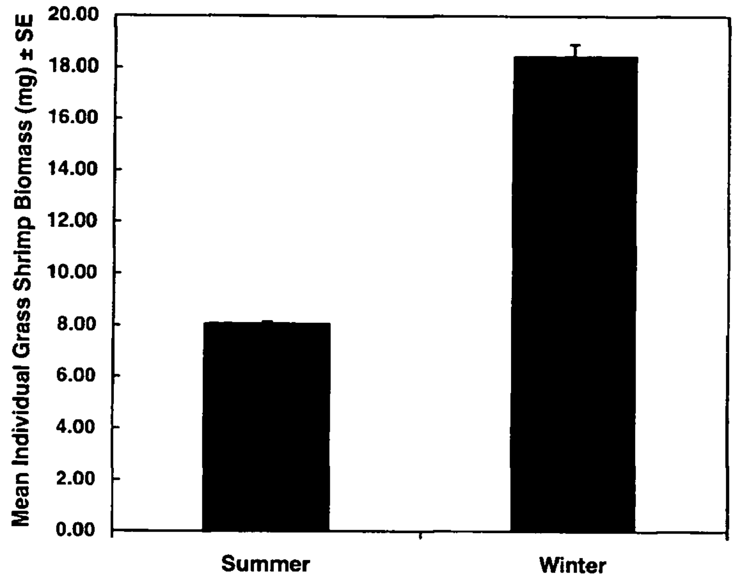

Fig. 4. Mean biomass of individual grass shrimp (± SE) calculated on a seasonal basis.

Fig. 4. Biomasse individuelle moyenne de la crevette (± SE) calculée par saison.

trap was caught moving from the channel to the floodplain, while 3.0 shrimp on average were captured moving into the channel during the day (Fig. 5a). However, these numbers were not significantly different. At night, differences in horizontal movement were similar to the daytime trials and were not significant: 1.7 shrimp per trap were captured moving from the channel, and 4.5 moving in the opposite direction (Fig. 5b).

A mean of 0.6 shrimp was caught in both top and bottom traps in *Polygonum* beds during the day (Fig. 6a). At night, slightly more shrimp were captured in bottom (mean = 1.3 per trap) versus top (mean = 0.6 per trap) traps in *Polygonum* (Fig. 6b). The results of the Kruskal-Wallis test showed no significant difference in these numbers. However, in *Nuphar* beds, an interesting pattern emerged, whereby differences in mean number of shrimp caught in top (0.5) versus bottom (3.5) traps were significant during the day (p =

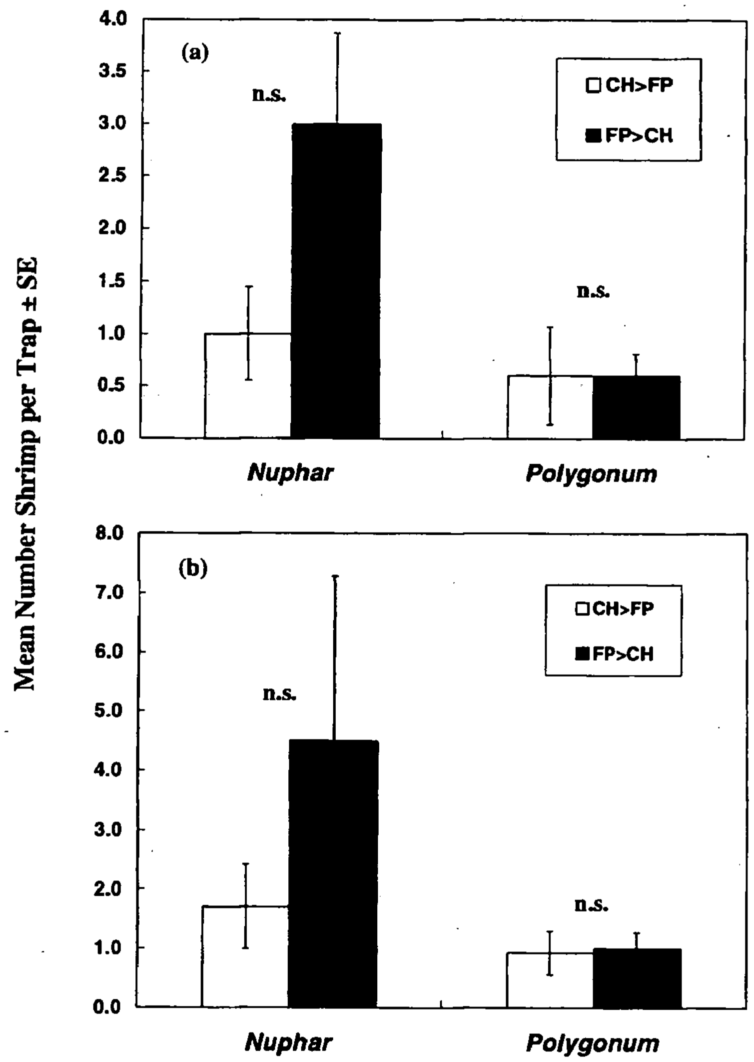

Fig. 5. Mean number ± SE of *P. paludosus* captured moving from the channel to the floodplain (CH > FP) and from the floodplain to the channel (FP > CH) during the day (a) and at night (b).

Fig. 5. Nombre moyen (± ES) de *P. paludosus* capturés en migration du canal → lit majeur (CH > FP) et dans le sens inverse pendant le jour (a) et la nuit (b).

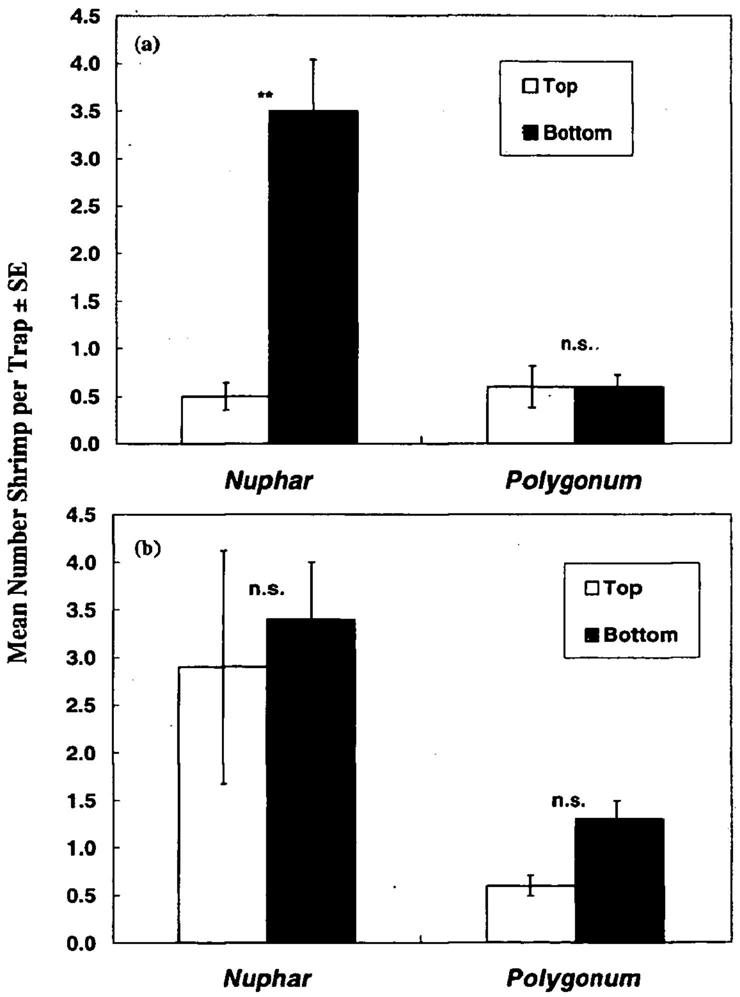

Fig. 6. Mean number ±SE of *P. paludosus* captured in top and bottom Breder traps (a) during the day and (b) at night. Significant differences at p<0.05 denoted by double asterisks.

Fig. 6. Nombre moyen (± ES) de *P. paludosus* capturés en surface et au fond à l'aide de pièges Breder (a) pendant le jour et (b) la nuit. Les différences significatives à p < 0.05 sont notées par un double astérisque.

0.0343; Fig. 6a). At night, 3.4 shrimp were caught in bottom traps and 2.9 were caught in top traps, which was not statistically significant (Fig. 6b).

3.3. Growth studies

Results from the grass shrimp growth studies showed at least some growth on all food treatments (Fig. 7). However, no significant net growth occurred on FPOM ($p = 0.3072$), with a mean net weight gained of only 1.99 ± 1.90 mg per shrimp after 150 degree-days. *Polygonum* leaves resulted in significant net growth after 150 degree days ($p = 0.0012$), with a mean increase of 4.03 ± 1.18 mg per shrimp. Periphyton on *Nuphar* stems resulted in the highest net growth overall, with a mean increase of 6.69 ± 3.04 mg per shrimp. However, there was no significant difference in net growth between shrimp grown on *Polygonum* leaves and shrimp grown on periphyton from *Nuphar* stems (Fig. 7).

4. Discussion and conclusions

With respect to distribution and abundance, it was shown that *P. paludosus* overwhelmingly preferred *Polygonum* beds to *Nuphar* beds. This trend differed from summer to winter when considering the numbers of grass shrimp, but was consistent throughout the year when considering biomass. Differences in mean shrimp size in the summer compared to the winter may help explain this disagreement in season by plant interactions between tests examining numbers and those examining biomass. The increase in average shrimp biomass in the winter samples makes up for the lower numbers of shrimp per sample and results in an insignificant interaction term when considering values for biomass instead of numbers.

Results indicated that summer samples contained shrimp in their early adult life, and winter samples appeared to be composed of this same cohort near the end of their life cycle. Additional sampling in early March confirmed that extremely high densities of larval shrimp (150-500 shrimp/sample) were being recruited into the populations. This is contrary to the findings of Kushlan & Kushlan (1980), who concluded that the percentage of ovigorous females was highest in the summer and fall, when water levels are the highest. This difference could be due to the altered hydrology of the Kissimmee River Pool B remnant channel.

The partially restored section of the Kissimmee River, where the study was conducted, was subject to stage management regimes. This may have confounded the detection of any inherent diel horizontal movement pattern because when water was being drawn down,

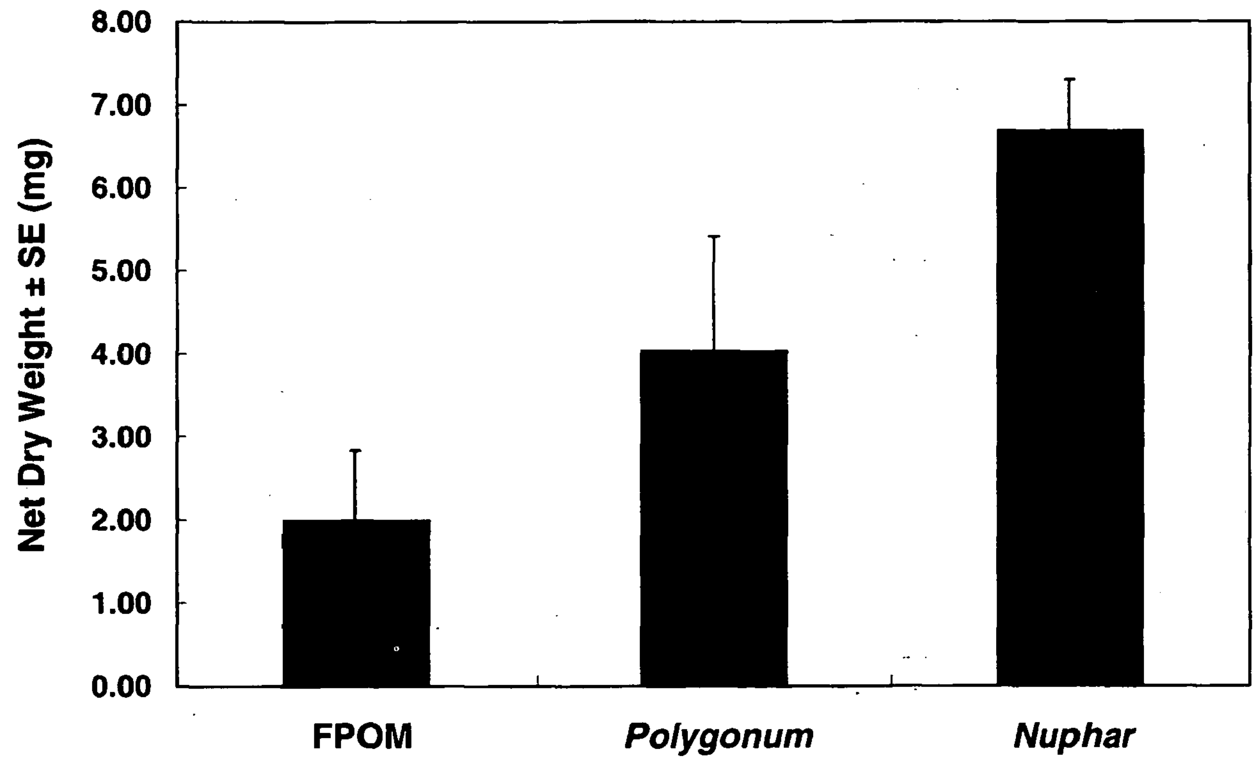

Fig. 7. Net dry weight of *P. paludosus* in each of the three food treatments. Data derived by subtracting the mean initial weight from each dried shrimp that survived the growth experiment.

Fig. 7. Poids sec net de *P. paludosus* pour chaque type de nourriture testée. Données obtenues en soustrayant le poids moyen initial au poids sec de chaque crevette ayant survécu à l'expérience.

shrimp were more likely to move out of the floodplain. Conversely, when water levels were increasing, shrimp had a greater opportunity to use the riparian marsh habitat.

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

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

Growth studies showed that senescent *Polygonum* leaves and *Nuphar*-derived periphyton both resulted in significant growth. Periphyton appeared to be the most nutritious food source for grass shrimp, although the net growth was not significantly higher for periphyton than it was for *Polygonum* leaves. This is consistent with the classification of *P. paludosus* as a facultative scraper/shredder (Merritt et al. 1999). Periphyton often provides a more balanced diet than live macrophytes, due to periphyton's low C/N ratio and the large quantities of cellulose and lignin in macrophytes which results in the decreased digestibility of macrophyte proteins (Cummins & Klug 1979). It may actually be more nutritious than microbially-conditioned *Polygonum* leaves, with the lack of significance simply a result of inadequate replication due to shrimp mortality during the growth experiment. At best, grass shrimp are choosing habitat that provides them with adequate food. If periphyton really provides a more nutritious food source than macrophyte leaves, grass shrimp were choosing a habitat with less than optimal food.

In summer, dissolved oxygen occasionally dropped to near-zero levels in *Polygonum* beds, while the decrease was not nearly as severe in *Nuphar* beds (Fig. 2). Thus, dissolved oxygen levels are probably not significant in driving grass shrimp habitat selection. Therefore, there must be some sort of trade-off for *P. paludosus* in choosing *Polygonum* habitat over *Nuphar*.

Grass shrimp preference for *Polygonum* could be a result of an inherent preference for physically-complex habitat. *Polygonum* beds may have provided better refuge areas for *P. paludosus* compared to *Nuphar* communities. Several studies examining the relationship between habitat complexity and macroinvertebrate habitat choice support this hypothesis (Crowder & Cooper 1982, Stoner & Lewis 1985). Vulnerability to predators is often inversely related to habitat complexity (Coen et al. 1981), and this is well documented for the Decapoda. Crayfish density in lakes increased with the degree of macrophyte cover, and this relationship was modified by decreased vulnerability (i.e., increased prey size) to predators (Stein & Magnuson 1976). The distribution of some marine species of *Palaemonetes* has been positively correlated with increased habitat complexity (Khan et al. 1997), and this factor also has been shown to reduce predatory efficiency by reducing prey capture rates (Crowder & Cooper 1982). Khan et al. (1997) suggested that characteristics of the macrophytes (physical complexity) and the shrimp (residual predator conditioning) were important factors in observed grass shrimp distributions. Therefore, it is reasonable that *P. paludosus* capitalizes on this increased protection from predators provided by the complex habitat of *Polygonum* beds.

In diet studies of largemouth bass from the channelized river, grass shrimp and mosquitofish comprised most of their food (Trexler 1995). It is possible that the observed grass shrimp distributional pattern is due to lower predation in *Polygonum* than in *Nuphar* communities. The relatively low dissolved oxygen (DO) in *Polygonum* may have conferred an advantage to *P. paludosus* by reducing the number of fish predators present in these beds, thereby increasing grass shrimp survival. Furse et al. (1996) found that changes in DO, particularly declines below stressful levels, were the primary influence in largemouth bass habitat use and overall movement patterns. They found that largemouth bass used both *Nuphar* and *Polygonum* macrophyte communities almost equally overall, but were more likely to be found in areas where DO > 2 mg/L throughout the year. Whitmore et al. (1960) showed that largemouth bass showed strong avoidance of habitats with DO levels < 1.5 mg/L, while Petit (1973) reported that they stopped feeding at 2 mg/L; at 1 mg/L, all died within 11 hours. In each of these studies, increasing avoidance in vegetation occurred as temperatures increased, suggesting that the high temperatures in the Kissimmee River Pool B remnant channel would contribute even more to fish stress related to low DO. As metabolic needs increase due to high temperatures, their tolerance to low DO would decrease even more. The fact that DO sometimes falls below 2.5 mg/L in *Polygonum* beds (Fig. 2) due to the low subsurface light and heterotrophic nature of these communities suggests that largemouth bass were more likely to choose *Nuphar* beds over *Polygonum* beds. In addition, Miranda & Pugh (1997) found that largemouth bass density was highest in areas of intermediate macrophyte cover, suggesting that *Nuphar* beds would likely be more favorable for larger bass than *Polygonum* beds. Therefore, grass shrimp inhabiting high-density *Polygonum* beds would be less likely to have contact with their fish predators than those living in *Nuphar*.

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

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

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