CONTRASTING PATTERNS OF HABITAT USE BY PRAWNS AND CRAYFISH IN A HEADWATER MARSH OF THE ST. JOHNS RIVER, FLORIDA

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ABSTRACT

We compared seasonal patterns of habitat use by the prawn Palaemonetes paludosus and the crayfish Procambarus alleni in Blue Cypress Marsh Conservation Area, Florida. Prawn densities were similar to those found in other oligotrophic wetlands of southern Florida, whereas crayfish densities were much greater than reported previously for other wetlands in the area. Prawns and crayfish had strikingly different patterns of habitat use. Prawn density and biomass were similar in wet prairies and sloughs, whereas crayfish density and biomass were significantly higher in wet prairies. Within habitats, the abundance of prawns and crayfish generally increased with increasing structural complexity and the abundance of crayfish generally decreased with increasing water depth. Differences in risk of predation, frequency of agonistic encounters, food availability, and other factors likely contributed to observed patterns of habitat use. Because of differences in their ability to burrow and avoid concentration into dry-season refugia, prawns and crayfish responded very differently to seasonal variation in hydrologic conditions. Prawn densities were initially low (following a severe drought) and then increased during much of the study period, whereas crayfish densities were relatively stable throughout the study period. Overall, it appears that prawns are more responsive to antecedent hydrologic conditions and crayfish are more responsive to the availability of suitable habitats such as wet prairies.

The expansive freshwater wetlands of southern Florida, U.S.A., are seasonally dynamic habitat mosaics that are generated by differences in topography, hydrology, and nutrient inputs. For example, sloughs, emergent wet prairies, and sawgrass stands are interspersed with one another and form local gradients of increasing habitat complexity and decreasing water depth (Jordan et al., 1997a). Differences in risk of predation, availability of food resources, and physiological conditions among these habitats result in a spectrum of risks and opportunities for resident organisms and often generate patterns of differential habitat use. The relative quality of habitats changes as seasonal fluctuations in water level affect their accessibility to mobile organisms. Importantly, habitat use by different species reflects underlying differences in behavior and physiology.

The crayfish Procambarus alleni (Faxon), a common species in marshes of southern Florida, is not distributed randomly among available habitats. Instead, this species prefers densely vegetated habitats such as wet prairies and sawgrass (Jordan, 1996; Jordan et al., 1996a). Differences in risk of predation and cover-seeking behavior likely contribute to this pattern of habitat use (Jordan et al., 1996b). During seasonal droughts, crayfish burrow into the peat substrate rather than increasing their use of deeper sloughs. The effect of drought on population regulation is mediated by burrowing because crayfish are less vulnerable to dessication and predation from the large numbers of wading birds and other opportunistic predators that aggregate around dry-season refuges such as sloughs.

In contrast to crayfish, the freshwater prawn Palaemonetes paludosus (Gibbes) does not have specialized behavioral or physiological mechanisms for dealing with drought and is sensitive to severe drying events (Kushlan and Kushlan, 1980; Jordan, 1996).
Because prawns are vulnerable to seasonal droughts, they may use deeper slough habitats more than crayfish. However, little research has examined habitat use by prawns in the marshes of southern Florida, and it is unclear whether this species has strong habitat preferences that vary seasonally. Both prawns and crayfish are critical species in food webs of freshwater marshes of southern Florida because they serve as intermediate consumers linking production of periphyton and detritus with higher trophic groups (Gunderson and Loftus, 1993; Browder et al., 1994; Frederick and Spalding, 1994). Although the importance of prawns and crayfish to marsh food webs is widely recognized, relatively little research has examined variation in the distribution and abundance of these decapods within wetland landscapes. This oversight is significant because food-web structure is often intimately linked with underlying habitat structure (Polis et al., 1997).

We examined seasonal patterns of habitat use by prawns and crayfish in a headwater marsh of the upper St. Johns River, Florida. Specifically, we compared abundance and biomass of prawns and crayfish in emergent wet prairies and sloughs of the Blue Cypress Marsh Conservation Area during a 40-month field study. We also examined relationships between plant biomass (i.e., habitat complexity), water depth (i.e., hydrology), and the abundance of decapods within wet-prairie and slough habitats to compare the responses of these two species.

**MATERIALS AND METHODS**

This study is part of a larger research project designed to provide prerestoration data on the diversity and abundance of aquatic macrofauna in the headwater marshes of the St. Johns River and to identify potential indicator taxa. Accordingly, the following descriptions of the study area, collection methods, and statistical analyses largely follow Jordan et al. (1996a, 1997b).

We conducted research within Blue Cypress Marsh Conservation Area (hereafter BC), which is part of a larger marsh management system that forms the headwaters of the St. Johns River in central and southern Florida (27°41′N, 80°44′W). The BC is a 11,938 ha marsh habitat mosaic composed of sloughs, emergent wet prairies, and other aquatic habitats (Lowe, 1986; Jordan et al., 1997a). Sloughs comprise approximately 7% of BC, are relatively deep, and are characterized by floating mats of Utricularia and Nymphaea. Wet prairies comprise approximately 20% of BC, are relatively shallow, and are characterized by emergent sedges and grasses (e.g., Panicum, Eleocharis, and Rynchospora). More detailed descriptions of sloughs and wet prairies are provided by Lovelace (1989), Gunderson (1994), and Jordan et al. (1997a).

Similar to other subtropical wetlands (e.g., the Florida Everglades), BC experiences seasonal variation in rainfall and is characterized by distinct wet and dry seasons. We used an aluminum throw trap (100 × 100 × 75 cm) to collect prawns and crayfish. Throw traps provide quantitative estimates of macrofaunal abundance (Kushlan, 1981; Freeman et al., 1984; Chick et al., 1992; Jordan et al., 1997b) and is one of the few quantitative methods available for sampling aquatic macrofauna in densely vegetated habitats (Rozas and Minello, 1997). Estimates of crayfish abundance may be biased because this method does not capture burrowing crayfish. Therefore, we only compare our results to other studies that used throw traps or similar enclosure methods to capture non-burrowing crayfish. Although biased, above-ground estimates provide a realistic picture of the abundance of crayfish available to wading birds and other predators in wetland habitats.

We measured water depth to the nearest centimeter inside each trap. Plants were then uprooted and shaken to dislodge any macrofauna, placed in a mesh bag, and spun to remove excess water prior to measuring plant biomass to the nearest 0.1 kg. We then passed a bar seine with 3.0-mm stretch mesh through the trap until three consecutive empty sweeps were obtained. Prawns and crayfish were preserved in 10% buffered Formalin and returned to the laboratory to be counted and weighed by species to the nearest 0.001 g wet weight. Recently, a second species of crayfish, Procambarus fallax (Hagem), was collected in southern Florida (Hendrix and Loftus, 2000); however, no specimens of P. fallax were found in archived samples from BC.

We collected decapods every other month between August 1992 and December 1993, and then quarterly from February 1994 through November 1995 (n = 16 sampling periods). Collections were made at three wet prairie sites and three slough sites that were separated by at least 0.5 km. We selected study sites that were large enough to accommodate repetitive sampling across the entire study period and that were accessible by airboat. Three throw-trap samples were obtained from within each site during each sampling month (n = 288 total traps). We avoided resampling locations that had been sampled previously. Samples were averaged to calculate mean water depth, plant biomass, density, and biomass of prawns and crayfish for each site during each sampling period. A subset of crayfish data (1992–1993) were reported elsewhere (Jordan et al., 1996a) and are included herein for comparative purposes.

We transformed response variables to meet assumptions of parametric analyses; however, we present non-transformed data in figures because they produced similar results. Density and biomass data were log_{10}-transformed after adding 1 to each value. We used repeated measures analyses of variance (ANOVA) to examine spatial (i.e., between sloughs and wet prairies) and temporal (i.e., among months) effects on response variables. This statistical approach corrects for the temporal autocorrelation that arises from repeated measurements through time (Winer et al., 1991; Milliken and Johnson, 1992). Finally, we performed correlation analyses to examine relationships between decapped densities and habitat characteristics (i.e., water depth and plant biomass).

**RESULTS**

We collected 6,681 prawns (558 g) and 4,171 crayfish (3,701 g), yielding about 23
Table 1. Results of repeated measures analyses of variance testing for the effects of habitat type, month, and the month × habitat interaction on transformed estimates of density and biomass of prawns. Asterisks denote statistically significant effects when \( P < 0.05 \).

<table>
<thead>
<tr>
<th>Source</th>
<th>df</th>
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<th>P</th>
<th>R²</th>
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<td>Prawn density:</td>
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<td></td>
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<td></td>
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<tr>
<td>Habitat</td>
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<td>10.993</td>
<td>0.0009*</td>
<td>60</td>
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<td>0.2579</td>
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</tr>
<tr>
<td>Month</td>
<td>15</td>
<td>0.124</td>
<td>1.515</td>
<td>0.2645</td>
<td>11</td>
</tr>
<tr>
<td>Month × Habitat</td>
<td>60</td>
<td>0.081</td>
<td>1.062</td>
<td>0.3611</td>
<td>2</td>
</tr>
<tr>
<td>Prawn biomass:</td>
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<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Habitat</td>
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<td>1.660</td>
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<td>0.842</td>
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<tr>
<td>Month</td>
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<td>0.2645</td>
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<tr>
<td>Month × Habitat</td>
<td>60</td>
<td>0.081</td>
<td>1.062</td>
<td>0.3611</td>
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Prawns per m² (2 g per m²) and 14 crayfish per m² (13 g per m²). Prawn density and biomass estimates did not differ significantly between wet prairies (22 prawns per m²; 2 g per m²) and sloughs (24 prawns per m²; 2 g per m²) (Table 1, Fig. 1). In contrast, crayfish were significantly more abundant in wet prairies (25 crayfish per m²; 2 g per m²) than in sloughs (3 crayfish per m²; 2 g per m²) (Table 2, Fig. 2). Habitat accounted for 71 and 78% of the variation observed in crayfish abundance and biomass, respectively (Table 2), whereas this effect accounted for little of the variation observed in prawn abundance and biomass (Table 1).

Relationships between habitat structural features and decapod densities differed between species and habitats. Prawn densities were positively correlated with plant biomass (i.e., habitat complexity) within sloughs (\( r = 0.306, P = 0.0344 \)) and wet prairies (\( r = 0.404, P = 0.0044 \)), whereas crayfish densities covaried with plant biomass only in wet prairies (\( r = 0.354, P = 0.0136 \)). Crayfish densities were negatively correlated with water depth in sloughs (\( r = -0.399, P = 0.0050 \)) and wet prairies (\( r = -0.353, P = 0.0141 \)), whereas prawn densities were not significantly affected by water depth in either habitat.

Patterns of seasonal variation in densities and biomass differed between prawns and crayfish. Prawn density and biomass estimates were temporally variable, with the month effect accounting for 60 and 50% of the variation observed in these variables (Table 1, Fig. 1). In contrast, crayfish density and biomass estimates were much less variable, and the month effect accounted for little of the variation observed (Table 2, Fig. 2). Prawn densities increased in both habitats during the first 2.5 years of the study and then declined during the last year. Crayfish densities did not increase consistently during the sampling period, but rather peaked in wet prairies during seasonal drying events. Patterns of habitat use did not vary significantly among sampling periods (Figs. 1, 2), and the habitat × month interaction accounted for little of the variation observed in decapod density or biomass (Tables 1, 2). Finally, densities of prawns and crayfish were uncorrelated in both sloughs and wet prairies.

**DISCUSSION**

Prawns and crayfish occupy a diversity of lentic and lotic systems in southern Florida, with standing stocks varying considerably among these systems. Densities of prawns (23 per m²) within BC are similar to those observed within emergent marshes of oligotrophic wetland systems (25–34 prawns per m²; Kushlan and Kushlan, 1980; Jelks, 1991; Jordan, 1996), but substantially lower than within vegetated habitats of eutrophic systems such as the Hillsborough River and Lake Okeechobee (215–275 prawns per m²; Beck and Cowell, 1976; Chick, 1992). In contrast, densities of crayfish (14 per m²) within BC are higher than those observed within other oligotrophic wetland systems (e.g., 1–4 crayfish per m²; Kushlan and Kushlan, 1979; Jelks, 1991; Jordan, 1996) and eutrophic lakes and rivers (e.g., < 1 crayfish per m² in
Lake Okeechobee; Chick, 1992) of southern Florida. Floating mats of water hyacinths in a south Florida drainage canal are the only habitat that supported densities of crayfish (> 8 per m²; Godley, 1980) similar to those of the marshes of BC. In general, these data suggest that eutrophic riverine and lacustine systems support significantly higher densities of prawns, whereas oligotrophic wetland systems generally support higher densities of crayfish. However, the vast areal extent of marsh systems in southern Florida (i.e., headwater marshes of St. Johns River, floodplain marshes of the Kissimmee River, Everglades) translates into considerable system-wide production of both prawns and crayfish.

A central focus of this research was to determine the relative importance of slough and wet-prairie habitats to marsh decapods within BC. Patterns of habitat use differed between prawns and crayfish: prawns generally used both wet prairies and sloughs, whereas crayfish were consistently more abundant in wet prairies than in sloughs. Habitat use by crayfish in BC is consistent with results from a diversity of aquatic systems, wherein crayfish
Table 2. Results of repeated measures analyses of variance testing for the effects of habitat type, month, and the month × habitat interaction on transformed estimates of density and biomass of crayfish. Asterisks denote statistically significant effects when \( P < 0.05 \).

<table>
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<tr>
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tend to be most abundant in structurally complex habitats (Hobbs, 1991). Although prawns used both wet prairies and sloughs in the northern Everglades, they were significantly more abundant in the latter habitat (Jordan, 1996). Previous researchers have noted higher densities of prawns in vegetated habitats than in adjacent patches of sand or mud devoid of vegetation (e.g., Beck and Cowell, 1976), suggesting that structural complexity is also important to prawns. Although slough habitats are structurally less complex than wet prairies (Loveless, 1959; Gunderson, 1994; Jordan et al., 1997a), they provide substantially more structure than non-vegetated patches of sand and mud. Prawn densities were positively correlated with increasing plant biomass (i.e., habitat complexity) within wet prairies and sloughs. Therefore, although we did not find differences in prawn densities between habitats, structural complexity does appear to affect the distribution of prawns at the microhabitat level. Densities of crayfish were also correlated with habitat complexity within wet prairies, but not within sloughs where they were rarely found.

The distribution of decapods both within and between habitats is influenced by a variety of factors. For example, predation is a pervasive force structuring aquatic communities, and relative differences in risk of predation between sloughs and wet prairies may have contributed to patterns of habitat use by decapods. Although relatively rare in seasonally dynamic wetlands such as BC and the Everglades, densities of largemouth bass (Micropterus salmoides Lacepède) and other large, predatory fishes are higher in sloughs than in wet prairies (Dineen, 1984; Loftus and Kushlan, 1987; Wiechman, 1987; Jordan, 1996). Crayfish and prawns actively select habitats that provide the greatest amount of cover from predators (Stein and Magnuson, 1976; Godley, 1980; Blake and Hart, 1993; Garvey et al., 1994; Alberstadt et al., 1995; Jordan, 1996; Jordan et al., 1996b). Furthermore, vulnerability of crayfish and prawns may be lower in structurally complex habitats because the ability of their predators to detect and capture prey decreases with increasing habitat complexity (Heck and Crowder, 1991). For example, survival rates of P. alleni exposed to predatory largemouth bass increase with increasing habitat complexity (Jordan et al., 1996b). Use of both sloughs and wet prairies by prawns appears enigmatic considering the higher densities of predatory fishes and presumably increased risk of predation within sloughs. However, laboratory experiments indicate that prawns are also vulnerable to predation by crayfish and decrease their use of refugia in the presence of agonistic crayfish (Jordan, 1996). Positive correlations between prawn densities and habitat complexity within both sloughs and wet prairies indicate that prawns are using the most complex portions of each of these habitats. Thus, habitat use by prawns may reflect behavioral responses to predatory fishes in sloughs and agonistic crayfish in wet prairies. Similarly, negative correlations between crayfish densities and water depth may in part reflect avoidance of deeper water often occupied by large, predatory fishes. Finally, habi-
tat-specific differences in food availability, physiological conditions (e.g., dissolved oxygen levels), and other factors also likely influence use of sloughs and wet prairies by decapods. Critical experiments are needed to determine how habitat-use decisions of decapods are affected by risk of predation (including intraguild predation and cannibalism), food availability, physiological conditions, and other factors operating within the wetland mosaics of southern Florida.

Freshwater marshes of southern Florida are seasonally dynamic, alternating between distinct wet (summer and fall) and dry (winter and spring) seasons. For example, water levels in most of BC were below the marsh surface immediately prior to the beginning of this study. Seasonal drying events occurred during each year of the study; however, water levels did not drop below the marsh surface in most of BC during these drying events. Seasonal expansion and contraction of inundated marsh surface affects prawns and crayfish differently because of their distinct life histories (Kushlan and Kushlan, 1979, 1980). Prawns do not have specialized behavioral
or physiological mechanisms for dealing with drought and are sensitive to severe drying events (Kushlan and Kushlan, 1980). Therefore, the depressed densities of prawns at the beginning of the study period likely reflect drought-related mortality (Kushlan, 1974). Prawn densities increased throughout much of the study, likely because water levels did not drop below the marsh surface and there was little concentration and concomitant drought-related mortality of prawns. In contrast, crayfish excavate burrows and are tolerant of drought conditions. This tolerance explains why densities of crayfish were relatively high at the beginning and throughout the duration of this study.

Concentration of crayfish into wet prairies during seasonal drying events and avoidance of relatively deep waters likely contributed to negative correlations observed between crayfish densities and water depth. Observed peaks in crayfish densities in wet prairies during seasonal drying events also were concomitant with seasonal peaks in recruitment (Jordan et al., 1996a). Importantly, crayfish do not appear to concentrate appreciably into sloughs and other topographic depressions (e.g., alligator holes and ponds) during severe seasonal drying events (Godley, 1980; Jordan, 1996). Crayfish densities actually declined within sloughs of the northern Everglades during a severe drought (Jordan, 1996). Crayfish apparently concentrate in structurally complex habitats such as wet prairies and sawgrass as marsh water levels decline, and then burrow into the substrate when surface waters become restricted to sloughs, alligator holes, and ponds (Kushlan and Kushlan, 1979; Jordan, 1996; Jordan et al., 1996a). Although prawn densities did not increase in sloughs during the relatively mild seasonal drying events that occurred during this study, prawn densities averaged 425 per m² in sloughs during a severe marsh drawdown in the northern Everglades (Jordan, 1996). Seasonal concentration of prawns and other aquatic prey is critical to the foraging behavior and reproductive success of wading birds and other predators living in wetland systems (Godley, 1980; Kushlan and Kushlan, 1980; Frederick and Spalding, 1994; Ogden, 1994). Therefore, annual differences in the extent of marsh drying can profoundly affect the success of taxa dependent upon seasonal concentrations of prey.

In summary, our results indicate that the distribution of decapods varies at ecologically relevant spatial (i.e., within habitats, among habitats, among marsh systems) and temporal scales (i.e., among seasons, among years). Moreover, differences in the life histories of prawns and crayfish result in species-specific responses to spatial and temporal variation within wetland systems. Given their sensitivity to changes in environmental conditions, we recommend that prawns and crayfish be included in monitoring programs designed to evaluate the efficacy of restoration efforts in wetland systems such as the upper basin of the St. Johns River, Everglades, Lake Okeechobee, and floodplain marshes of the Kissimmee River.

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LITERATURE CITED


Hendrix, A. N., and W. F. Lofus. 2000. Distribution and relative abundance of the crayfishes Procambarus alleni (Faxon) and P. falax (Hagen) in southern Florida.—Wetlands 20: 194–199.


