SPATIAL ECOLOGY OF THE CRAYFISH PROCAMBARUS ALLENI IN A FLORIDA WETLAND MOSAIC

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Abstract: We investigated patterns of differential habitat occupation by the crayfish Procambarus alleni, a numerically abundant and trophically important species in freshwater marsh systems of southern Florida. Crayfish were collected from emergent wet prairies and sloughs in marshes forming the headwaters of the St. Johns River, Florida between August 1992 and December 1993. In addition to differences in plant species composition, wet prairies had greater plant biomass and lower water depths than sloughs. Mean density and biomass of crayfish were significantly higher in the densely vegetated wet prairies (28 per m²; 26.9 g per m²) than in aquatic sloughs (3 per m²; 1.5 g per m²). Crayfish density increased with increasing plant biomass (i.e., habitat complexity) in wet prairies, whereas crayfish density decreased with increasing water levels (i.e., hydoperiod) within slough habitats. Recruitment occurred throughout the study, and the majority of crayfish collected were small in size (< 1.0 g). Ovigerous females were rarely collected and were found only in wet prairies. Differences in relative risk of predation, food availability, or a combination of these factors are likely generating differences in habitat occupation by the crayfish P. alleni in this wetland habitat mosaic. Efforts to restore and manage freshwater marshes in southern Florida (e.g., Everglades, Lake Okeechobee, Kissimmee River, St. Johns River) would benefit by considering spatial aspects of the ecology of indicator taxa such as crayfish.

Key Words: crayfish, Procambarus alleni, habitat occupation, spatial ecology, habitat complexity, reproduction, restoration ecology

INTRODUCTION

The freshwater marshes of southern Florida are comprised of mosaics of aquatic sloughs, sawgrass (Cladium jamaicense Crantz) stands, emergent wet prairies, and other distinct habitat types (Loveless 1959, Lowe 1986, Wood and Tanner 1990, Gunderson 1994). Aquatic sloughs are deeper habitats characterized by floating mats of Utricularia spp. and Nymphaea odorata Ait., whereas wet prairies are relatively
shallow habitats characterized by emergent sedges and grasses (e.g., *Panicum hemitomon* Schult., *Eleocharis* spp., and *Rhynchospora* spp.). These habitat mosaics provide a wide spectrum of opportunities and risks for their associated aquatic macrofauna (*sensu* Wiens 1976). That is, each habitat type has a characteristic array of food resources, predators, and potential competitors that may all affect the demographics of resident species (e.g., Fretwell and Lucas 1970, Holt 1987, Pulliam 1988, Pulliam and Danielson 1991, Rosenzweig 1991, Kadmon 1993). Overall, insufficient attention has been paid to the role that spatial heterogeneity plays in structuring populations and assemblages of aquatic macrofauna in wetland systems, especially with respect to important trophic groups and keystone species (Andrew and Mapstone 1987, DeAngelis and White 1994).

Evidence for differential habitat occupation and habitat-specific demographics of aquatic organisms in the wetland habitat mosaics in southern Florida has been slow to emerge. Early studies on such important prey taxa as the crayfish *Procambarus alleni* (Faxon) (Kushlan and Kushlan 1979), the grass shrimp *Palaeomonetes paludosus* (Gibbes) (Kushlan and Kushlan 1980), apple snails *Pomacea paludosa* (Say) (Kushlan 1975), and fishes (Kushlan 1976, 1980) focused primarily on the effects of hydroperiod, with little emphasis on spatial aspects of the ecology of these species. Loftus and Kushlan (1987) provided qualitative evidence that sloughs, sawgrass stands, and wet prairies differed with respect to fish assemblage structure. Additionally, a recent reinterpretation of the results of Kushlan (1976) indicates that the described shift in fish assemblage structure was not due directly to prolonged hydroperiod but rather to a sampling-related change in habitat structure (Loftus and Eklund 1994). Rader (1994) found qualitative differences in the composition of macroinvertebrate assemblages occupying slough and sawgrass habitats of the central Everglades. Jordan et al. (1994) showed that the fishing spider *Dolomedes triton* was much more abundant in sawgrass stands than in either wet prairies or sloughs.

In practice, is it necessary to know whether habitats vary in their relative ability to contribute to marsh productivity? Certainly this is the case when considering the large scale conversion of habitats that has occurred throughout southern Florida. For example, thousands of hectares of sawgrass stands, sloughs, and emergent prairies have been converted into virtual monocultures of cattail (*Typha* spp.) via alterations in hydrologic and nutrient regimes (Richardson et al. 1990, Gunderson 1994). Habitat differences in marsh productivity have potentially important consequences for management within the marsh systems of southern Florida. Large-scale habitat conversion of these marshes has had a large impact on these systems, yet the consequences of these actions on the spatially explicit demographics of species residing within the system are poorly understood. For example, the dramatic declines in wading bird populations are likely due directly or indirectly to alteration of the marshes of southern Florida (Ogden 1994). Understanding the spatial aspect of marsh ecology should enhance the success of restoration efforts, particularly for important taxa such as crayfish, fishes, alligators, and wading birds (Gunderson and Loftus 1993, DeAngelis and White 1994).

The crayfish *Procambarus alleni* (Faxon) has been identified as a critical species in the food webs of freshwater marshes of southern Florida (e.g., Frederick and Spalding 1994). For example, *P. alleni* is an important constituent in the diets of wading birds (Kushlan and Kushlan 1975, Kushlan 1977, Frederick and Spalding 1994), alligators *Alligator mississippiensis* (Daudin) (Fogarty and Albury 1968), swamp snakes *Regina alleni* (Garman) (Godley 1980), and pig frogs *Rana grylio* Stejneger (Ligas 1960). It is also likely that this species is an important consumer, affecting populations of plants, macroinvertebrates, and small-sized fishes (e.g., Lodge and Lorman 1987, Feminilla and Resh 1989, Savino and Miller 1991). Although the importance of *P. alleni* to marsh food webs is widely recognized, little research has addressed how this species is distributed among habitats. Considering the prominent role that crayfish have in freshwater marshes, identification of habitat-specific differences in crayfish demographics should provide important information relative to marsh restoration efforts and management (Robertson and Frederick 1994). This study provides the first examination of habitat occupation patterns by *P. alleni*, the only epigean species of crayfish found in southern Florida (Hobbs 1942). Specifically, we compared the relative abundance and biomass of crayfish in two distinct wetland habitats: emergent wet prairies and sloughs. We also examined relationships between habitat complexity (i.e., plant biomass), hydrology (i.e., water depth), and the abundance of crayfish within wet prairie and slough habitats.

### STUDY AREA AND METHODS

**Study Area**

We conducted this study in the Blue Cypress Marsh Conservation Area (hereafter referred to as BCMCA) in Indian River County, Florida. BCMCA (27°41'N, 80°44'W) is a 11,938 ha marsh comprising a habitat mosaic of emergent wet prairies, sawgrass stands, and aquatic sloughs (Lowe 1986). Other habitats include Blue Cypress Lake (2,630 ha) and varying amounts of
woody (e.g., *Taxodium*, *Salix*) and mixed herbaceous plant communities. BCMCA is part of a larger marsh management system that forms the headwaters of the St. Johns River. The St. Johns River Water Management District and The U.S. Army Corps of Engineers are working jointly to restore this system and manage it for flood protection, wildlife and fishery resources, enhanced water quality, and maintenance of water supply (Miller et al. 1993).

Sampling Methods

We collected crayfish by throwing an aluminum throw trap (100 × 100 × 75 cm) into the desired habitat and pressing it firmly into the substrate. This technique provides quantitative estimates of macrofaunal abundance (e.g., Kushlan 1981, Freeman et al. 1984, Chick et al. 1992) and is one of the few quantitative methods available for sampling aquatic macrofauna in densely vegetated habitats (e.g., Jordan et al. 1994). Water depth was measured to the nearest centimeter inside each trap prior to removal of plants. Relative coverage of above-ground vegetation was visually estimated, and then plants were uprooted and shaken to dislodge any macrofauna. We placed all plants in a mesh bag, which was then spun to remove excess water prior to measuring plant biomass to the nearest 0.1 kg. After we removed plants, a bar seine with 3.0-mm stretch mesh was then passed through the trap until three consecutive empty sweeps were obtained. Crayfish were preserved in 10% buffered formalin and returned to the laboratory to be counted and weighed to the nearest 0.001 g wet weight. Eggs were removed from ovigerous females, counted, and weighed collectively to obtain a wet biomass estimate of egg production.

Design and Analyses

We collected crayfish from wet prairie (*n* = 3 sites) and slough habitats (*n* = 3 sites), which comprise roughly 20% and 7% of the vegetated portion of the BCMCA system, respectively. Sites were separated by at least 0.5 km within the habitat mosaic of wet prairies and sloughs found within BCMCA. Within each of these habitats, three traps (subsamples) were randomly collected. We averaged values from the three trap subsamples to calculate mean water depth, plant biomass, crayfish density, and crayfish biomass for each site during each sampling visit. Sampling was performed bimonthly (except August 1993) at each of these sites from August 1992 through December 1993 (*n* = 8).

Water depth and wet plant biomass data were normalized by log_{10} transformation. Crayfish density and biomass data were log_{10} transformed after adding 1.0 to each value. Kendall's rank concordance test was used to compare the relative abundance of plant species between habitats (Sokal and Rohlf 1981). Repeated measures analyses of variance (ANOVA) were used to test for spatial (i.e., between sloughs and wet prairies) and temporal (i.e., among months) differences in water depth, plant biomass, crayfish density, and crayfish biomass. Repeated measures ANOVA corrects for the temporal autocorrelation that arises from repeated measurements through time and also prevents temporal pseudoreplication (Winer et al. 1991, Milliken and Johnson 1992). Partial correlation analyses were performed to examine the relationship between crayfish density, plant biomass, and water depth within each habitat type (Sokal and Rohlf 1981).

### RESULTS

Wet prairie and slough habitats were distinct from one another with respect to structure (i.e., plant species composition and plant biomass) and water depth (Table 1). Structurally, wet prairie sites were much more complex than slough sites and were dominated by the emergent *P. hemiemon*, with *Sagittaria lancifolia* and *Eleocharis elongata* being seasonally subdominant. Sloughs were typically dominated by floating aquatics, especially *Nymphaea odorata* and *Utricularia* spp. There was little concordance in the ranked relative
abundance of plant species between wet prairies and sloughs (Kendall’s tau = -0.2, p=0.3188). Mean plant biomass was about three times greater (F_{1,4}=35.7, p=0.0039) in wet prairies (3.6 kg per m²) than in sloughs (1.3 kg per m²). Plant biomass did not vary significantly among months (F_{1,28}=2.9, p=0.1045), and there was no interaction between habitat type and month (F_{1,28}=1.5, p=0.2771). Sloughs (47.3 cm) were significantly (F_{4,16}=163.6, p=0.0002) deeper than wet prairies (29.8 cm) throughout the study period (Figure 1). Water depth varied significantly among months (F_{4,16}=139.7, p=0.0001), generally decreasing over the study period (Figure 1). Habitat type and month interacted significantly (F_{4,28}=6.6, p=0.00319) to affect water depth.

A total of 2,268 crayfish (2.042 g) were collected from within 144 traps, yielding about 16 crayfish per m² (14 g per m²). Both crayfish density and biomass estimates were significantly higher for wet prairie sites than slough sites (Figure 2, Table 2). Average densities ranged from 3 crayfish per m² in sloughs to 28 crayfish per m² in wet prairies, whereas average biomass ranged from 1.5 g per m² to 26.9 g per m² in these habitats, respectively. Habitat type explained about 70% and 85% of the observed variation in crayfish density and biomass estimates, respectively.

The relationship between crayfish density and habitat structure differed between the two habitat types. Partial correlation analysis indicated that plant biomass was positively correlated with crayfish density within wet prairies (r=0.641, p=0.0005), whereas these variables were unrelated within sloughs (p>0.05). Water depth was negatively correlated with crayfish density within slough sites (r=-0.686, p=0.0004), whereas...
these variables were unrelated within wet prairies (p>0.05).

Estimates of crayfish density were temporally variable, with the month effect accounting for 8% of the observed variation (Figure 2, Table 2). For wet prairies, the highest average density of crayfish (47 per m²) was found in June 1993, and the lowest density (19 per m²) occurred in December 1993. For sloughs, the highest average density of crayfish (8 per m²) was also found in June 1993, but the lowest density (< 1 per m²) occurred in August 1992 at the beginning of the study. Probably as a result of recruitment, temporal variation in crayfish abundance was somewhat decoupled from variation in crayfish biomass. That is, in wet prairies, peak biomass (39 g per m²) occurred in February 1993 but had dropped to about 18 g per m² by June 1993. However, inter-month variability of crayfish biomass was non-significant and only accounted for 2% of the observed variation (Figure 2, Table 2). Crayfish smaller than 1.0 g in mass represented the most abundant size class during all months of the study (Figure 3).

Habitat type and month interacted weakly (p=0.1140) to affect crayfish density estimates (Table 2). That is, the density of crayfish in wet prairies showed no consistent change through time, whereas the density of crayfish in slough habitats generally increased (Figure 2). However, the density of crayfish in sloughs was always considerably lower than in wet prairies. The interaction between habitat type and month did not significantly affect crayfish biomass estimates (Table 2).

Only 13 (<1%) of the 2,268 crayfish collected during this study were ovigerous (no attempt was made to sex non-gravid individuals). All ovigerous females were found in wet prairie sites and ranged in size from 1.0 to 6.3 g wet weight, although 86% of these were greater than 2.0 g wet weight (mean weight = 3.8 ± 1.7 SD). Clutch size ranged from 56 to 247 progeny (0.108–0.834 g wet weight). The thirteen ovigerous females collected produced a total of 1,810 eggs. Clutch size varied positively with female weight (r=0.852, p=0.0001), but female size was not related
to the size of individual offspring \((r=0.154, p=0.6228)\).

**DISCUSSION**

Our results indicate that crayfish are differentially occupying sloughs and emergent wet prairies within BCMCA. Previous research in stream and lake systems has shown that crayfish tend to occupy more complex habitats (e.g., higher plant biomass, higher stem density) that provide more refuge (e.g., Stein 1977, Rabeni 1985, Gore and Bryant 1990, Garvey et al. 1994). Our findings are consistent with patterns of habitat occupation observed in a northern Everglades habitat mosaic (Arthur R. Marshall Loxahatchee National Wildlife Refuge, Palm Beach County, Florida; F. Jordan, unpublished data), where crayfish densities in wet prairies were significantly higher than in sloughs and alligator holes.

The overall density (16 per m²) of *P. alleni* found in this study is higher than estimates from other marsh systems in Florida. For example, Kushlan and Kushlan (1979) found that the average density in southern Everglades habitats was 0.2 per m². Loftus et al. (1990) found average densities of 1.3 crayfish per m² in a later study carried out in the southern Everglades. The hyacinth-choked canals of Rainey Slough (Glades County, Florida) supported about 10 crayfish per m², although peak densities reached 61 per m² (Godley 1980). Jelks (1991), working in isolated wetlands in Sarasota County, Florida, found 2.5 crayfish per m². Density estimates in the expansive marshes of the northern Everglades ranged from 2.1 crayfish per m² in sloughs and alligator holes up to 4.0 crayfish per m² in wet prairies (F. Jordan, unpublished data). These data sets cover a broad suite of hydrologic conditions and range from one to seven years in duration. Of course, the above comparisons of crayfish standing crops are even more dramatic when we consider wet prairie sites (28 per m² in BCMCA) separately. The underlying reason for this disparity among marsh systems is unclear. For example, there is little difference in the vegetational structure of prairies sampled in BCMCA and those sampled in the northern Everglades (Lowe 1986). Also, the different types of enclosure traps used in the above studies provide comparable estimates of macrofaunal abundance (Chick et al. 1992).

Why were crayfish so much more abundant in wet prairies than in sloughs within BCMCA? Although not examined directly in this study, there is correlative evidence that predation, hydrology, and habitat complexity interact to determine patterns of abundance in *P. alleni*. Because of its importance as a food resource in the trophic webs of freshwater marshes in southern Florida, it is likely that predation influences population size and habitat occupation by *P. alleni*. Feeding studies on such varied taxa as wading birds (Kushlan and Kushlan 1975, Kushlan 1977, Frederick and Spalding 1994), alligators (Fogarty and Albury 1968), swamp snakes (Godley 1980), and pig frogs (Ligas 1960) indicate that *P. alleni* is the dominant dietary component. Further, limited tethering studies performed during February 1993 indicate that predation rates are high (40% in 12 h) in BCMCA (unpublished data). Predators regulate population size of crayfish in other systems. For example, centrarchid fishes seem to regulate the abundance of *Orconectes* spp. in Ozark stream systems (Rabeni 1992). Centrarchids, along with other larger piscine predators (i.e., gars and bowfin), are more abundant in the deeper water sloughs and alligator holes of the southern (Lofus and Kushlan 1987) and northern (F. Jordan, unpublished data) Everglades. Similar patterns of predatory fish distribution in BCMCA could lead to higher predation rates in slough habitats.

Predation rates may be higher in slough habitats because piscine predators have increased foraging efficiency in less complex habitats (Crowder and Cooper 1982, Savino and Stein 1982, Werner et al. 1983, Heck and Crowder 1991). For example, Garvey et al. (1994) experimentally demonstrated that predation rates on *Orconectes* spp. increased with decreasing habitat complexity. Although predation may directly account for observed differences in the numbers of crayfish in wet prairie and slough habitats, it may also indirectly generate these patterns. That is, crayfish may be moving into less risky (i.e., more complex) or avoiding more risky (i.e., less complex) habitats when they detect potential predators (Stein and Magnuson 1976, Blake and Hart 1993, Garvey et al. 1994). Crayfish also orient towards cover in the absence of predators (i.e., Alberstadt et al. 1995), but this is likely an evolutionarily "hard-wired" behavioral response to predation that results in the same distribution pattern.

In addition to between-habitat differences, we found strong correlative evidence for variation in crayfish abundance at the microhabitat level. That is, crayfish seemed to respond strongly to features that varied within sloughs (i.e., water depth) and wet prairies (i.e., plant biomass). In sloughs, crayfish density decreased with increasing depth (i.e., prolonged hydroperiod). The average size and abundance of piscine predators increases with increasing depth and prolonged hydroperiod in these south Florida marsh systems (Kushlan 1976, Lofus and Eklund 1994; F. Jordan, unpublished data for the northern Everglades). In wet prairies, crayfish density increased with increasing habitat complexity (i.e., plant biomass). The ability of aquatic and wading bird predators to detect and capture their prey...
(e.g., crayfish) varies inversely with increasing habitat complexity and water depth (Crowder and Cooper 1982, Savino and Stein 1982, Werner et al. 1983, Heck and Crowder 1991). Thus, within-habitat patterns of crayfish distribution could be related to differences in predation pressure.

Factors other than predation are also likely affecting the patterns of habitat occupation by crayfish observed in this study. Differences in food resources between habitats probably contribute significantly to differences in crayfish production. Crayfish are omnivorous and consume significant quantities of aquatic plants (e.g., Feminella and Resh 1989, Olsen et al. 1991, Hart 1992, Creed 1994). For example, Feminella and Resh (1989) found that the crayfish *P. clarkii* (Girard) controlled the abundance of aquatic macrophytes in a California freshwater marsh. Further, they found that *P. clarkii* was significantly more abundant in beds of aquatic macrophytes than in surrounding unvegetated areas. In our study, standing crops of aquatic plants were significantly higher in wet prairies than in sloughs, and the abundance of *P. alleni* was positively correlated with plant biomass (i.e., food availability) within wet prairies. However, there was no evidence for a decline in plant biomass within the wet prairies of BCMCA during the study period (ANOVA: $F_{1,16} = 1.14$, $p = 0.4009$). Overall, the patterns of crayfish distribution found in this study could be explained by between-habitat differences in the availability of food, the relative risk of predation, or a combination of these factors. Clearly, additional studies are needed to separate the importance of aquatic plants as a food resource versus their value as a refuge from potential predators.

The high frequency of small-sized (i.e., < 1 g) crayfish collected throughout the study (see Figure 3) suggests that recruitment occurred continuously during the sampling period. Previous researchers have reported continuous reproduction of *P. alleni* in subtropical, south Florida marshes (Kushlan and Kushlan 1979, Godley 1980), and the paucity of ovigerous females was also noted in these systems. Female *P. alleni* apparently retreat into burrows until their eggs hatch (Hobbs 1942; Florida Game and Freshwater Fish Commission, unpublished data). Our absolute density and biomass estimates may be biased downward due to the absence of ovigerous females, but this bias is unlikely to significantly affect the relative abundance of *P. alleni* between habitats. Steady, year-round recruitment and “loss” (i.e., predation and/or emigration) of larger individuals explains the relatively small amount of variability in crayfish density (8%) and biomass (2%) accounted for by the month effect in our ANOVAs. Inter-month variability was driven more by hydrologic conditions than recruitment patterns (see Figure 1). Crayfish densities varied inversely with water levels, as reflected in an overall (both habitats combined) negative linear correlation between these variables ($r = -0.546$, $p < 0.0001$). Similar to this study, Kushlan and Kushlan (1979) found that crayfish density and water depth (i.e., prolonged hydropressure) were negatively related, possibly due to increased predation pressure. Another (perhaps more parsimonious) explanation for the observed negative correlation is that, as water levels drop and inundated marsh surface area decreases, crayfishes are concentrated into the remaining flooded habitat.

A lack of basic life history information has led to concern over crayfish conservation and management in Florida (Caine 1978, Franz and Franz 1990, Robertson and Frederick 1994). Additionally, crayfish conservation may be linked to the breeding success of wading birds (e.g., Gunderson and Loftus 1993, Frederick and Spalding 1994, Ogden 1994). As previously mentioned, *P. alleni* is an important component of food webs in the freshwater marshes of southern Florida. Wading birds scale their foraging decisions at both the level of individual habitats (Hoffman et al. 1994) and at the level of different wetland systems throughout their respective ranges (Holling 1992, Robertson and Frederick 1994). Therefore, enhanced secondary productivity at such a relatively localized scale as the wet prairies within BCMCA can have an impact at a regional scale (Robertson and Frederick 1994). Focusing exclusively on either wet prairies or sloughs within BCMCA would have led to misleading conclusions about the distribution of *P. alleni* within this habitat mosaic and misrepresented the importance of the area to wading birds. This study demonstrates that restoration efforts in the Everglades, Lake Okeechobee, Kissimmee River, and the upper basin of the St. Johns River would benefit from the incorporation of spatial aspects of the ecology of trophically important taxa such as the crayfish *P. alleni*. Specifically, we suggest that monitoring efforts be stratified with respect to dominant habitat types (Jordan et al. 1994, Streever et al. 1995), especially those plant taxa that are being targeted for reduction or enhancement (e.g., cattail, sawgrass, *Hydrilla*).

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