

## PREDATION, HABITAT COMPLEXITY, AND DISTRIBUTION OF THE CRAYFISH *PROCAMBARUS ALLENI* WITHIN A WETLAND HABITAT MOSAIC

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**Abstract:** The crayfish *Procambarus alleni* is abundant in densely vegetated habitats within the freshwater wetland mosaics of central and southern Florida. We performed laboratory experiments to determine whether habitat preference and/or predation could account for habitat use by this species. First, groups of crayfish were placed into tanks divided evenly into vegetated and non-vegetated sides, and habitat use was measured during the day and night. Crayfish preferred vegetated habitats during both the day and night, although use of non-vegetated habitats increased significantly at night. Next, different size classes of crayfish were exposed to predatory largemouth bass (*Micropterus salmoides*) in experimental tanks of varying habitat complexity (i.e., plant biomass). Bass reduced survival of small-sized crayfish but had no effect on larger crayfish. Larger crayfish also seemed to prey upon smaller crayfish. Susceptibility of crayfish to predation decreased with increasing habitat complexity. Experimental results are consistent with field observations and indicate that predators and habitat complexity play important roles in determining the distribution and daily activity of *P. alleni* within wetland habitat mosaics.

**Key Words:** *Procambarus alleni*, *Micropterus salmoides*, habitat selection, predator avoidance

### INTRODUCTION

Natural aquatic systems are spatially heterogeneous and often form mosaics comprised of different habitat types (e.g., littoral vs. pelagic zones, pools vs. riffles, depositional vs. erosional banks). These habitat mosaics provide a spectrum of opportunities and risks for their associated aquatic macrofauna in that each habitat type has a characteristic array of food resources, predators, and potential competitors, which may all affect the demographics of resident species (Pulliam 1988). Ultimately, differences in these factors can account for differential habitat use by species- and habitat-specific assemblage composition (Wiens 1976). For example, differences in the relative risk and intensity of predation

can result in higher densities of prey fishes and invertebrates in densely vegetated habitats (e.g., sea-grass beds, vegetated littoral zones) than in adjacent non-vegetated habitats (Heck and Crowder 1991). Overall, predators seem to play prominent roles in structuring aquatic communities by reducing or eliminating prey populations, causing shifts in habitat use, acting as selective agents in the evolution of behavior and morphology, and effecting changes in species interactions throughout food webs (see reviews in Kerfoot and Sih 1987).

Although the regulatory importance of aquatic predators is recognized for well-studied systems such as streams and lakes, little effort has been made to quan-

tify their role in regulating the abundance and distribution of prey organisms in seasonally dynamic freshwater wetlands (DeAngelis and White 1994). Throughout central and southern Florida, freshwater marshes are comprised of mosaics of aquatic sloughs, sawgrass stands, emergent wet prairies, and other distinct habitat types (Loveless 1959). Field sampling efforts have shown that aquatic macrofauna tend to use these habitats non-randomly (e.g., Loftus and Kushlan 1987, Jordan et al. 1994). Perhaps the most striking example of differential habitat use in these freshwater marshes involves the crayfish *Procambarus alleni* (Faxon). This trophically important (Robertson and Frederick 1994) species is generally much more abundant in densely vegetated habitats, which generally support fewer predatory fishes (Dineen 1984, Loftus and Kushlan 1987). Jordan et al. (1996) found that crayfish densities were significantly ( $\approx 900\%$ ) greater in wet prairies than in sloughs within the upper basin of the St. Johns River (Indian River County, Florida; Figure 1). Furthermore, they found that the density of crayfish increased with increasing plant density (Figure 1). Quantitative sampling in the northern Everglades (Palm Beach County, Florida) also indicated that *P. alleni* densities were significantly ( $\approx 200\%$ ) higher in sawgrass stands and wet prairies than in sloughs (F. Jordan, unpublished data). Jordan et al. (1996) hypothesized that habitat use by *P. alleni* was most likely due to aquatic predators, either directly through differential predation or indirectly through predator-mediated habitat selection.

Predators (especially fishes) can regulate the size of crayfish populations (e.g., Rabeni 1992) and strongly mediate habitat use by crayfish (e.g., Stein and Magnuson 1976, Stein 1977, Garvey et al. 1994). It seems likely that predation plays an important role in determining the distribution of *P. alleni*, primarily because this species comprises a significant portion of the diet of predators such as wading birds, alligators, swamp snakes, pig frogs, and predatory fishes (Robertson and Frederick 1994). These predators rely primarily on visual and/or tactile cues to locate crayfish, which may lead to decreased foraging efficiency in densely vegetated habitats due to reductions in their ability to detect and successfully capture vagile prey such as crayfish (Heck and Crowder 1991). Therefore, persistent differences in the complexity (e.g., plant stem density or biomass) of these marsh habitats may result in differential rates of predation on crayfish and ultimately lead to the evolution of anti-predator behavior (i.e., preference for increased cover). We performed laboratory experiments to determine what role, if any, predation plays in determining observed patterns of habitat use by *P. alleni*. First, we assessed behavioral preference for vegetated and non-vegetated habitats and

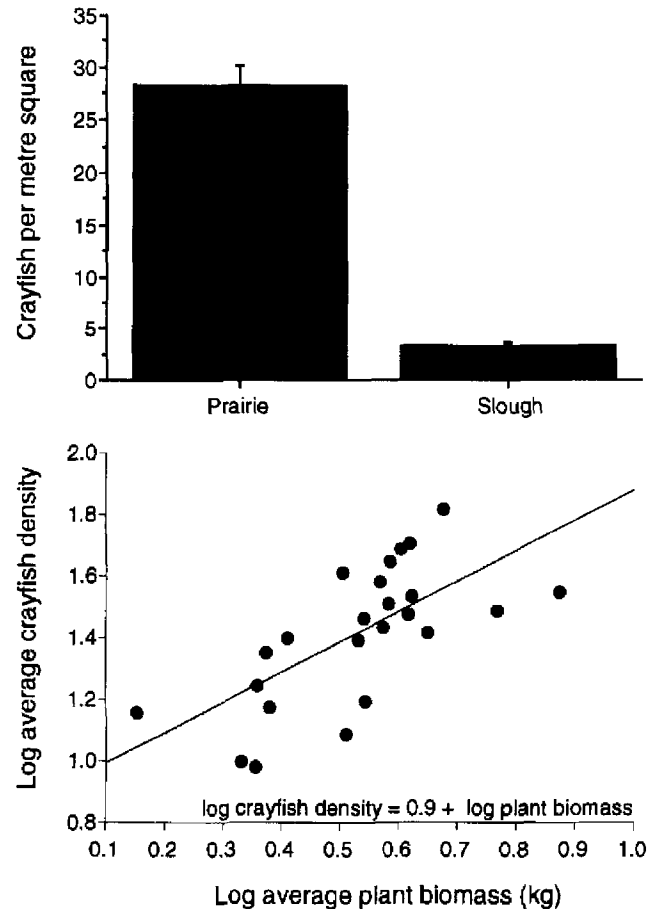


Figure 1. Top: densities of crayfish (means +1 SE) in emergent wet prairies and sloughs in the Blue Cypress Marsh Conservation Area, which is located within the upper basin of the St. Johns River, Indian River County, Florida. Bottom: relationship between  $\log_{10}$ -transformed densities of crayfish and  $\log_{10}$ -transformed plant biomass in wet prairie sites. This regression is significant ( $F_{1,22} = 18.2$ ,  $p = 0.0003$ ) and plant biomass explains 45% of the observed variation in crayfish densities. Data from Jordan et al. (1996) and unpublished data (F. Jordan).

determined if preferences varied between day and night (Habitat Selection Experiment). Second, we assessed size-specific survival of crayfish exposed to predatory largemouth bass (*Micropterus salmoides*) under different levels of habitat complexity (Predation Experiment).

## METHODS

### Animal Collection and Maintenance

Crayfish were collected from emergent wet prairies within the upper basin of the St. Johns River; largemouth bass were collected from Lake Yale in Lake County, Florida. Crayfish and bass were maintained separately in outdoor holding tanks with recirculating

water systems. Bass were fed crayfish and small fishes *ad libitum*, whereas crayfish were fed flake food *ad libitum*. Predators were not fed for 48 h prior to experiments to standardize hunger levels. Individual crayfish were used only once in an experiment.

#### Habitat Selection Experiment

This experiment tested whether groups of crayfish preferred vegetated or non-vegetated habitats and whether preferences varied between day and night. Four rectangular plastic tanks (62-cm length  $\times$  47-cm width  $\times$  47-cm height) were placed in a small clearing on the campus of Jacksonville University (Duval County, Florida). The bottom of each tank was covered with 2–3 cm of sand and filled with  $\approx$ 120 L of tap water to a depth of 41 cm (0.29-m<sup>2</sup> surface area, 0.12-m<sup>3</sup> or 119-L volume). Two distinct habitats were created within each tank by placing simulated vegetation on one side of the tank and leaving the other side of the tank bare sand. Placement of vegetated and non-vegetated habitats was randomly assigned and then reversed between trials. Vegetation was simulated by tying 22 bipartite strips of dark green plastic (2-cm width  $\times$  30-cm length) to a sheet of mesh buried beneath the sand substrate. Vegetation was stocked at a density of 154 strands per square metre, which approximates the complexity of emergent wet prairies in central and southern Florida (F. Jordan, unpublished data). Simulated vegetation was used to avoid confounding predator avoidance behavior with differential food availability (i.e., omnivorous crayfish feed on plants; Feminella and Resh 1989).

Sand, water, and vegetation were added to tanks between 8:00 and 8:30 EST on 30 September 1995 and allowed to settle for 3 hours. Nine crayfish were then added to each tank (11:00–11:30 EST), and the number of crayfish occupying the non-vegetated side of the tanks was measured once in the afternoon (16:00–17:00 EST) and once in the evening (21:00–22:00 EST). Crayfish were collected on the following morning, and the process was repeated again on two separate dates (5 October 1995 and 6 October 1995) with new crayfish being used on each date. Count data from the 12 trials (i.e., 4 tanks  $\times$  3 dates) were converted into proportions, and paired t-tests were used to compare numbers of crayfish using vegetated and non-vegetated sides and to test for changes in habitat use between day and night observation periods. Date of trial was ignored because a preliminary analysis of variance indicated that this factor did not affect crayfish habitat selection. Further, analysis of residual plots from this preliminary analysis indicated that data transformation was unnecessary.

#### Predation Experiment

This experiment tested whether habitat complexity (i.e., plant biomass) and/or predatory largemouth bass affected survival of crayfish. Thirty-six cylindrical, plastic tanks (48-cm diameter and 43-cm height) were set up in our laboratory. Tanks were filled with  $\approx$ 65 L of tap water to a depth of 36 cm (0.18-m<sup>2</sup> surface area, 0.06-m<sup>3</sup> volume). Stems of the common wetland plant *Ludwigia repens* Forst. (hereafter *Ludwigia*) were collected from local ephemeral ponds, rinsed thoroughly, and then added to the plastic tanks. No extraneous macroinvertebrates were found when the tanks and vegetation were carefully searched for surviving crayfish at the end of the experiment. One of three habitat complexity treatments was randomly assigned to each tank: low complexity (0 kg of *Ludwigia* stems), medium complexity (0.45 kg of *Ludwigia* stems), or high complexity (1.35 kg of *Ludwigia* stems). The plant biomass used in medium and high habitat complexity treatments is typical of slough and emergent wet prairie habitats in central and southern Florida (Jordan et al. 1994, Jordan et al. 1996; F. Jordan, unpublished data). Tanks were filled on 21 December 1995 and allowed to settle for 24 h before adding crayfish. Tanks were aerated during the experiment and mean ( $\pm$ 1 SE) dissolved oxygen levels did not differ ( $F_{2,29} = 2.4$ ,  $p = 0.1104$ ) among low ( $9.1 \pm 0.1$  mg/l), medium ( $9.3 \pm 0.4$  mg/l), and high ( $9.1 \pm 0.4$  mg/l) habitat complexity tanks. Lights were maintained on a 12L:12D cycle during the experiment.

One large (26–30 mm carapace length), one medium (21–25 mm carapace length), and two small (16–20 mm carapace length) crayfish were added to each tank on the morning of 22 December. Mean weights ( $\pm$ 1 SE) for these crayfish size classes were  $4.3 \pm 0.2$  g,  $2.4 \pm 0.4$  g, and  $1.1 \pm 0.1$  g, respectively. Individual bass (122  $\pm$  3 mm standard length) were randomly assigned to half of the low, medium, and high habitat complexity tanks, and the remaining tanks served as predator controls. The number of crayfish surviving after five days was used as the response variable in an analysis of variance testing for the effects of predator (present or absent [i.e., controls]), habitat complexity (low, medium, or high), and the interaction between these factors. Levene's homogeneity of variance test and inspection of residual plots indicated that data transformation was unnecessary prior to analysis. Least-squares (LS) means were compared to determine which means differed when main or interaction effects were significant.

#### RESULTS

Crayfish responded strongly to the available habitats, although the magnitude of their response varied

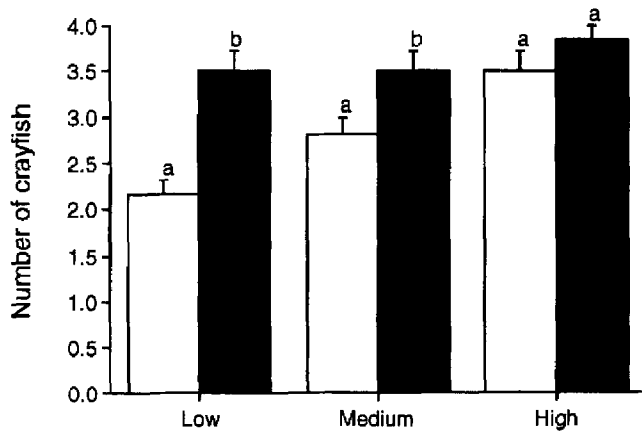


Figure 2. Proportions of crayfish (means +1 SE) occupying vegetated and open sand portions of behavioral tanks during the day and night. Letters designate means that differ significantly within a time period (paired *t*-tests; see text for details).

with time of day (Figure 2). During the day, crayfish used vegetated habitats significantly (91%) more than non-vegetated habitats ( $t = 27.5$ ,  $p = 0.0001$ , 11 df). Crayfish use of vegetated habitats was still greater than use of non-vegetated habitats in the evening ( $t = 4.5$ ,  $p = 0.0009$ , 11 df), but there was a significant (31%) increase in use of non-vegetated habitats relative to daytime use ( $t = 8.2$ ,  $p = 0.0001$ , 11 df).

Overall, bass reduced survival of crayfish by 22% relative to controls, and predation accounted for 30% of the variation observed in survival rates (Table 1). Survival varied with crayfish size; no large or medium sized crayfish were eaten during the five-day experiment, whereas bass reduced survival of small-sized crayfish by 92%, 58%, and 25% (relative to stocking densities) in the low, medium, and high complexity tanks, respectively.

Crayfish survival was significantly greater in high complexity tanks than in low and medium complexity tanks (which did not differ), and habitat complexity accounted for 23% of the variation in crayfish survival (Table 1). The effects of habitat complexity on crayfish survival varied with predator presence, which resulted in a significant interaction between these factors (Table 1). Crayfish survival did not differ among habitats in tanks that lacked predators, whereas crayfish survival increased with increasing habitat complexity in the presence of predatory bass (Figure 3). Comparison of least-squares means indicated that predatory bass reduced the survival of crayfish greatly (37%;  $p = 0.0001$ ) in low complexity tanks, less so (23%;  $p = 0.0233$ ) in medium complexity tanks, and little (<4%;  $p = 0.2414$ ) in high complexity tanks.

Survival of small sized crayfish in control tanks was reduced significantly (10%; Figure 3) relative to stock-

Table 1. Analysis of variance testing for the effects of predator presence, habitat complexity, and their interaction on the number of crayfish surviving after five days.  $R^2$  is the percentage of variation in the response variable accounted for by a particular effect.

Source	DF	MS	F	P	$R^2$
Model	5	2.2	9.6	0.0001	62
Predator	1	5.4	23.3	0.0001	30
Complexity	2	2.1	9.0	0.0008	23
Predator × Complexity	2	0.8	3.3	0.0493	9
Error	30	0.3			

ing density ( $t = 3.1$ ,  $p = 0.0070$ , 17 df). Specifically, there were 25% reductions in the numbers of small-sized crayfish surviving in low ( $t = 2.2$ ,  $p = 0.0756$ , 5 df) and medium ( $t = 2.0$ ,  $p = 0.0756$ , 5 df) complexity tanks relative to stocking densities, but only marginal reductions (9%) in the high complexity tanks ( $t = 1.0$ ,  $p = 0.3632$ , 5 df). Although no intact crayfish bodies were recovered, we did find remains in some tanks, suggesting that small-sized crayfish were being eaten by larger conspecifics.

## DISCUSSION

*Procambarus alleni* showed a strong preference for habitats containing simulated vegetation relative to adjacent habitats containing only bare sand. Since there were no differences in food availability or water chemistry between these habitats, it seems likely that crayfish were selecting the habitat that was likely to provide the greatest amount of cover (i.e., reduced risk of predation). Other crayfish species tend to select habitats that provide the most cover from predators (Stein

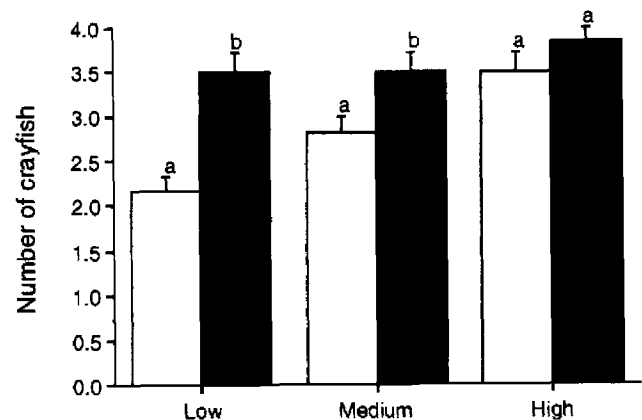


Figure 3. Numbers of crayfish (means +1 SE) surviving after five days as a function of predator presence (open bars) or absence (closed bars) and habitat complexity. For each level of habitat complexity, means with different letters are significantly different ( $p < 0.05$ , LS means).

and Magnuson 1976, Stein 1977, Garvey et al. 1994). In addition to selecting complex habitats that provide more cover, many crayfish species also increase their activities at night (Hobbs 1991), which is when most predatory freshwater fishes (e.g., bass, sunfishes, gar) are quiescent. We found that *P. alleni* substantially increased use of non-vegetated habitats at night. Preference for complexly vegetated habitats and increased nocturnal activity support the idea that crayfish are behaviorally minimizing their vulnerability to predatory fishes.

Habitat preferences observed in this study are highly concordant with results of quantitative sampling performed in the freshwater marshes of central and southern Florida, where *P. alleni* densities were substantially higher in densely vegetated wet prairies than in thinly vegetated sloughs (Jordan et al. 1996; F. Jordan, unpublished data). Therefore, observed patterns of habitat use in the field may reflect strong selection for increased cover (Stein and Magnuson 1976, Stein 1977, Garvey et al. 1994) because predatory fishes are much more abundant in sloughs than in complexly vegetated habitats such as emergent wet prairies and sawgrass stands (Dineen 1984, Loftus and Kushlan 1987; F. Jordan, unpublished data).

Our second experiment is consistent with previous research that has shown that crayfish are susceptible to predatory fishes. Susceptibility decreases significantly as crayfish reach sizes too large to be handled by predatory fishes such as largemouth bass in the freshwater marshes of central and southern Florida. Size selectivity on crayfish seems to be more a function of the defensive abilities of large-sized crayfish rather than gape limitation per se (e.g., Stein and Magnuson 1976, Garvey et al. 1994). Other types of predators (e.g., wading birds, alligators) are likely to prefer and take larger crayfish because of increased handling efficiency relative to predatory fishes. We also found that survival of small crayfish in tanks lacking predators was significantly lower than stocking densities, suggesting intraspecific predation (i.e., cannibalism). Size-based dominance hierarchies are common in crayfish (Hobbs 1991), and frequently lead to strong negative intraspecific and interspecific effects (e.g., Garvey et al. 1994). Typically, different sized crayfish fight for limited shelter space, resulting in the loser having increased vulnerability to predators (Garvey et al. 1994).

Crayfish constitute a significant portion of the diets of predatory fishes in many aquatic systems. For example, Rabeni (1992) found that smallmouth bass (*Micropterus dolomieu* Lacepède) and rock bass (*Ambloplites rupestris* Rafinesque) relied heavily on crayfish (*Orconectes* spp.) in an Ozark stream system. Further, he estimated that about half of the crayfish biomass in

this system was consumed by smallmouth bass and rock bass, which appeared to be the primary agents of crayfish mortality. Largemouth bass and warmouth sunfish (*Lepomis gulosus* Cuvier) consume significant numbers of *P. alleni* in central and southern Florida (unpublished data of F. Jordan and the Florida Game and Freshwater Fish Commission, West Palm Beach, FL). Juveniles and small adult crayfish (0.1–1.0 g dry weight) are most vulnerable to predatory fishes (Stein and Magnuson 1976, Stein 1977, Rabeni 1992, Garvey et al. 1994, this study), which frequently results in predator-induced demographic bottlenecks occurring around these size-age classes. Jordan et al. (1996) found that relatively few *P. alleni* recruited into larger size classes (i.e., >1.0 g wet weight) during their 18-month study, indicating a possible demographic bottleneck.

We found that the survival of *P. alleni* increased as a function of increasing habitat complexity, which also appears to hold for other crayfish species. For example, survival of *Orconectes* spp. exposed to predatory bass (*Micropterus* spp.) increased with increasing habitat complexity (Stein and Magnuson 1976, Garvey et al. 1994). Enhanced survival in more complex habitats is likely due to reductions in the ability of visually-oriented predators to detect and successfully capture prey (Heck and Crowder 1991). Intraspecific predation rates were lowest in high habitat complexity tanks, indicating that adult crayfish may also suffer decreased foraging efficiency in complex habitats. Both the lowered foraging efficiency (this study) and abundance (Dineen 1984, Loftus and Kushlan 1987; F. Jordan, unpublished data) of predators likely contribute to the relatively high abundance of *P. alleni* in emergent wet prairies and sawgrass stands in the wetland habitat mosaics of central and southern Florida (Jordan et al. 1996; F. Jordan, unpublished data). That is, complex habitats provide more refuges from predators and facilitate the coexistence of predators and vulnerable species and sizes of prey (e.g., Huffaker 1958, Hixon and Beets 1993, Beck 1995).

Variation in the frequency and duration of inundation is generally viewed as the most important factor regulating the abundance of aquatic organisms and determining community composition in seasonally dynamic freshwater wetlands (e.g., Kushlan 1976, 1987, Murkin and Kadlec 1986, Neckles et al. 1990, Batzer and Resh 1992, Batzer et al. 1993). However, little effort has been made to determine how other factors (e.g., predation, habitat heterogeneity) affect community composition in wetland systems (Prejs and Prejs 1992, DeAngelis and White 1994). Our results indicate that predation and habitat complexity both affect survival of the crayfish *P. alleni* and at least partially account for patterns of habitat use by this crayfish ob-

served in the field. Different hydrologic conditions (e.g., duration of inundation) are going to favor different predator assemblages (e.g., predatory arthropods vs. large fishes), which in turn will cause changes in habitat-specific prey assemblage structure. Therefore, a general model of assemblage regulation in wetland systems should not be based solely on hydrology but should also incorporate the direct and indirect effects of predators and habitat complexity.

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#### LITERATURE CITED

- Beck, M. 1995. Size-specific shelter limitation in stone crabs: a test of the demographic bottleneck hypothesis. *Ecology* 76:968-980.
- DeAngelis, D.L. and P.S. White. 1994. Ecosystems as products of spatially and temporally varying driving forces, ecological processes, and landscapes: a theoretical perspective. p. 9-27. *In* S.M. Davis and J.C. Ogden (ed.) *Everglades: the Ecosystem and its Restoration*. St. Lucie Press, Delray Beach, FL, USA.
- Dineen, J.W. 1984. The fishes of the Everglades. p. 258-268. *In* P.J. Gleason (ed.) *Environments of South Florida: Present and Past II*. Miami Geological Survey, Coral Gables, FL, USA.
- Feminella, J.W. and V.H. Resh. 1989. Submersed macrophytes and grazing crayfish: an experimental study of herbivory in a California freshwater marsh. *Holarctic Ecology* 12:1-8.
- Garvey, J.E., R.A. Stein, and H.M. Thomas. 1994. Assessing how fish predation and interspecific prey competition influence a crayfish assemblage. *Ecology* 75:532-547.
- Heck, K.L., Jr. and L.B. Crowder. 1991. Habitat structure and predator-prey interactions in vegetated aquatic systems. p. 281-299. *In* S.S. Bell, E.D. McCoy, and H.R. Mushinsky (ed.) *Habitat Structure: the Physical Arrangement of Objects in Space*. Chapman and Hall, New York, NY, USA.
- Hixon, M.A. and J.P. Beets. 1993. Predation, prey refuges, and the structure of coral-reef fish assemblages. *Ecological Monographs* 63:77-101.
- Hobbs, H.H., III. 1991. Decapoda. p. 823-858. *In* J.H. Thorp and A.P. Covich (ed.) *Ecology and Classification of North American Freshwater Invertebrates*. Academic Press, New York, NY, USA.
- Huffaker, C.B. 1958. Experimental studies on predation: dispersion factors and predator-prey oscillations. *Hilgardia* 27:343-383.
- Jordan, F., H.L. Jelks, and W.M. Kitchens. 1994. Habitat use by the fishing spider *Dolomedes triton* in a northern Everglades wetland. *Wetlands* 14:239-242.
- Jordan, F., K.J. Babbitt, C.C. McIvor, and S.J. Miller. 1996. Spatial ecology of the crayfish *Procambarus alleni* in a Florida wetland mosaic. *Wetlands* 16:134-142.
- Kerfoot, W.C. and A. Sih. 1987. *Predation: Direct and Indirect Effects on Aquatic Communities*. University Press of New England, Hanover, NH, USA.
- Kushlan, J.A. 1976. Environmental stability and fish community diversity. *Ecology* 57:821-825.
- Kushlan, J.A. 1987. External threats and internal management: the hydrologic regulation of the Everglades. *Environmental Management* 1:109-119.
- Kushlan, J.A. and M.S. Kushlan. 1979. Observations on crayfish in the Everglades Florida. *Crustaceana, Supplement* 5:115-120.
- Loftus, W.F. and J.A. Kushlan. 1987. Freshwater fishes of southern Florida. *Bulletin of the Florida State Museum, Biological Sciences* 31:147-344.
- Loveless, C.M. 1959. A study of the vegetation of the Florida Everglades. *Ecology* 40:1-9.
- Murkin, H.R. and J.A. Kadlec. 1986. Responses by benthic macroinvertebrates to prolonged flooding of marsh habitat. *Canadian Journal of Zoology* 64:65-72.
- Neckles, H.A., H.R. Murkin, and J.A. Cooper. 1990. Influences of seasonal flooding on macroinvertebrate abundance in wetland habitats. *Freshwater Biology* 23:311-322.
- Prejs, K. and A. Prejs. 1992. Importance of predation in regulating density of meio- and macrofauna in seasonal tropical waters. *Hydrobiologia* 242:77-86.
- Pulliam, H.R. 1988. Sources, sinks, and population regulation. *American Naturalist* 132:652-661.
- Rabeni, C.F. 1992. Trophic linkage between stream centrarchids and their crayfish prey. *Canadian Journal of Fisheries and Aquatic Sciences* 49:1714-1721.
- Robertson, W.B. and P.C. Frederick. 1994. The faunal chapters: contexts, synthesis, and departures. p. 709-737. *In* S.M. Davis and J.C. Ogden (ed.) *Everglades: the Ecosystem and its Restoration*. St. Lucie Press, Delray Beach, FL, USA.
- Stein, R.A. 1977. Selective predation, optimal foraging, and the predator-prey interaction between fish and crayfish. *Ecology* 58:1237-1253.
- Stein, R.A. and J.J. Magnuson. 1976. Behavioral response of crayfish to a fish predator. *Ecology* 57:751-761.
- Wiens, J.A. 1976. Population responses to patchy environments. *Annual Reviews in Ecology and Systematics* 7:81-120.

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