

Everglades Crayfish Final Report

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[USGS Cooperative No. 14-16-0009-1571]

Funding Source:
U.S. Department of Interior, Bureau Information Needs
South Florida Ecosystem Restoration Program

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Report History

This project was initiated to understand the role of crayfish in the Everglades aquatic community. Previous research into the species composition of ephemeral and sustained bodies of water within the myriad of ecotones present in Everglades National Park (ENP) and Big Cypress National Preserve (BICY) suggested that a single species, *Procambarus alleni* (Faxon), was capable of inhabiting these locales equally. The plasticity of this species appeared remarkable. With the goal of resolving habitat use and characterizing this plasticity, I devised an experimental design, which employed throw trapping to determine density in a range of hydroperiods. The two-year project identified four locations where crayfish would be identified and collected.

I found a second species of crayfish, *P. fallax* (Hagan) that inhabited the longer hydroperiod study sites. This discovery provided a reasonable answer to our initial question of plasticity; however it altered the focus of our original proposal. Determining the life history characteristics of both species and identifying how the two species were using each of our originally selected sites became the new direction. This final report provides three sections that address these topic areas and a fourth section that reviews literature pertinent to crayfish ecology in the Florida Everglades.

The initial discovery of *P. fallax* and the relationship between hydroperiod and species composition was included in a submission to Wetlands. The relative abundance of *P. fallax* was found to vary predictably with hydroperiod both in historic and recent collections. *P. alleni* was prevalent in those locations that were flooded for 11 months and dominated in those flooded for less than 10 months.

The literature provides information regarding *P. alleni* life history, however little is known about *P. fallax*. Thus, the second section of this report was written to detail the life history of *P. fallax*. The format of the section follows the guidelines for submission of a manuscript to the Journal of Crustacean Biology. *Procambarus fallax* is unique in that this

species does not burrow during reproduction and oviposition. In comparison to other subtropical procambarids, *P. fallax* conducts the full complement of life history tasks in the flooded habitats of Shark Slough, ENP. Because of this fully submerged lifestyle, aquatic predators may structure habitat use; thus density of life history stages with varying susceptibility to predation were monitored over the two year study in two adjacent habitats. When physical conditions allowed, *P. fallax* was found in higher densities in sawgrass (*Cladium jamaicense*) than spikerush (*Eleocharis* spp.). The fact that sawgrass is found in shallower water than spikerush and has a more stout physical structure probably reduces predation by large bodied aquatic fishes and wading birds. Densities in both habitats increased when *P. fallax* used sawgrass over spikerush.

The third section of this report describes *P. alleni* life history and *P. fallax* life history in locations where both species are found, such as East Slough and Raccoon Point. *Procambarus alleni* is found in shorter hydroperiod sites and burrows during the dry season. Reproduction and oviposition occurs in the burrows and juveniles are released as habitats are reflooded in the spring. Life history characteristics of *P. alleni*, including the seasonality of burrowing, size at maturity, maximum size, habitat use, sex ratio, and fluctuations in juvenile and adult density by season, are presented. In Raccoon Point *P. fallax* was found in significantly higher densities in a large cypress dome when compared to other, smaller domes. The size and depth of the large dome maintained habitat with flooded vegetation throughout the dry season. Both of these qualities have been discussed by previous authors (Hobbs, 1942) as suitable habitat for *P. fallax*. Finally, a short section is dedicated to the effects of a dual species crayfish assemblage on predators of crayfish, particularly wading birds. I hope that the few conclusions and multiple queries enclosed in the following pages will direct research to further address the topics of crayfish distributional patterns and their impact on the surrounding community.

Section 1

Distribution and relative abundance of the crayfishes *Procambarus alleni* (Faxon)
and *P. fallax* (Hagen) in southern Florida

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Abstract: The Everglades crayfish (*Procambarus alleni* Faxon) is the only species reported from Everglades National Park (ENP) and Big Cypress National Preserve (BICY). However, we identified a second species, *Procambarus fallax* (Hagen), from these two locations. *P. fallax* has been a member of the community prior to 1985 and has been misidentified as *P. alleni*. We provide a method for distinguishing specimens of these morphologically similar species. Species relative abundance varied predictably with hydroperiod (length of inundation) in recent collections and in historic samples. *Procambarus fallax* relative abundance was highest in sites characterized by long hydroperiod and prolonged inundation.

Key Words: *Procambarus alleni*, *Procambarus fallax*, hydroperiod, Everglades, Shark Slough

INTRODUCTION

Crayfishes are distributed throughout most aquatic habitats in Florida (Hobbs 1942). Because crayfish can assimilate detritus into protein in one trophic step (Momot 1984), they are efficient energy links to higher trophic levels (Lorman and Magnuson 1978). In the Everglades region of southern Florida (Figure 1), crayfish are a major prey item in the diet of the striped swamp snake, *Regina alleni* (Godley 1980), pig frogs, *Rana grylio* (Stejneger), fishes such as largemouth bass, (*Micropterus salmoides* Lacepede) and warmouth (*Lepomis gulosus* Cuvier) and wading birds such as glossy ibis, *Plegadis falcinellus* and white ibis, *Eudocimus albus* (Gunderson and Loftus 1993). Despite its ecological role, life-history aspects of crayfish in the Everglades have not been well studied.

A single species of crayfish, *Procambarus alleni* (Faxon), is reported from southern Florida counties and the Everglades (Hobbs 1942, Kushlan and Kushlan 1979, Gunderson and Loftus 1993). In Everglades National Park (ENP) *P. alleni* inhabits ephemeral pools and flooded marshes ranging in salinity from 0 to 18 ppt (Conover and Reid 1972, Loftus et al. 1990). During seasonal drydowns, *P. alleni* burrows, where copulation and oviposition occur (Rhoades 1970). Reflooding of dry land brings crayfish to the surface with attached young. In flooded wetlands (Jordan et al. 1996) showed that *P. alleni* actively selected vegetated substrates to avoid predation by fishes and conspecifics in the upper basin of St. Johns River. In laboratory studies Bovbjerg (1956 and 1959) determined that *P.alleni* aggression was responsible for density dependent movement and dominance hierarchies.

In this study of *P. alleni*, we hoped to explain a broad tolerance to hydrologic regimes, spanning sites that were inundated for several months to those that remained flooded throughout the year. However, early in the study it became apparent that the presence of a second species, *Procambarus fallax* (Hagen), explained extensive habitat use by crayfish. Hobbs (1942) first described the ecology of *P. fallax* and its range, which is enclosed to the west by the Suwanee

River, to the north by Georgia and to the south by Lake Okeechobee. Palm Beach County was thought to form the southern limit, yet we collected *P. fallax* in Miami-Dade county near the southern extent of freshwater marshes in Florida. To determine if *P. fallax* had been present in Everglades National Park for several decades or had recently immigrated into the system, we analyzed collections of crayfish dating from the early 1980's. Besides treatment of specialized feeding by the striped swamp snake on *P. fallax* (Franz 1977), this species has not been included in discussions of Florida crayfish since 1942. These historical records and a spatial examination of *P. fallax* and *P. alleni* distribution conducted in 1996 provide the most recent contributions to crayfish ecology in the Everglades.

METHODS

To examine the current spatial distribution of *P. alleni* and *P. fallax*, we chose sampling sites that typified dry and wet conditions. Since vegetation and substrate are indicative of hydrology (Gunderson 1989, Loftus et al. 1990, David 1996), site selection was based largely on these two criteria. Additionally, each study site was located within several kilometers of a hydrologic monitoring station to quantify the hydroperiod. We defined short-hydroperiod sites as those flooded less than nine months per year, intermediate as flooded from nine to eleven months, and long-hydroperiod locations as flooded from eleven to twelve months. The sampling locations, in order of driest to wettest, were the Rocky Glades, East Slough, Raccoon Point, and Shark Slough (Figure 1). Rocky Glades is composed of limestone karst and muhly grass (*Muhlenbergia filipes* Curtis) with pockets of marl providing habitat for sparse sawgrass (*Cladium jamaicense* Crantz). East Slough also has a limestone with marl substrate, however spikerush (*Eleocharis cellulosa* Torr.) is a vegetative component indicating longer hydroperiod than Rocky Glades. Raccoon Point is a matrix of intermediate hydroperiod cypress prairies

composed of limestone, marl sediment, and dominated by beak rush (*Rhynchospora* spp.) and longer hydroperiod cypress domes with peat substrate, submerged aquatic vegetation, and tall stands of cypress (*Taxodium* spp.). We established plots on the interface of the two habitats and characterized them by the hydroperiod of the dome. Shark Slough is a long hydroperiod, mixed spikerush and sawgrass marsh with peat alluvium.

We collected crayfish primarily in throw traps (methods described by Loftus and Eklund 1994). However in locations which were not amenable to this collection method, such as Rocky Glades site, we used Gee[®] passive fish traps. The possibility of exclusion of a species by passive traps was assessed by deploying them while throw trapping.

Prior to the collection of data, male crayfishes of both species were sent for identification to Richard Franz at the Florida Museum of Natural History in Gainesville. After verifying that the color pattern found on each species (Figure 2) matched form I pleopod morphology (R. Franz pers. comm.), we identified crayfishes in the field and released them unharmed. Crayfishes were measured (carapace length), sexed, and labelled according to species.

We tested the response of species relative abundance to hydrology in two ways. First, species relative abundance was related to hydroperiod in 1996 over locations that spanned a hydrologic gradient. We analyzed composition from three sites ranging in hydroperiod from eleven to twelve months. Second, species relative abundance was related to hydrologic fluctuations at a single location over time. We analyzed archived crayfish data from Shark Slough that was obtained from 1985 to 1997.

We sampled four plots in East Slough and Shark Slough and three plots in Raccoon Point to determine the correlation between hydroperiod and species relative abundance. Hydroperiod was calculated by correlating local water depth to a continuous hydrologic monitoring station (East Slough- 205, Raccoon Point-BCA5, Shark Slough-P33) on the date of crayfish sampling. Hydroperiod, which was defined as the number of days flooded, of all sites was determined from November 1995 to November 1996. After arcsine transforming the ratio of *P. fallax* abundance

to total crayfish abundance, we calculated the Pearson product moment correlation between hydroperiod and *P. fallax* relative abundance.

To determine if *P. fallax* and *P. alleni* relative abundance vacillated due to annual variations in hydrology, we examined archived throw-trap samples from 1985 to 1997 in central Shark Slough. Additionally, by reviewing archived samples we could determine if *P. fallax* was a long-standing member of the community or a recent immigrant. Since color patterns were lost by both species in the archival process, we examined male pleopod morphology (see Hobbs, 1942), assuming that male relative abundance is an index of species relative abundance. Sex ratio did not vary in 1996 and 1997 for either species (ANOVA of arcsine transformed male to total ratio; *P. fallax* in Shark Slough $F_{2,11} = 4.26$, $p = 0.96$, and *P. alleni* in Raccoon Point $F_{2,10} = 4.46$, $p = 0.22$). We determined local water depth and hydroperiod using a continuous depth gauge (P-33) near the collection site and computed number of days flooded for each year. After arcsine transforming the proportion of *P. fallax* males to total males, we calculated the Pearson product-moment correlation between number of wet days and proportion of *P. fallax* males.

RESULTS and DISCUSSION

Both *P. alleni* and *P. fallax* were collected in throw traps and Gee[®] traps in the study sites. *Procambarus alleni* was collected from Rocky Glades, Raccoon Point, and East Slough sites, which we characterized as short to intermediate hydroperiod (Figure 1). *Procambarus fallax* was taken in Shark Slough, East Slough, and Raccoon Point in intermediate to long hydroperiod samples.

Collections from 1996 revealed that species distribution followed a hydrologic gradient: *P. alleni* was collected in locations distinguished by seasonal drydowns while *P. fallax* was typically found in habitats characterized by prolonged flooding. Crayfish from Rocky Glades, which was flooded only 168 days in 1996, were composed entirely of *P. alleni*. Plots in Shark

Slough, East Slough and Raccoon Point contained both species (Figure 3). *P. fallax* relative abundance was significantly correlated to hydroperiod ($r = 0.751$, $p = 0.008$) in these sites. Hobbs (1942) similarly captured *P. fallax* in long hydroperiod locations. Further, his collections revealed partitioning of habitat by *P. fallax* and *P. alleni* based on hydrologic conditions. During the wet season, *P. fallax* and *P. alleni* were captured together in flooded ditches. However, during the seasonal drydown, *P. alleni* was collected from burrows in the now dry ditch while *P. fallax* was found in a still flooded, contiguous stream (Hobbs 1942).

The alternation of species composition due to hydrology is apparent in the Shark Slough throw trap collections from 1985 to 1997 (Figure 3). *Procambarus fallax* relative abundance was positively correlated with number of days flooded annually ($r = 0.68$, $p = 0.011$). Duration and frequency of dry season water loss has been shown to affect the density and composition of amphibian (Pechmann et al. 1989), ENP fish (Loftus and Eklund 1994, DeAngelis et al. 1997), and Big Cypress National Preserve invertebrate (Leslie et al. 1997) communities. Crayfish have been assumed to be exempt from the pressures of drydowns in ENP (Frederick and Callopy 1989), perhaps by assuming that all crayfish collected were *P. alleni* and capable of burrowing, however this does not appear to be the case. *P. fallax* relative abundance is sensitive to the duration of flooding.

Analysis of archived data indicated that *P. fallax* has been a member of the central Shark Slough marsh community since 1985 (Figure 4) and perhaps earlier. Previous researchers in southern Florida probably caught *P. fallax* but did not distinguish them from *P. alleni*. We therefore provided a method for distinguishing the two species in fresh collections (Figure 2). Gunderson and Loftus (1993) reported the single species of crayfish captured in ENP as *P. alleni*; however, crayfish from throw-trap samples spanning 1985 to 1997 indicate that *P. fallax* was also present. Several behavioral characteristics, which might have facilitated the capture and identification of *P. alleni* from ENP, include: habitation by *P. alleni* of shorter hydroperiod locations which often border roads, construction of conspicuous chimneys at the entrance to its

burrows, and overland movements following rain events (Hobbs 1942, pers. observations). In contrast, *P. fallax* is less likely to be captured because it inhabits longer hydroperiod locations that are less accessible, constructs simple burrows without chimneys (Hobbs 1942), and does not appear to travel across land. Our records of *P. fallax* probably do not represent a range expansion, but rather an extension of the reported distribution based on misidentifications or lack of recognition.

Hydroperiod, which describes the duration of drydown, does not capture the loss of refuge through sequential dessication of microdepressions. For example, water may remain in refugia that is recharged through groundwater and isolated rain events. This facet of the landscape was crucial to determining the effects of drydowns on marsh fish abundance (DeAngelis et al. 1997), and the same may be true of hydrologically sensitive species of crayfish. *Procambarus fallax*, while being outcompeted during drydowns, maintained a reduced presence in the community (Figure 3), perhaps through microdepressions. Ultimately, the mechanisms responsible for the observed shifts in composition are unknown and warrant further investigation. Still, species composition is dictated by hydroperiod in the Everglades, and crayfish may indicate widespread shifts of Everglades fauna to alterations in hydrology.

Much of the flora and fauna of the Everglades can be related to hydrology. Soil composition, vegetation, and fauna are correlated to hydroperiod depending upon scale (Gunderson 1994). Soil accretion occurs on the level of centuries, vegetation composition on the order of decades (Gunderson 1994, Busch et al. 1998), and marsh fishes on the order of months provided the underlying trophic structure has not been altered (Loftus and Eklund 1994). Change in crayfish species composition due to hydrology appears to occur in one to two years (Figure 4). However, unlike the response of marsh fishes to hydrology, which may be complex due to the interaction of multiple species, the crayfish assemblage is composed of two easily identified members whose presence-absence is correlated to hydrologic regime. Since the historical data provided here are from a single location, additional sites which span a gradient of hydroperiods

are required to fully explore the relationship between crayfish species and hydrology. With species specific hydroperiod requirements in hand, we can estimate the historical distributions of crayfish through historical water flow and depth profiles (e. g. Fenema et al. 1994) and synthesize pre-drainage species distributions that fostered wading bird success in the system. Moreover, understanding the crayfish and hydroperiod relationship may provide a predictive tool for assessing alternative hydromanagement scenarios.

ACKNOWLEDGEMENTS

We would like to thank the many hours contributed by Shawna Baker, Americorp members Liz Morgan and Jessica Stevenson, the lab space and input provided by Joel Trexler, the review by Joe Pechman, and the financial support provided by the Biological Resource Division of the United States Geological Service through the efforts of D. DeAngelis, W. Kitchens, and G. Ronnie Best.

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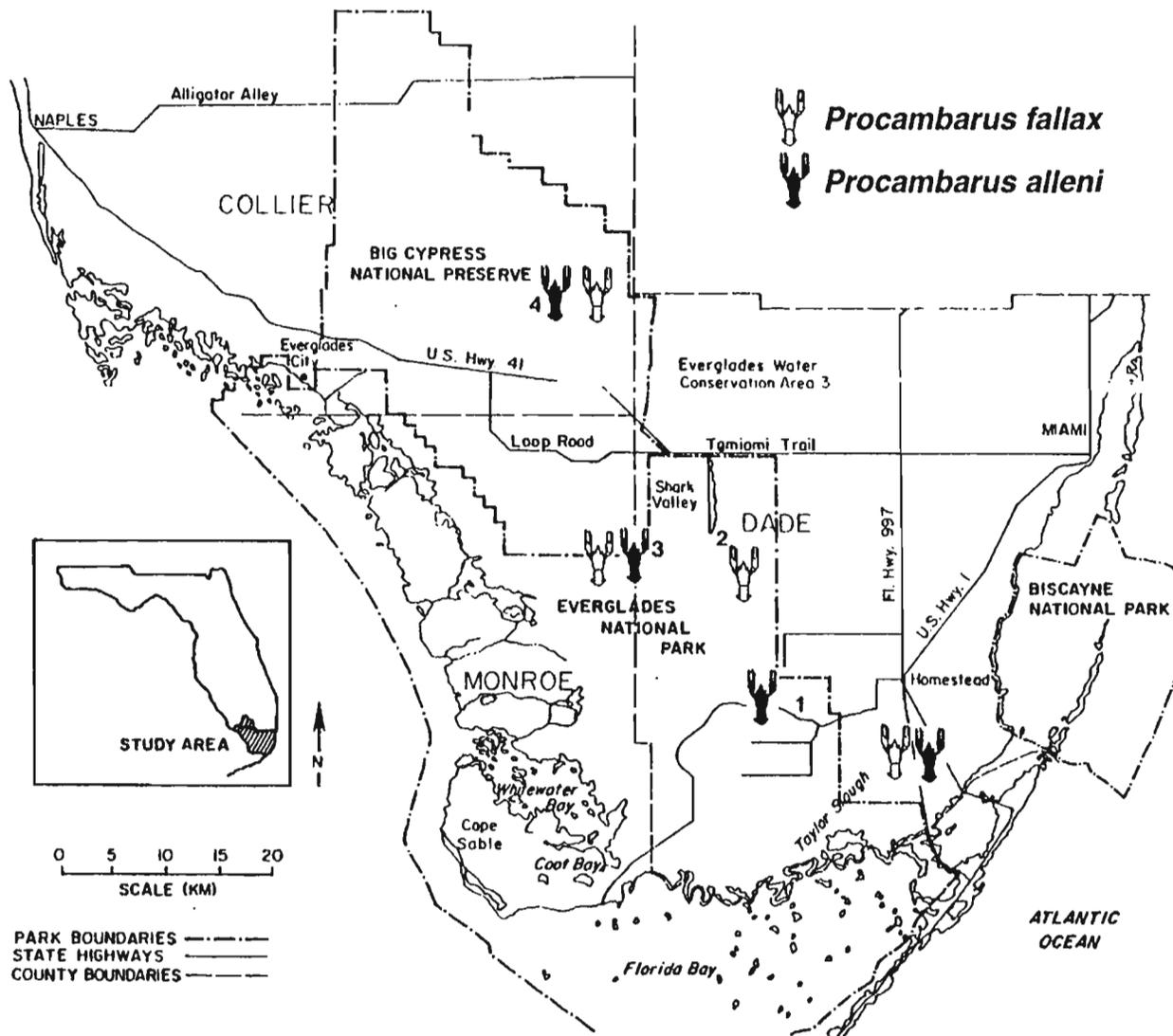


Figure 1. Crayfishes were collected from Taylor Slough, Rocky Glades (1), Shark Slough (2), East Slough (3), and Raccoon Point (4). Crayfish icons indicate occurrence at a sampling location.

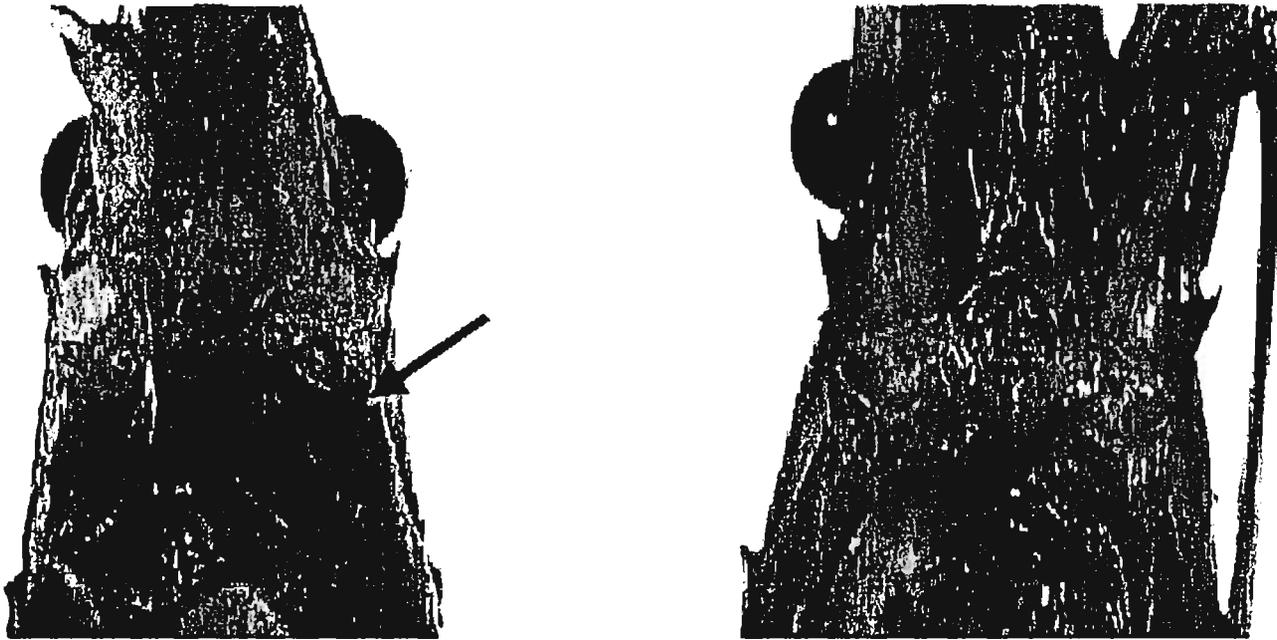


Figure 2. Ventral view of anterior cephalothorax. *P. alleni* (left) has conspicuous markings anterior of oral cavity. *P. fallax* (right) lacks this coloration.

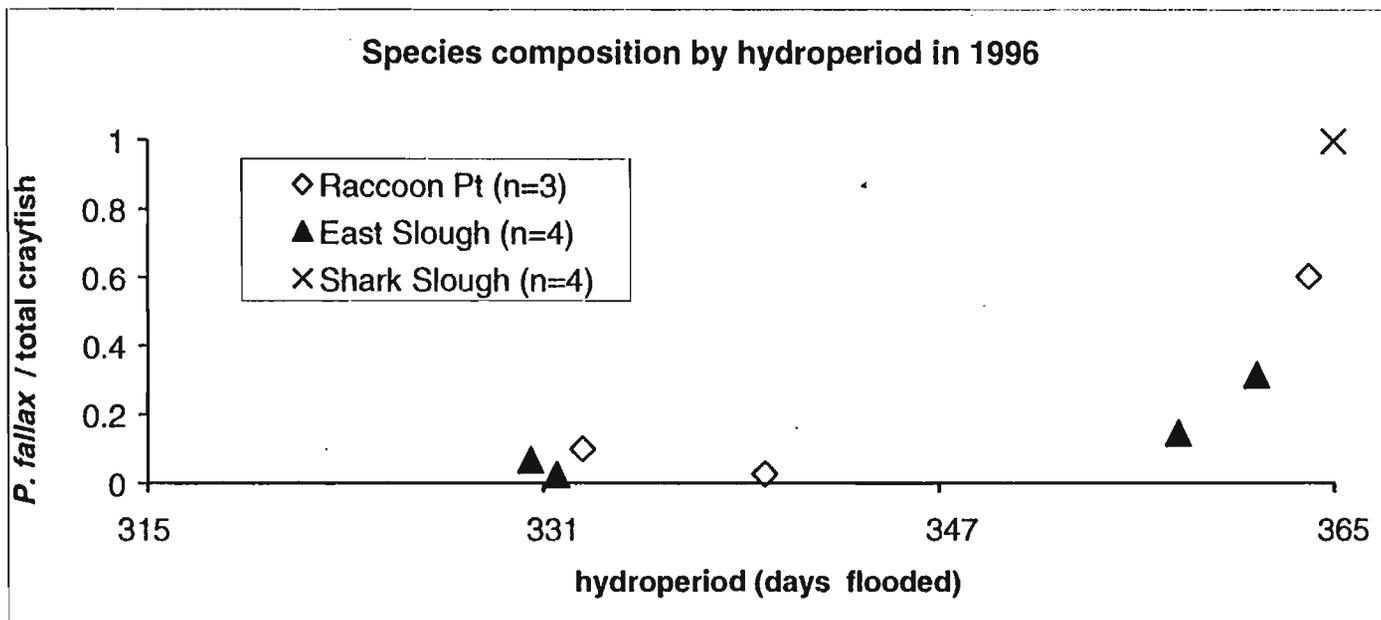


Figure 3. Proportion of *P. fallax* to total crayfish in 1996 from three sites with varying hydroperiod . Each replicate plot within a site is presented. *P. fallax* proportion is positively correlated to days flooded ($r = 0.751$, $p = 0.008$).

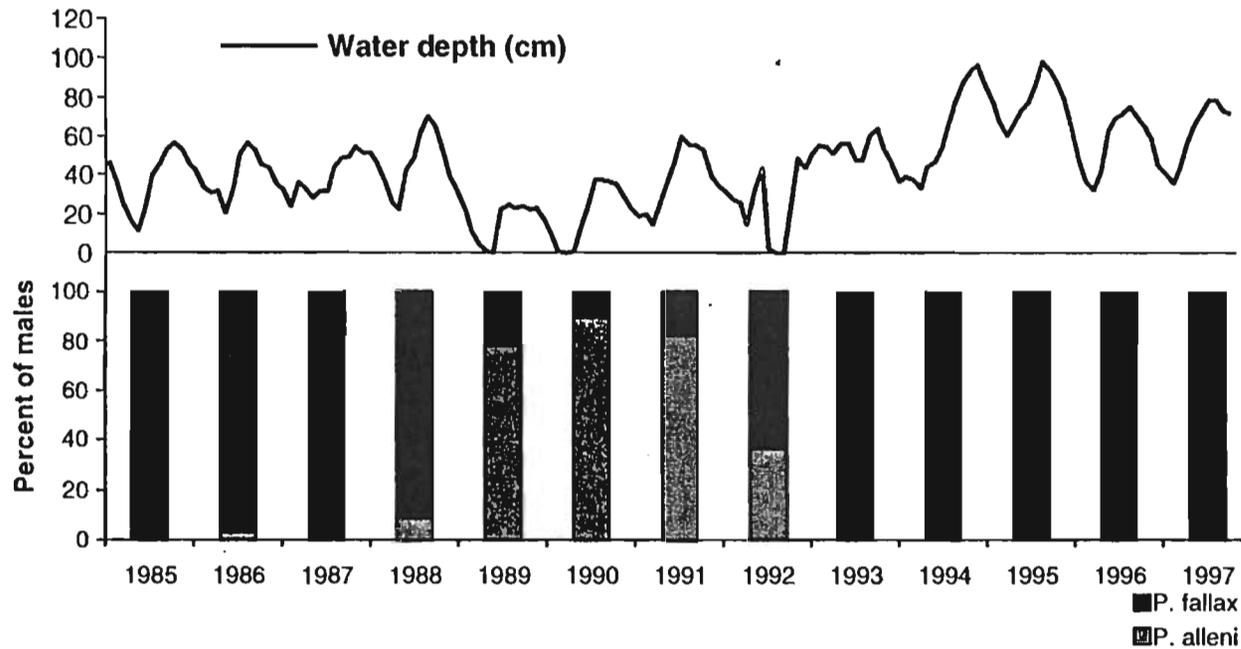


Figure 4. Relative composition of *P. alleni* and *P. fallax* males in relation to average monthly water depth in Shark Slough. *P. fallax* percent of total males is positively correlated to days flooded per year ($r = 0.68$, $p = 0.011$).

Section 2

Life History of the Slough Crayfish, *Procambarus fallax* (Hagen)

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ABSTRACT

Procambarus fallax was ~~discovered~~ ^{IDENTIFIED FROM FIRST COLLECTIONS} in November 1996 in Shark Slough which is ^{approximately 100K} well south of its ^{KNOWN} reported distribution. Shark Slough, like other locations further north in which *P.*

¹⁾ *fallax* has been collected, ^{IS} remains flooded throughout the year. In contrast ^{MOST OF EVERGLADES} to other procambarids found in the subtropics, the fulfillment of the myriad of life ^{COMPLETION ALL HISTORY STAGES} processes by *P. fallax* in a ^{PERENNIAL} flooded habitat is rare. We provide ^{FOR} a description of ^A certain life history characteristics of this species, and ^{DESCRIBE} report on the ^{IN LONG-HYDRO PERIOD} special conditions experienced by this species ^{due to a fully flooded}

~~lifestyle.~~ **HABITATS.**

^{BECAUSE} Due to the presence of aquatic predators ^{ARE PRESENT DURING ALL LIFE STAGES OF} throughout all stages of development ^{P. FALLAX} in the flooded marshes of the Everglades, we investigated ^{USE BY DIFFERENT STAGES} the role of habitat utilization by sampling two

vegetation types. ^{OCCURRED AT} *Procambarus fallax* was found in higher densities in sawgrass versus spikerush ^{HABITAT}

in one of two years. During the first year, *P. fallax* used both habitats, however the utilization changed with season. During the second year, *P. fallax* adults in a reproductive state (Form I males and ovigerous females) ^{OCCURRED} were found in sawgrass more often than ^{IN} spikerush. An increase in ^{THE DENSITY OF} juvenile ^S density in both sawgrass and spikerush accompanied the second year. Given the physical structure of sawgrass, the fact that it is found in shallower locations, and the morphology of piscine predators, sawgrass is a preferred habitat when physical conditions allow.

INTRODUCTION

Studies of burrowing crayfish are common, yet few studies exist that describe the life cycle of a fully aquatic species of crayfish. Most subtropical procambarids inhabit flooded locations during the wet season and reproduce in burrows during the dry season. *P. clarkii*, perhaps the most thoroughly studied species of the genus, follows this pattern (Hobbs, 1989) as do *P. acutus acutus* (Romaine and Lutz, 1989), *P. zonangulus* (Burras et al., 1995), *P. alleni* (Hobbs, 1942, Rhoades, 1970), and *P. hayi* (Payne, 1972). Variation in burrow use was addressed by Hobbs (1942), who described three levels: 1) primary burrowers inhabit burrows for the majority of their life 2) secondary burrowers maintain burrows throughout the year but may

be found occasionally on the surface during or shortly following precipitation, and 3) tertiary burrowers utilize burrows during droughts or for reproductive periods. Unfortunately little room exists to describe those species that are fully aquatic, even in the reproductive period. Perhaps this is due to the infrequency of collecting such crayfish and subsequently studying their life history.

Procambarids are the most specious of the astacids and perhaps the most specialized in habitat requirements (Hobbs, 1988). Although they range from middle North America through central America, the hub of radial dispersion is located at the base of the Appalachian Mountains (Hobbs, 1988). The types of habitats utilized by procabarids is diverse, particularly in the region surrounding this hub. Thus, we would expect crayfish in this region to inhabit localities in a fashion that would limit competition with other species of crayfish in the region.

Two species of crayfish have been collected in Everglades National Park (ENP) and Big Cypress National Preserve (BICY) (Hendrix and Loftus, in press). Both species would be classified as tertiary burrowers, although particular life-history characteristics are different. *Procambarus alleni* (Faxon) is similar to *P. clarkii* in its life-cycle: maturation in approximately a year, excavation of burrows upon water loss, reproduction, oviposition, and hatching in burrows (Bovbjerg, 1959, Rhoades, 1970, Wygoda, 1981). The life cycle of *P. fallax* (Hagan) occurs in fully flooded conditions, presumably without the aid of a burrow. Because the life cycle of *P. fallax* has not been studied in any detail and this species tends to dominate annually flooded habitats in ENP, we initiated a two year study of its life history.

P. fallax has been described in a single instance by Hobbs (Hobbs, 1942) since its initial description by Hagen (Hagen, 1870). *P. fallax* was collected by Hobbs throughout most of the Florida panhandle, bordered on the north by Georgia and on the south by canals leading from Tampa Bay to Lake Okeechobee (Hobbs, 1942). The species is typically found in heavily vegetated microhabitats which remain flooded for most of the year (Hobbs 1942; Hendrix and Loftus in press). *P. fallax* was collected in Flagler, Citrus, Hillsborough, Sumter and Seminole

counties sympatrically with several species, including *P. alleni*. However, during the dry season, when *P. alleni* was collected from burrows in dry tributaries, *P. fallax* was captured in contiguous streams (Hobbs, 1942). Burrow excavations conducted throughout ENP and BICY revealed only *P. alleni*. Although *P. fallax* may be found both allopatrically and sympatrically with *P. alleni* throughout ENP and BICY (Hendrix and Loftus in press), this investigation presents life history characterizations from a single allopatric population in Shark Slough, ENP.

Crayfish that undergo the full array of life-cycle complexities in submerged habitats are susceptible to amphibian and piscine predators. Amphibian predators of crayfish in Florida wetlands include pig frogs, *Rana grilio*, (Ligas, 1960) and two-toed amphiuma (*Amphiuma means*). Previous research has indicated that largemouth bass (*Micropterus salmoides*) structure crayfish distributions in lakes (Garvey et al., 1994) and Florida freshwater wetlands (Jordan et al., 1996b). Thus, we would expect distribution by *P. fallax* in our study plots to reflect susceptibility to predation. The substrate of Shark Slough is composed of muck soils that do not provide a mechanical refuge. However, refuge is available in the roots and culms of macrophytes. To test the utilization of habitat, we sampled crayfish from two vegetation types with different shoot density and culm stoutness.

METHODS

Study Location:

Shark Slough is the largest slough contained in Everglades National Park (Figure 1). The central portion maintains water for the longest duration and the lateral areas, namely the northeast, dry seasonally. The hydroperiod (duration of inundation) of Shark Slough is caused by a combination of, topography, recent hydrologic history, local rain events, and water management. In particular water management is significant to central Shark Slough since it receives the majority of hydrologic input into ENP (Light and Dineen, 1994). In response to

hydrology, the central section of the slough is comprised of dense, monotypic stands of sawgrass (*Cladium jamaicense*) and spikerush prairie (*Eleocharis* spp.). Fire, peat deposition, and hydrology determine the boundary between these two species (Herndon et al., 1991, Busch et al., 1998). Periphyton (a floating complex of algae and plant material) is a common element of sloughs, and bladderwort (*Utricularia* spp.) is often present with it (Busch et al., 1998). The annually flooded habitats of Shark Slough are composed of limestone rock overlain with organic peat (Busch et al., 1998).

Sampling Design:

We sampled spikerush and sawgrass habitats during March, July, and November of 1996 and March, July, and December of 1997. Four plots, each divided into a 25m x 50m rectangular section of sawgrass and a contiguous 25m x 50m rectangular section of spikerush, were sampled. Seven throw trap samples were collected in each habitat type per plot on each of the six sampling events, except March 1996, in which three plots were sampled at five throw trap samples per habitat.

Throw trapping was used to sample crayfish (Loftus and Eklund, 1994, Jordan et al., 1996), due to the limited bias associated with this method (Turner and Trexler, 1997). The trap was constructed of a cube of copper tubing, around which was stretched and sewn a mesh exterior. The bottom was pushed into on the substrate and trapped animals were removed with a bar seine and dip nets. The sampled area of substrate measured 1 m².

Prior to searching for crayfish, we measured: water depth, water temperature, vegetation shoot density by species, estimated areal coverage of vegetation and estimated areal coverage of periphyton. Areal coverage for periphyton and vegetation was measured by two or more technicians stating their estimate of the cover simultaneously. Both periphyton and vegetation estimates were rounded to 25% increments (values of 25%, 50 %, etc. were entered into data

sheets). Additionally, temperature probes were placed in spikerush to measure temperature throughout the duration of the study.

We identified crayfish to species based on coloration (Hendrix and Loftus, in press) in the field. Sex, carapace length, and in the case of ovigerous females, fecundity were measured. Further, an assessment was made on the reproductive stage of the males. Male procambarids display secondary sexual characteristics including enlarged chelae and ischial hooks when form I (reproductively active) and lack these characteristics when form II (inactive) (Hobbs 1991). Because females typically do not display similar external secondary sexual characteristics, female maturity was determined by the presence of eggs on the abdomen. After measurement, crayfish were returned unharmed to the sampling location.

During July and November 1997, we attempted to define the bias associated with throw-trapping. Crayfish caught from previous throw traps were marked by clipping the uropod and introduced into a new throw trapping sample. Animals were acclimated for approximately five minutes while physical and vegetation parameters were measured. Individuals were used in tests only once to ensure a response similar to uncaptured crayfish. We hypothesized that 1) all sizes of crayfish were sampled equally and 2) both sawgrass and spikerush were sampled with the same efficiency.

Instead of calculating mean size at maturity (MSAM), we determined the probability of being mature at a given size (probability). The probability method uses the mean, standard deviation and distribution (a Normal distribution in our case) to determine maturity, in contrast to the mean only in MSAM. To determine the probability of maturity, the following series of manipulations were completed for each, ovigerous females and form I males, separately: reproductively active individuals (FI males and ovigerous females) were classified in 1mm intervals, the size-frequency distribution was compared to a Normal distribution and tests of normality were conducted (Shapiro Wilk test of Normality) using SPSS (SPSS, 1998). A 29mm female in berry, was not included in the determination of mean size at maturity of females, as she

was 4 mm larger than the next largest female and had a significant effect on the distribution of the data (Test of Normality, Shapiro Wilk statistic with largest ovigerous female = 0.898, 24 d.f. $p = 0.020$, Shapiro Wilk statistic without largest ovigerous female = 0.961, 23 d.f., $p = 0.488$). Finally, the cumulative normal density function defined above was used to assign the probability of maturity to the reproductively inactive (FII males and females without eggs) portion of the population.

We attempted to determine the difference in mature individuals calculated by the two methods. The number of mature females and males were calculated by the probability and MSAM methods for each sampling event (six total, three in each year). We defined the number of mature animals in the following manner:

$$\text{number mature} = \sum [\text{Pr}(\text{mat})_x] \times (\text{count}_x), \text{ where}$$

$\text{Pr}(\text{mat})_x$ = Probability of maturity at size x determined from either the mean size at maturity (MSAM) or the probability of maturity based on a cumulative Normal curve (probability)
 count_x = number of crayfish of size x .

The two methods were tested for similarity in classifying *P. fallax* adults by a pairwise t-test.

We calculated biomass by summing the dry weight of individuals found in a throw trap. To determine individual dry weight, a length-dry weight regression was calculated. We collected animals that spanned the size range found in the field, dried them in an oven for 5 days at 60°C, and weighed them. We used the relationship $\text{wt} = a(\text{CL})^b$, where wt = weight, CL = carapace length, and a, b = parameters.

Habitat use

Habitat use by juveniles, non-reproductively active adults (NRA), and reproductively active adults (RA), was determined by repeated measures analysis of variance (ANOVA). Densities of each of the life history stages were tested separately. Tests for homogeneity of variance after log transformation were also completed for each life history stage. Due to the nature of repeated measures ANOVA, the number of time periods to be compared must be less

than or equal to $(n-1)$, where $n = 4$ in all samples except March 1996 when $n = 3$. Thus, we compared juvenile densities of March 1996 to July 1996 (restricted to two dates as March 1996 had only three plots), and March, July, and December 1997. NRA adults were compared in July and November 1996 in the first comparison and March, July, and December 1997 in the second. FI males were compared in July and November 1996 in the first comparison, and March, July, and December, 1997, in the second. Finally, the density of ovigerous females was compared in March and November 1996, and was compared in March and December 1997.

RESULTS

1667 *P. fallax* were collected in 170 throw trap samples from March 1996 to December 1997, and ranged from 5.0 to 32 mm CL. Although *P. fallax* was not identified as a species present in Shark Slough until after July 1996, crayfish collected in Shark Slough from November 1996 to December 1997 consisted solely of *P. fallax*. Further, preserved crayfish collected from Shark Slough in another, concurrent study during 1996 were only *P. fallax* also (Hendrix and Loftus in press). We therefore assumed that crayfish collected from this location during 1996 and 1997 were *P. fallax*.

Water depth and temperature varied predictably with season in the two sampling years (Fig 2a and b). The seasonal trends of temperature and water depth were similar although the sinusoidal curve of water depth appeared to trail that of temperature. Temperature in both years ranged from 10 to 35 degrees, and summer temperatures were generally 27 degrees. In 1996 the rate of drydown (the slope of the line from January to May of 1996, Fig 2b) was more intense than 1997, which led to a shallower dry season minimum water depth. On average, water depth in sawgrass was 12cm less than contiguous spikerush due to peat deposition beneath sawgrass.

Vegetation cover, shoot density, and periphyton cover varied throughout the study but, unlike temperature and water depth, seasonal patterns were not evident (Figure 3). Vegetation

cover was high in all samples, but in July and December 1997 spikerush vegetation cover declined below 50% (Figure 3a). Shoot density increased from 100 to 200 shoots m^{-2} with a seasonal decline in the summer of 1997 (Figure 3b). Although it appeared that spikerush abundance was declining in our study sites, December 1997 spikerush density was 200 shoots m^{-2} , similar to peak densities in March 1997. Finally, periphyton cover was higher in spikerush in all samples (50 to 80%) than sawgrass (< 25%).

Life history

We collected 57 form I male *P. fallax* (~ 3% of the population) ranging in size from 14.7 to 31.0 mm CL and 27 *P. fallax* ovigerous females (~1.5%) ranging from 14.9 to 26.4 mm CL. Smaller crayfish (5-10 mm CL) were under-estimated by throw trap samples while larger crayfish (16-25 mm CL) were well represented (Figure 4)

The normal curves which approximated size at maturity of *P. fallax* F1 males and ovigerous females were similar, although males were slightly larger than females (Figure 5). Average size at maturity was 21.1 mm CL for males and 18.8 mm for females. The normal distributions used to calculate the number of mature males and females were $N(21.1, 14.4)$ and $N(18.1, 3.3)$, respectively, where $N(x, s^2)$ is a normal distribution with mean x and sampling variance s^2 .

The number of mature females was estimated similarly by both the MSAM and probability methods (Figure 6; pairwise t-test of log transformed adult female counts, $t = -0.704$, 5 df, $p = 0.513$). However, number of mature males was significantly underestimated by MSAM (Figure 6; pairwise t-test of log transformed adult male counts, $t = 3.37$, 5 d.f., $p = 0.021$).

Adult females were more prevalent in collections than adult males during the two year sampling (Figure 7). Non-ovigerous females were the largest component of the adult population although form II males and ovigerous females were seasonally dominant. Form I males were present in all collections, although they were more prevalent in November of both years (Figure

7). Ovigerous females were collected during all sampling events except July of 1996 and 1997 (Figure 7).

Females were found with both eggs and newly hatched young (Figure 8). Average egg fecundity was 41 eggs ranging from 6 to 130. The female with 6 eggs was not used in the regression between eggs and CL, as she had most probably lost a portion of her initial clutch. Egg number increased significantly with CL ($F_{1,14} = 11.6$, $p = 0.004$, $n = 16$, Figure 6). Average fecundity of instars was 29 ranging from 17 to 36 (Figure 8). Instar number also increased with size although the relationship was not significant ($F_{1,6} = 6.11$, $p = 0.056$, $n = 8$).

Ovigerous females were collected in March and late fall samples indicating that *P. fallax* breeding occurs asynchronously through the fall and spring. Additionally, juveniles greater than 5 mm CL were collected in all samples suggesting that breeding was occurring continuously. Still, trends in juvenile abundance indicate two cohorts are produced per year (Figure 8); one in spring and one in the fall. Peaks in juvenile abundance are evident and can be traced visually through maturity, particularly from July 1996 to March 1997 (Figure 9). From these cohorts, it appears that *P. fallax* matures in approximately a year and probably lives to two years. The spring 1996 cohort identified in March and July 1996 reached an average size larger than 20 mm CL in March 1997 and expired by December 1997 (Figure 9).

Habitat use

Crayfish biomass varied between habitats throughout the study (Figure 10). In 1996 average biomass was 0.34 and 0.35 g m⁻² in spikerush and sawgrass, respectively and in 1997, 0.52 and 0.9 g m⁻², respectively. The simultaneous change in biomass within each habitat (Figure 9, Table 1). suggests that crayfish shifted from sawgrass to spikerush between March and July 1996. In November 1996 through December 1997, biomass was consistently higher in sawgrass than spikerush and increased in both habitats during this period.

Densities of life history stages in spikerush and sawgrass were similar to fluctuations in biomass (Figure 11). Habitat use by RA and juveniles followed similar annual trends; in 1996 these two life history stages were found equally in sawgrass and spikerush but in 1997 were collected in higher densities in sawgrass (Table 2, Figure 11). RA increased due to higher ovigerous female density (from 0.12 to 0.23 m⁻²) and in F1 density (from 0.24 to 0.48 m⁻² in 1996 and 1997, respectively). Juvenile density also increased, from 1.83 m⁻² in 1996 to 3.91 m⁻² in 1997. In contrast, NRA density was similar in both years (1.62 m⁻² in 1996 and 1.59 m⁻² in 1997); NRA used spikerush preferentially in July 1996, yet used both vegetation types equally in all other months sampled (Figure 11, Table 2).

DISCUSSION

Our collections have shown that *P. fallax* conducts the full array of life history events in a flooded habitat. Copulation was observed in holding containers while animals were being measured, and it is likely that it occurs in the flooded marsh. Extrusion of eggs also occurs in the open marsh as females with eggs and young were collected from spikerush and sawgrass. While the construction of burrows was not addressed in this study, flooded peat soils become loosely aggregated into a flocculent boundary layer with little structure. Thus these two reproductive processes would occur either under the cover of macrophytes or in the loosely defined substrate. Copulation and oviposition, the aspects of life history most associated with burrows in subtropical procambarids, appear to occur in the habitats studied.

Reproduction occurred prior to November and after March both years. Although extrusion, hatching, and liberation of instars to juveniles occurred throughout this period, there appeared to be two pulses in juvenile abundance per reproductive season (Figure 8). Hobbs (Hobbs, 1942) similarly collected ovigerous *P. fallax* from flooded substrates in every month but

July with seasonal ovigery peaking in the fall and spring. Prolonged reproductive seasons with asynchronous breeding may be a function of habitat and environmental cues. For example, *P. clarkii*, a species known to burrow during the reproductive season, has adopted an almost fully lentic lifestyle in the littoral zone of Lake Naivasha, Kenya (Oluoch 1990). Crayfish may also possess certain hard wired responses to reproductive cues that occur more often in flooded subtropical environments. For example, photoperiod and temperature have been found to significantly influence seasonality of egg production (Huner and Lindqvist, 1991). In constant temperature and prolonged daylight treatments, which would be typical of a subtropical location, ovarian maturation continually recycled providing the opportunity for unabbreviated egg production (Stephens 1952; Huner and Lindqvist 1991). While the mechanism responsible for the prolonged breeding season of *P. fallax* is unknown, the presence of juveniles in the population throughout our collections indicates that breeding is stimulated for the majority of the year.

Length frequency histograms indicate that two cohorts are produced per year (Figure 9). These cohorts were followed through the duration of our study and provided rough estimates of time to MSAM (mean size at maturity) and lifespan. Crayfish born in the spring reached approximately 10 mm CL by July of the same year and 20mm CL by the following March. Crayfish born in the fall reached ~12mm CL by March of the following year and 20mm CL by the late fall of the same year. *Procambarus fallax* lives to approximately 2 years although a few members of the population may live to three. Temperature in the winter is somewhat cooler than the spring (Figure 2a), thus those individuals hatched in the spring will endure a higher temperature than their fall counterparts. Although the effects of temperature on growth of *P. fallax* has not been studied, temperature has been found to effect growth in procambarids (Penn, 1943, Caine, 1978, Taylor, 1990) For example, *P. spiculfer* in Georgia grew the fastest in the spring with subsequent reduction in growth during the summer (Taylor, 1990). Further, Caine (1978) indicated that the summer months of subtropical laltitudes, in which water temperatures are greater than 35°C, may limit growth in procambarid populations. The temperature in Shark

Slough averaged 25 °C in the spring and fall peaking above 35°C in the summer (Fig 1a).

Provided *P. fallax* responds similarly to temperature, patterns in cohorts may be a function of growth during optimal temperature regimes in the spring and fall as well as timing of ovigery.

The majority of *P. fallax* matured in a year, although some animals kept in laboratory aquaria reached sexual maturity within 6 months (Hendrix unpub. data). *Procambarus fallax* MSAM was smaller for females (18.1 mm CL) than males (21.1 mm CL). Mating typically employs the active manipulation of females by males during copulation (Mason, 1970, Ingle and Thomas, 1974); thus F1 males are larger than receptive females. The variance in size of F1 males (14.4) was also greater than ovigerous females (3.3). Because of this range of sizes in sexually mature males, MSAM underestimated the number of mature males in the population (Figure 6). In general MSAM will underestimate the number of mature animals when the size range of reproductively active animals is broad. When applying MSAM to determine the number of mature individuals in a population, one assumes that the number of mature animals smaller than MSAM is equal to the number of immature animals greater than MSAM. In those months where MSAM underestimated the most number of mature males (March and July, 1996 and July 1997) cohort peaks were near 20mm CL (Figure 9), and this assumption was violated. Still, MSAM provides a useful comparison between species, and the MSAM of *P. fallax* is small compared to congeners. For example, *P. hayi* (Payne, 1972), *P. acutus acutus* (Huner, 1975), *P. clarkii* (Huner and Romaine, 1978), females begin to mature at 24 mm CL, 25 mm CL, 25mm CL, respectively. Not surprisingly, egg production per female in *P. fallax* is well below the average for the species listed above, as the quantity of eggs produced per female is a function of body size (Corey, 1991). However, *P. fallax* may produce more than one brood per reproductive season. Females held in captivity over several months had multiple broods, although the second was much reduced in egg number (Hendrix, unpublished data).

Habitat use

Both habitat types were used preferentially depending upon the year. In the summer of 1996 density in spikerush was higher than sawgrass in all life history stages (Figure 11, Table 2). While an entire host of possibilities exist to explain the observed alteration in distribution, water depth and temperature provide the most plausible, given the life history traits of *P. fallax*. In additional habitats within Shark Slough and Big Cypress National Preserve, *P. fallax* was unrestricted in spatial extent provided the locations were flooded for at least 11 months (Hendrix and Loftus, in press).

Between March and July 1996, average water depth reached the season low (Figure 2a). As water depth decreased, the habitat became more susceptible to fluctuations in temperature. Thus, water temperature fluctuated through a greater daily range concurrent with water loss (Figure 2a). Further, because temperature probes were located in spikerush habitat, which is approximately 12 cm deeper than sawgrass, crayfish in sawgrass most likely experienced fluctuations more severe than those in spikerush. *P. fallax* collected in additional areas of the Everglades watershed were found in seasonally flooded as well as permanently flooded throw trap samples during peak high water (November 1996), however dry season (March 1997) throw trap and burrow collections revealed *P. fallax* in flooded locations only (unpublished data). While the local response of *P. fallax* to ebbing water levels has not been studied, indirect evidence suggests that this species remains in flooded microhabitats when faced with dry downs.

In 1997 all life history stages except NRA were found in higher densities in sawgrass than spikerush. Reproduction occurred in sawgrass in 1997 as both form 1, ovigerous females, and juveniles were collected from sawgrass in significantly higher densities than spikerush (Figure 11, Table 2). However, NRA used both habitats in almost equal numbers throughout 1997 indicating that a similar risk of mortality was being experienced in both habitats. This phenomenon is most likely due to reaching a size at which predation risk was reduced. Still, RA were found in higher densities in sawgrass through this period suggesting that more complex

habitat was useful to reproduction. As a consequence, juvenile density in both habitats increased significantly through 1997 (Figure 11, Table 2) perhaps due to reduced risk of predation in sawgrass.

Predatory fishes structure the distribution of crayfish in stream communities (Stein and Magnuson, 1976). Recently molted individuals, juveniles, form I males, and ovigerous females were preferentially consumed in that order on a uniform substrate, however, given substrate preference, predation rates dropped for the same life-history stages in their preferred substrate (Stein, 1977). Further, habitat complexity has been shown to shape crayfish distributions in lake, stream, and wetland habitats (Stein, 1977, Rabeni, 1985, Garvey et al., 1994, Jordan et al., 1996b). The properties of sawgrass which make it a difficult habitat for crayfish predators include the stoutness of the culms and height of canopy which, in comparison to spikerush, may offer more restricted access to the habitat. Estimates of shoot density and vegetation cover indicates that sawgrass habitat was, on the average, more dense than spikerush (Figure 3). Additionally, sawgrass stands were found in shallower water than associated spikerush (Figure 2a). The predatory fishes most likely to consume *P. fallax* are largemouth bass (*Micropterus salmoides*), warmouth (*Lepomis gulosus*), and yellow bullhead catfish (*Ictalurus natalis*) and are typically not encountered in sawgrass (Loftus pers. comm). Additionally, wading birds prefer to fish in eleocharis marshes as opposed to sawgrass (Gunderson and Loftus, 1993, Hoffman et al., 1994) perhaps due to the prolonged hydrology and reduced physical barriers.

Wading bird foraging on crayfish

White ibis (*Eudocimus albus*), a known crayfish predator, is dependent upon hydrology for nesting success (Frederick and Callopy, 1989). As tactile foragers of marine and freshwater crustaceans, white ibis consume crayfish to feed developing nestlings (Kushlan and Kushlan, 1975, Kushlan, 1979, Frederick and Callopy, 1989, Frederick and Spaulding, 1994). Years in which bolus (regurgitant produced by the adults to feed nestlings) contained crayfish were

successful, whereas years in which crayfish and fish were absent, failed (Frederick and Callopy, 1989). Associated with the composition of food was a decrease in foraging flight distance indicating that crayfish were available locally. Nesting initiation and success has also been correlated with the severity of the dry down in spring; quick dry downs typically accompany successful nesting attempts (Frederick and Callopy, 1989, Bancroft et al., 1994). Previous work relating ibis foraging to crayfish availability presupposed that crayfish were unavailable during dry downs because they burrowed. While, the life history of *P. alleni* follows this trend (Hobbs, 1942, Rhoades, 1970), *P. fallax* may concentrate into deeper microhabitats (Figure 11).

Timing of prey availability is crucial to white ibis nesting success (Frederick and Callopy, 1989, Frederick and Spaulding, 1994). The availability of prey through the late dry season, when nestlings are still bound to their surroundings but in need of increasing caloric intake, is a crucial period for the parents. Thus, longer hydroperiod habitats that are available to foraging ibis will be lucrative at this stage of the breeding season (Ogden, 1994). Central Shark Slough, which is one of the longest hydroperiod locations in Everglades National Park, may serve this purpose. While little work has been devoted to determining overlapping foraging areas of white ibis and composition of crayfish species, it appears that a connection between ibis nesting success and importance of seasonal drydown may be linked through a hydroperiod dependent crayfish species. *Procambarus fallax* response to drydowns has not been studied, however it appears that their life history is characterized by elements that are not suited to a seasonal loss of water from the surface. As declining wading bird health is one of the prime motivations to restore Everglades wetlands, determining crayfish response to hydrology and their availability as prey to white ibis is paramount.

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Table 1. Repeated Measures Analysis of Variance (ANOVA) results for (a) biomass, (b) ovigerous females, (c) FI males, (d) non-reproductive adults (NRA), and (e) juveniles. All dependent variables were log (x + 1) transformed. Results are provided for the main effects of time (sampling month) and habitat (sawgrass and spikerush) and the interactive effect of time*habitat. p < 0.05 are in bold.

Biomass March and July 1996

Tests of Within-Subjects Effects

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
TIME	2.505E-02	1	2.505E-02	2.321	.178
TIME *	5.757E-02	1	5.757E-02	5.334	.060
HABITAT					
Error(TIME)	6.476E-02	6	1.079E-02		

Tests of Between-Subjects Effects

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
HABITAT	1.728E-02	1	1.728E-02	.668	.445
Error	.155	6	2.585E-02		

Biomass 1997

Tests of Within-Subjects Effects

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
TIME	.296	2	.148	12.763	.001
TIME *	4.585E-02	2	2.292E-02	1.978	.181
HABITAT					
Error(TIME)	.139	12	1.159E-02		

Tests of Between-Subjects Effects

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
HABITAT	.282	1	.282	11.454	.015
Error	.148	6	2.464E-02		

Table 2. Repeated Measures Analysis of Variance (ANOVA) results for (a), ovigerous females (b), FI males (c) non-reproductive adults (NRA), (d), juveniles. All dependent variables were log (x + 1) transformed. Results are provided for the main effects of time (sampling month) and habitat (sawgrass and spikerush) and the interactive effect of time*habitat. p < 0.05 are in bold.

a) Ovigerous females 1996

Tests of Within-Subjects Effects

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
TIME	2.190E-03	1	2.190E-03	.124	.737
TIME *	1.290E-02	1	1.290E-02	.731	.426
HABITAT					
Error(TIME)	.106	6	1.765E-02		

Tests of Between-Subjects Effects

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
HABITAT	3.252E-02	1	3.252E-02	1.058	.343
Error	.184	6	3.073E-02		

Ovigerous females 1997

Tests of Within-Subjects Effects

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
TIME	2.817E-04	1	2.817E-04	.027	.874
TIME *	2.029E-02	1	2.029E-02	1.977	.209
HABITAT					
Error(TIME)	6.159E-02	6	1.026E-02		

Tests of Between-Subjects Effects

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
HABITAT	.263	1	.263	40.864	.001
Error	3.867E-02	6	6.445E-03		

b) F1 male July and November 1996

Tests of Within-Subjects Effects

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
TIME	1.114E-03	1	1.114E-03	.107	.755
TIME *	8.515E-03	1	8.515E-03	.818	.401
HABITAT					
Error(TIME)	6.245E-02	6	1.041E-02		

Tests of Between-Subjects Effects

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
HABITAT	6.507E-04	1	6.507E-04	.041	.845
Error	9.415E-02	6	1.569E-02		

Form 1 males 1997

Tests of Within-Subjects Effects

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
TIME	.166	2	8.312E-02	2.824	.099
TIME *	3.630E-02	2	1.815E-02	.617	.556
HABITAT					
Error(TIME)	.353	12	2.943E-02		

Tests of Between-Subjects Effects

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
HABITAT	.349	1	.349	64.151	.000
Error	3.268E-02	6	5.447E-03		

c) NRA March and July 1996

Tests of Within-Subjects Effects

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
TIME	.189	1	.189	23.864	.008
TIME *	.858	1	.858	108.374	.000
HABITAT					
Error(TIME)	3.166E-02	4	7.916E-03		

Tests of Between-Subjects Effects

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
Intercept	3.937	1	3.937	43.360	.003
HABITAT	6.173E-02	1	6.173E-02	.680	.456
Error	.363	4	9.079E-02		

NRA 1997

Tests of Within-Subjects Effects

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
TIME	.506	2	.253	7.077	.009
TIME *	3.411E-03	2	1.706E-03	.048	.954
HABITAT					
Error(TIME)	.429	12	3.575E-02		

Tests of Between-Subjects Effects

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
HABITAT	.703	1	.703	14.632	.009
Error	.288	6	4.805E-02		

d) Juveniles March and July 1996

Tests of Within-Subjects Effects

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
TIME	1.211	1	1.211	1.480	.291
TIME *	5.434	1	5.434	6.640	.062
HABITAT					
Error(TIME)	3.274	4	.818		

Tests of Between-Subjects Effects

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
HABITAT	9.563	1	9.563	3.828	.122
Error	9.993	4	2.498		

Juveniles 1997

Tests of Within-Subjects Effects

Measure: MEASURE_1

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
TIME	3.761	2	1.880	36.068	.000
TIME *	.169	2	8.434E-02	1.618	.239
HABITAT					
Error(TIME)	.626	12	5.213E-02		

Tests of Between-Subjects Effects

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
HABITAT	1.472	1	1.472	17.113	.006
Error	.516	6	8.602E-02		

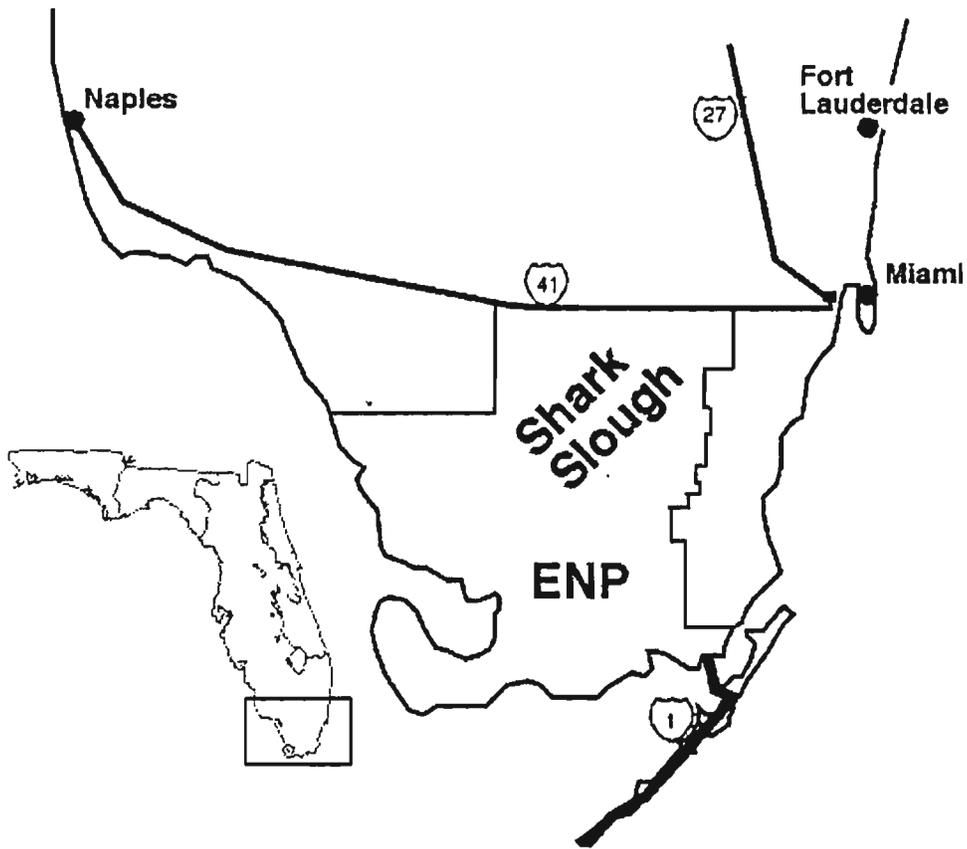


Figure 1. Crayfish were collected from Shark Slough in Everglades National Park (ENP) during 1996 and 1997.

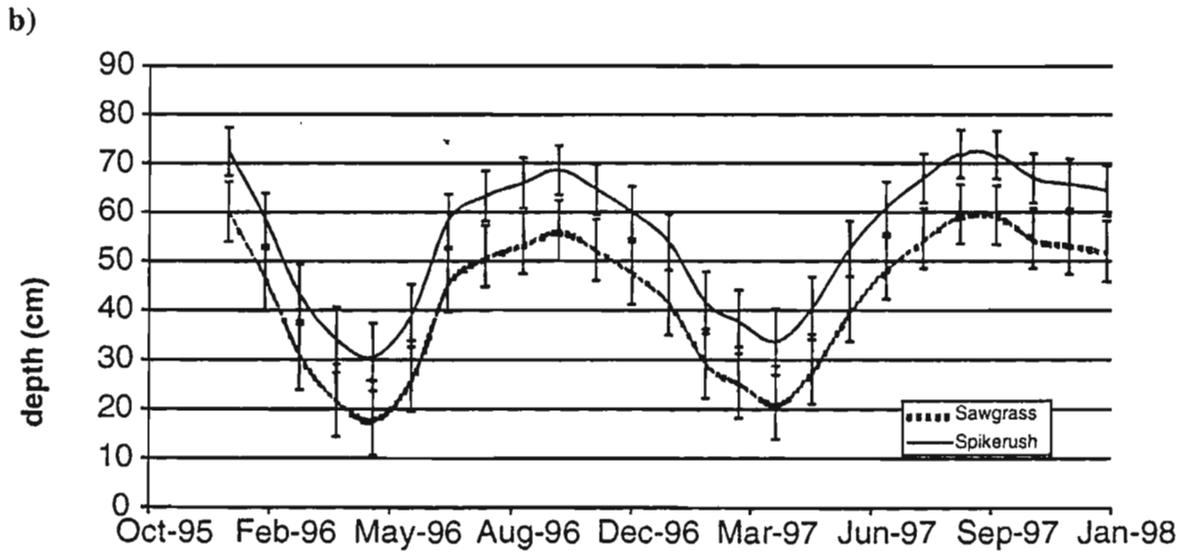
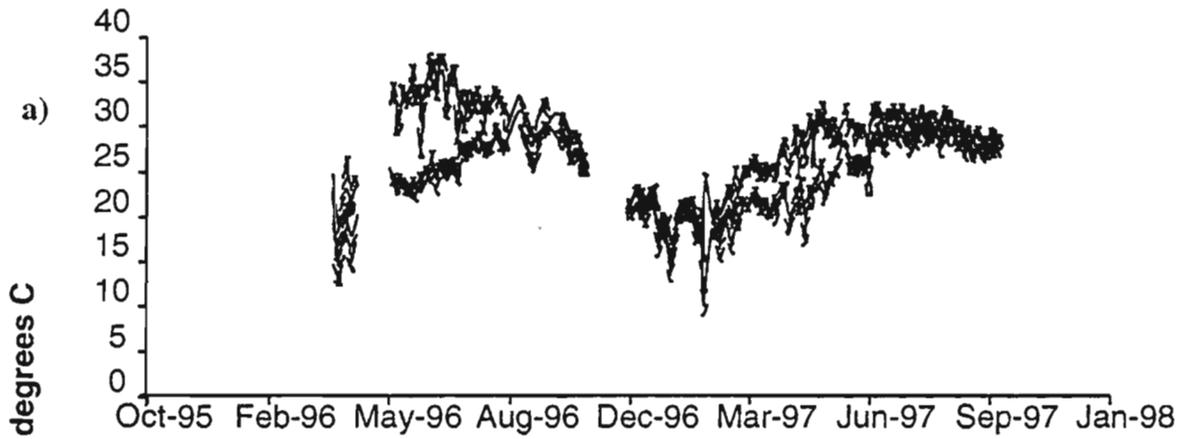


Figure 2. Temperature (a) and mean (± 1 SD) depth profiles (b) of central Shark Slough in 1996 and 1997. Daily minimum and maximum temperature are plotted in the top figure. The bottom figure plots the monthly average of depth in sawgrass and spikerush. Water depth in sawgrass averaged 12 cm less than depth in spikerush.

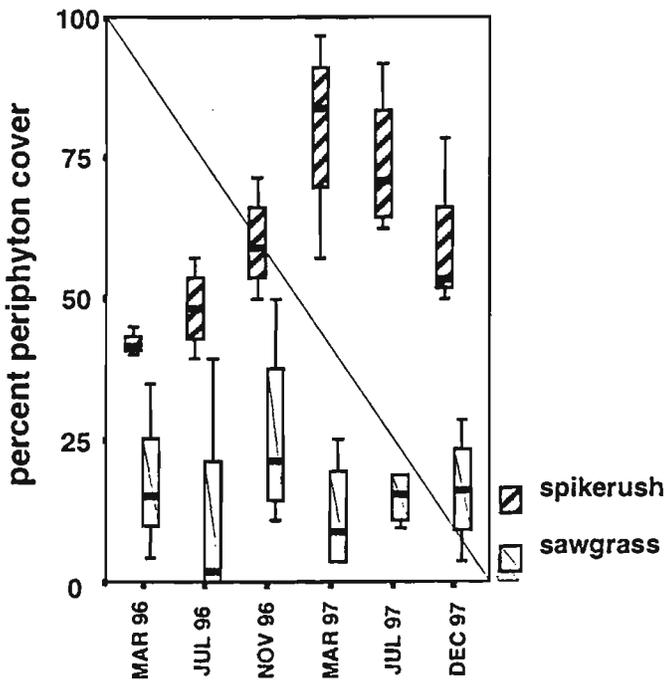
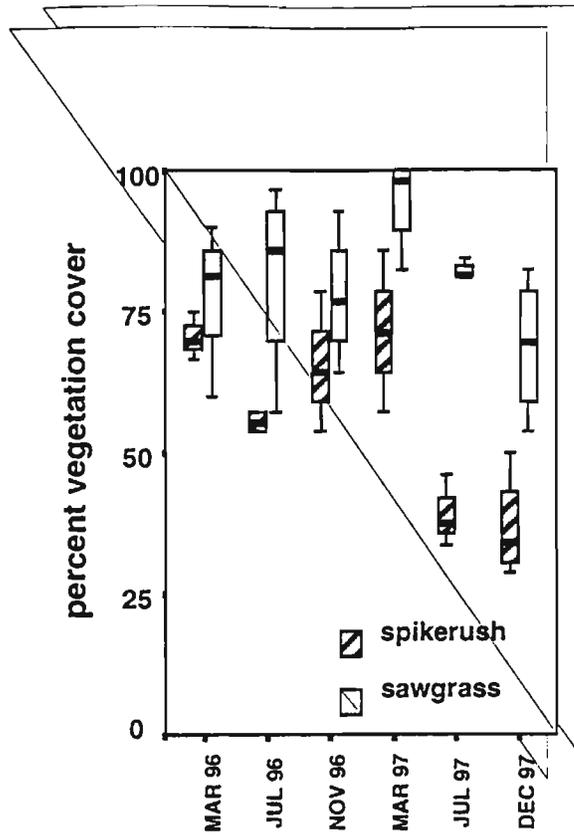
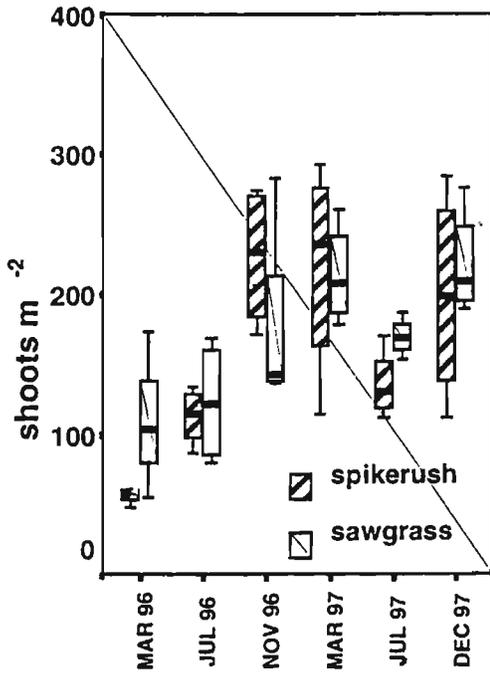


Figure 3. Shoot density (a) vegetation cover (b), and periphyton cover (c) in spikerush and sawgrass. Boxes indicate second and third quartiles with the median drawn across the box. Whiskers represent extreme values.

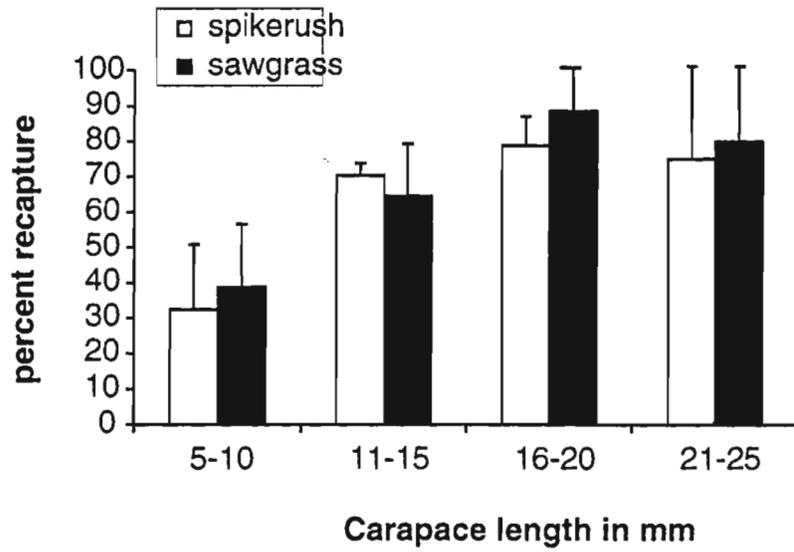


Figure 4. Percent *P. fallax* recaptured using throw traps in sawgrass and spikerush. Error bars represent one standard deviation.

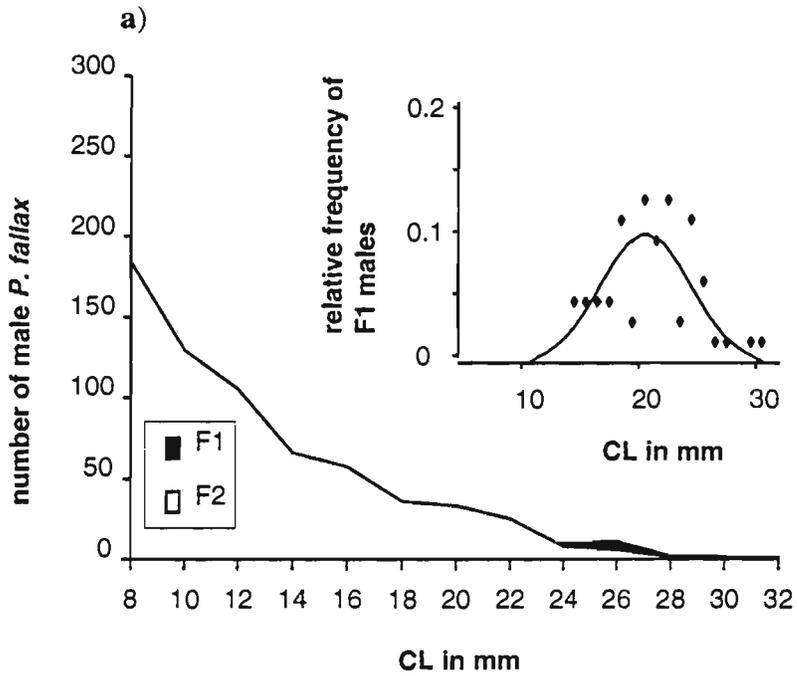
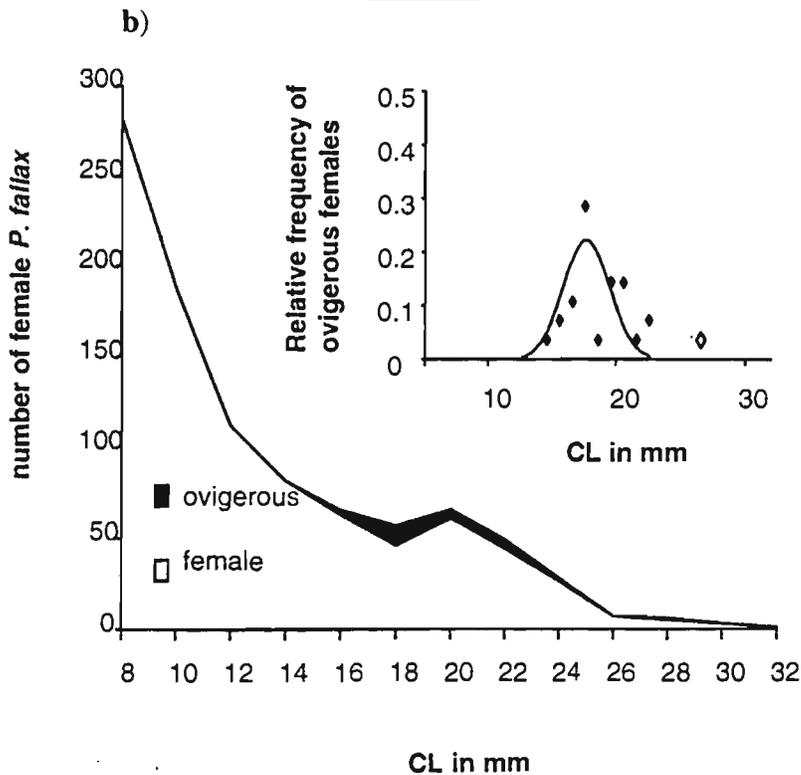


Figure 5. *P. fallax* male (a) and female (b) size distributions for 1996 and 1997 combined. Smaller Normal plots in upper right corners are the normal probability curves fit to the frequency of reproductive individuals (F1 and ovigerous females). The cumulative normal curve, indicated as $N(\mu, \sigma^2)$, was $N(21.1, 14.4)$ for males and $N(18.1, 3.3)$ for females. The open symbol in the bottom figure is an exceptionally large ovigerous female that was not included in the calculation of the female normal distribution.



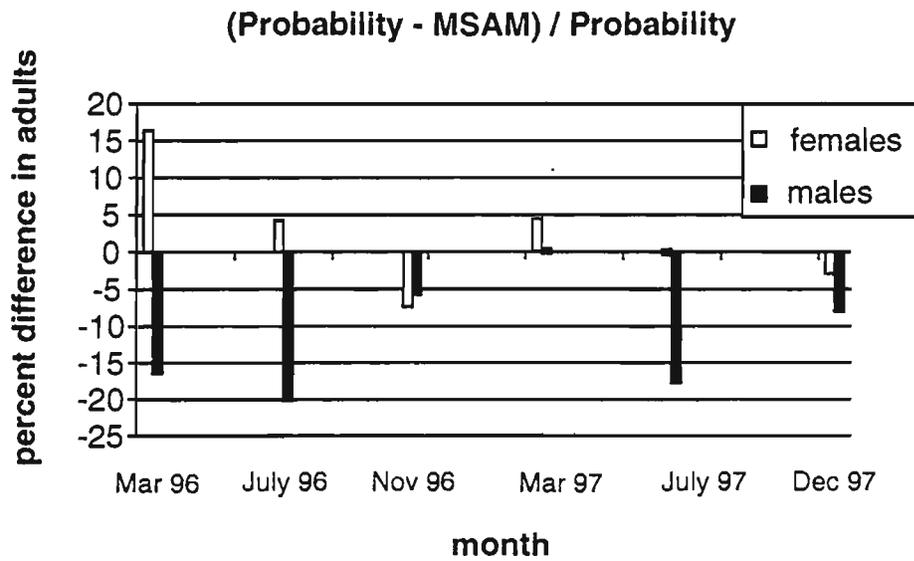


Figure 6. The difference between probability and Mean Size at Maturity (MSAM) methods for determining the number of mature adults. Negative values indicate that MSAM underestimated the number of mature individuals while positive values indicate overestimation.

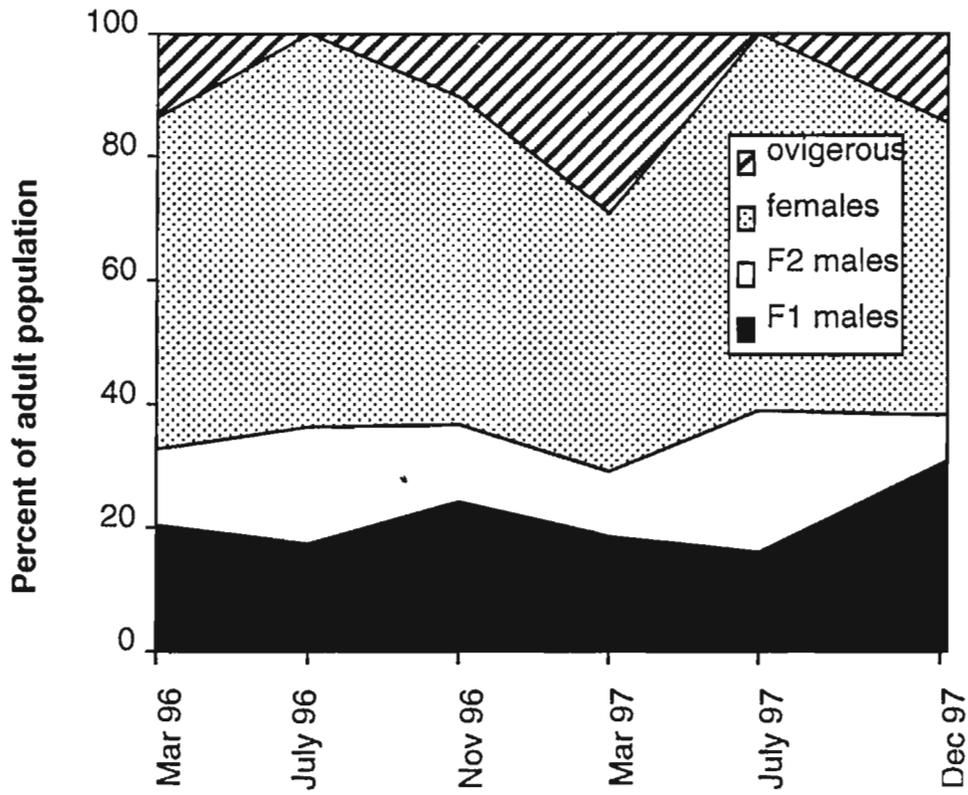


Figure 7. Adult composition by reproductive stage.

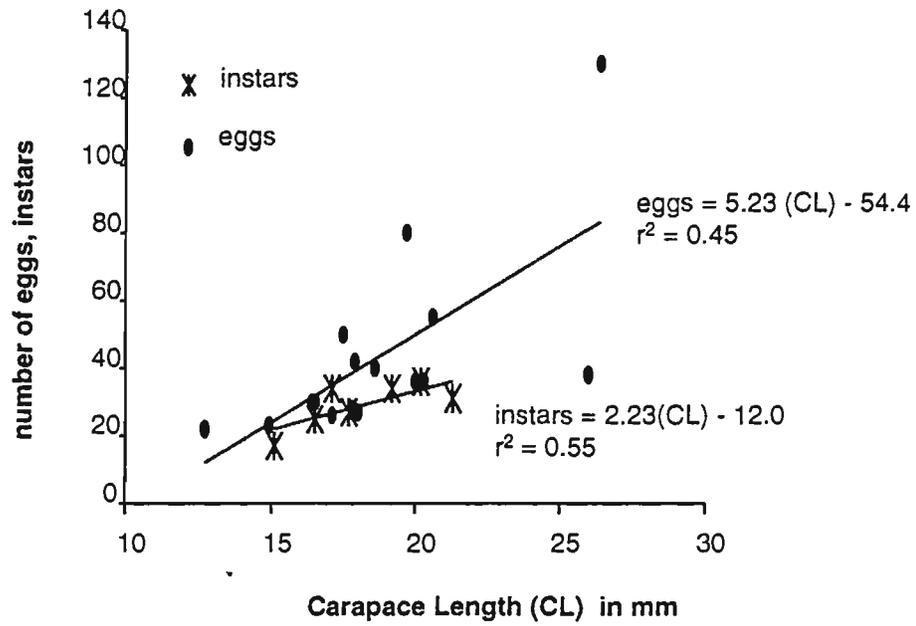


Figure 8. *Procambarus fallax* length-fecundity.

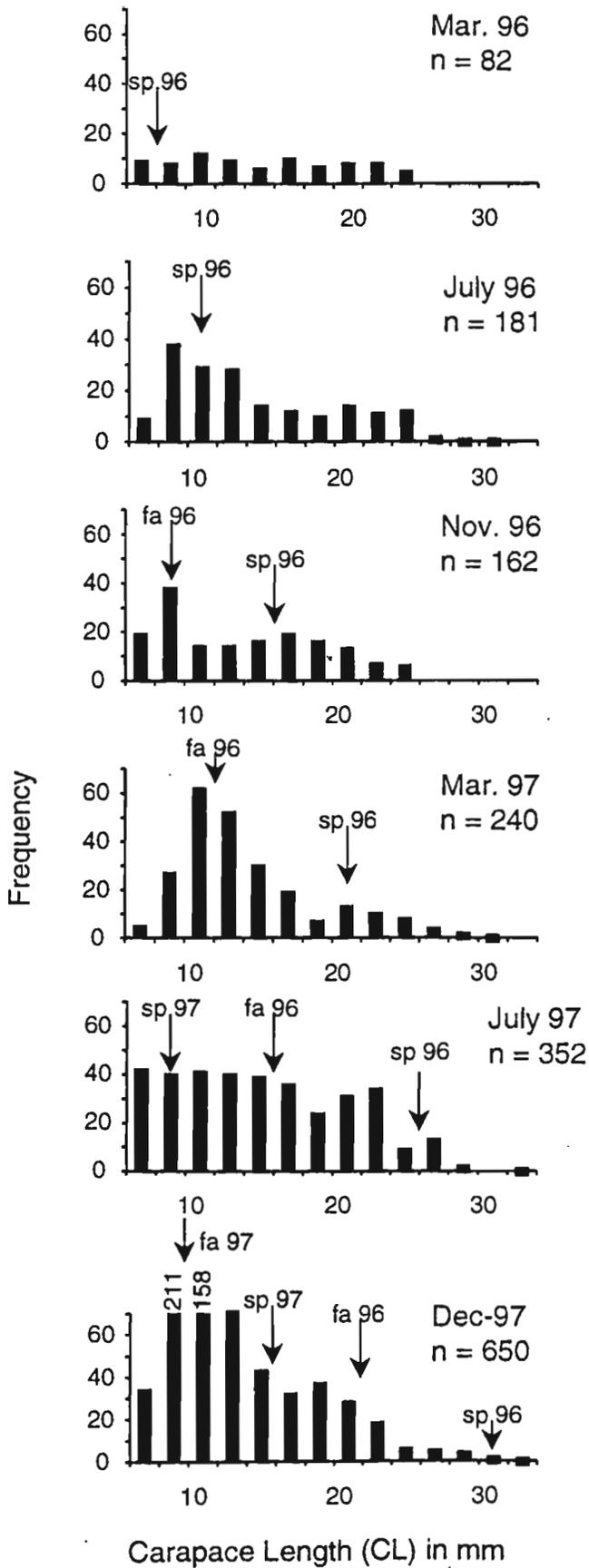


Figure 9. Size frequency distributions for each sampling period. Spring (sp) and fall (fa) cohorts were identified each year. Arrows represent the mean cohort size during sampling events in 1996 and 1997.

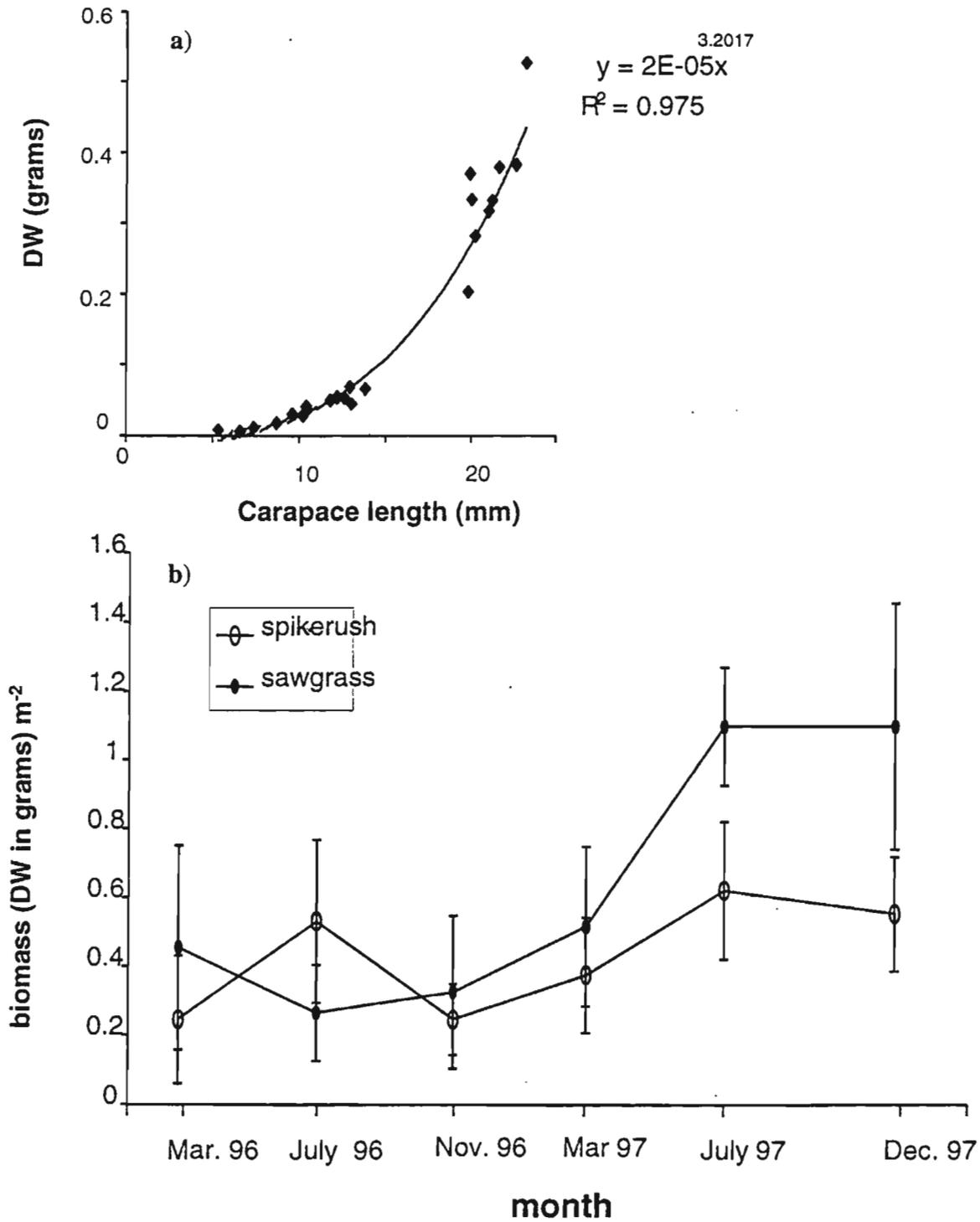


Figure 10. Carapace Length to dry weight (DW) regression (a) and seasonal variation in biomass of crayfish from sawgrass and spikerush habitats (b). Bars in (b) are +/- 1 SD.

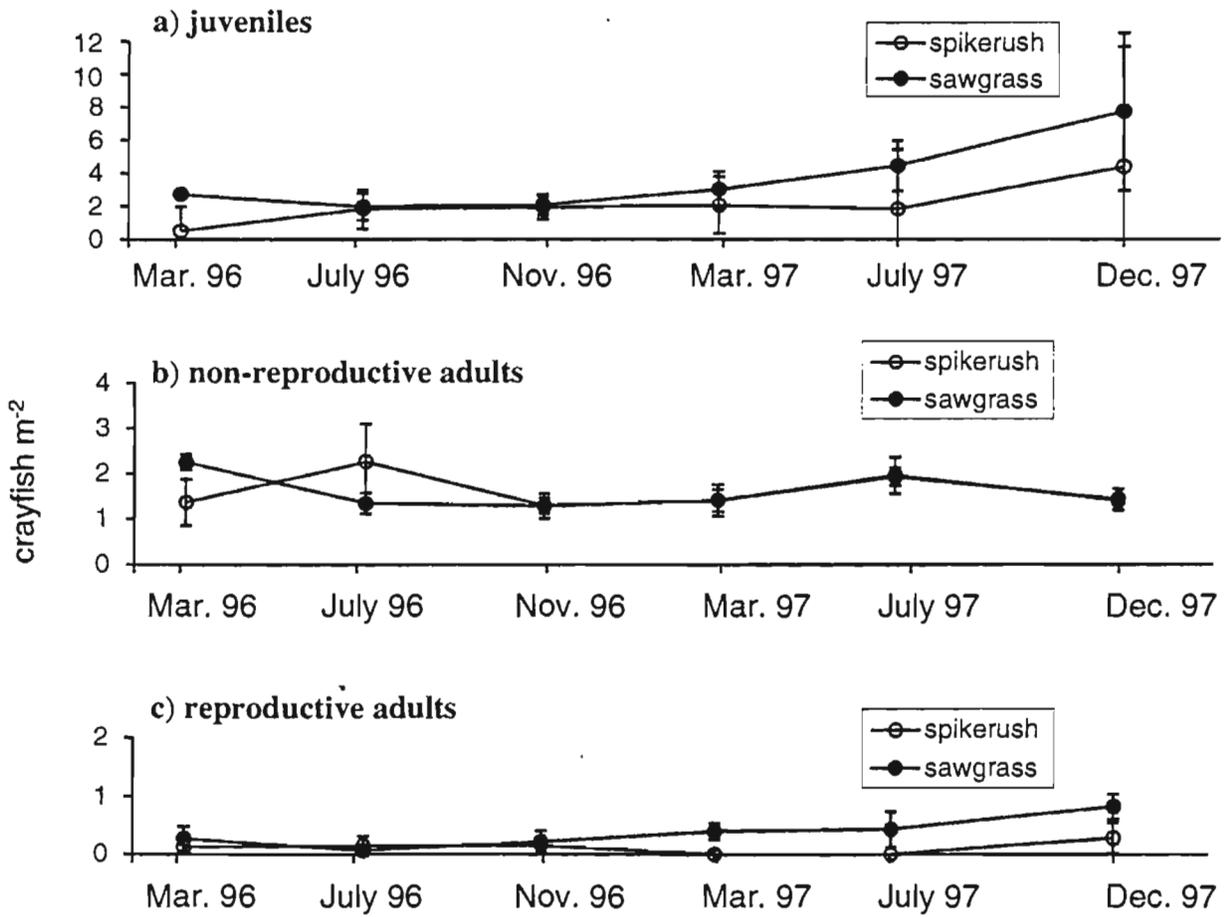


Figure 11. Density (± 1 s.d.) of *P. fallax* life history stages a) juveniles, b) non-reproductively active adults (NRA), and reproductively active adults (RA) in sawgrass and spikerush. Note difference in scale of the y axis.

Section 3 - TITLE?

Relevance of research

Objectives and Scope

The impacts of altered hydrology in Everglades National Park ENP and Big Cypress National Preserve (BICY) are widespread. An extensive canal structure, which attempts to drain agricultural land and provide substantial water for ENP, has created a patchwork of conflicting user groups bound by threads of carved limestone. Several species have been unable to utilize the resculpted landscape (such as the Cape Sable Sparrow, *Ammospiza maritima mirabilis*, Everglades snail kite, *Rostrhamus sociabilis plumbeus*, Wood stork, *Myceria americana*, and Florida panther, *Felis concolor coryi*) while others have had limited success in relation to historical presence (such as Glossy ibis, *Plegadis falcinellus*, and White Ibis, *Eudocimus albus*). Because the interactions of hydrology, forage species, and conspicuous predators are complex, and the forces affecting these relationships occur over varying spatial and temporal scales (DeAngelis, 1994), a holistic framework was developed from which to address these topics. The following investigation of the crayfish fauna of Everglades National Park and Big Cypress National Preserve represent an empirical contribution to ATLSS (Across Trophic Level System Simulation) which attempts to incorporate the complexity of the Everglades system into a modeling structure.

P. alleni and *P. fallax* research to date

The Everglades crayfish (*Procambarus alleni*) has been the topic of several investigations since it was described by Faxon (Faxon, 1884). Hobbs (Hobbs, 1942) collected *P. alleni* in lakes, marshes, drainage canals, and cypress stands. Several additional unpublished reports and published investigations which provided further insight into the life history of *P. alleni* are briefly summarized here. Rhoads (1970) described basic life history, reproductive

seasonality, and fecundity in crayfish from the southeastern area of the Everglades. Crayfish were excavated from burrows to obtain data on sex ratio, size-related fecundity, male morphology, and length-weight relationships. In an unpublished pilot study, Conover (1972), sampled *P. alleni* from several habitat types during January 1972. *P. alleni* was found in permanent ponds, temporary ponds, and prairie habitat that spanned salinities from 3.0 to 18 ppt. Kushlan and Kushlan (1979) reported on *P. alleni* sampled in Everglades National Park using mesh-and-frame pull traps from 1966 to 1972. The researchers concluded that water-level fluctuation led to increased crayfish biomass and density, presumably via decreased predation upon *P. alleni*. However, Loftus and Eklund (1994) found that pull traps bias collection data due to the unnatural conditions they provide (by forming water collecting depressions in an elevation sensitive substrate). Thus, conclusions made by Kushlan and Kushlan (1979) were erroneous. Evidence that *P. alleni* prefers highly vegetated habitats was provided by Jordan in both field (Jordan et al., 1996a) and laboratory (Jordan et al., 1996b) environments.

In the Rocky Glades region of Everglades National Park, *P. alleni* may provide the greatest biomass of any aquatic fauna as they have been collected in aggregations up to 100 crayfish per m² (Loftus, personal communication, Everglades National Park, Florida)! While this density was observed during an early summer recruitment event and may represent a short peak in abundance, Jordan (Jordan et al., 1996a) recorded a peak density of 27 g per m² (28 per m²) in the northern sloughs of the Everglades watershed and Taborsky (Taborsky, 1982) found *P. alleni* in culture ponds at densities up to 150 g wet weight per m².

Because crayfish can assimilate detritus into protein in one trophic step (Momot, 1984), they are efficient energy links to higher trophic levels (Lorman and Magnuson, 1978). In Everglades National Park (ENP), many predators have been shown to ingest *P. alleni*, including occasional consumers such as the snook (*Centropomis undecimalis*), American egret (*Casmerodius alba*), raccoon (*Procyon lotor*), opossum (*Didelphis virginiana*), otter (*Lutra canadensis*) (Rhoads, 1970), snail kite (*Rostrhamus sociabilis*) (Bennets et al, 1994), and

consumers dependent on *P. alleni* for a substantial portion of their diet including largemouth bass (*Micropterus salmoides*), warmouth (*Lepomis gulosus*), eastern glossy ibis (*Plegadis flacinellus*), American bittern (*Botaurus lentiginosus*), white ibis (*Eudocimus alba*), pied billed grebe (*Podilymbus podiceps*) and little blue heron (*Egretta caerulea*) (Rhoads, 1970; Gunderson and Loftus 1993). While *P. alleni* is consumed almost exclusively by several species of wading birds, little is known about the biology and ecology of this species. Robertson and Frederick (1994) stated that "As a dramatic example [of the poor understanding of the ecology of aquatic prey animals], next to nothing is known about the only species of crayfish (*P. alleni*) in the Everglades, which is a central food item for most wading birds and many fishes, anurans and reptiles."

Hobbs (1942) provides the first and only characterization of *P. fallax* since its initial description (Hagen, 1870). *P. fallax* has been collected throughout most of the Florida panhandle, bordered on the north by Georgia and on the south by canal structures leading from Tampa Bay to Lake Okeechobee. Prior to this study, Palm Beach County formed the southern extent of its range. The species is typically found in heavily vegetated habitats which provide water for most of the year. *P. fallax* was collected in Flagler, Citrus, Hillsborough, Sumter and Seminole counties in the company of *P. alleni* in flooded ditches. However, during the dry season, when *P. alleni* was collected from burrows in the dry ditch, *P. fallax* was captured in contiguous streams (Hobbs, 1942).

Methods

Study Locations:

Shark Slough, ENP

Shark Slough is the largest slough contained in Everglades National Park. Water levels vary throughout the slough with the central portion maintaining water for the longest duration and the lateral areas, nameley the northeast, drying seasonally. The hydroperiod (duration of inundation) of Shark Slough is caused by a combination of, topography, recent hydrologic history, local rain events, and water management. In particular water management is significant to the northwestern section as Shark Slough receives the majority of hydrologic input into ENP through gated structures in this area (Light and Dineen, 1994). In response to hydrology, the central section of the slough is comprised of dense, monotypic stands of sawgrass (*Cladium jamaicense*) and wet prairie composed primarily of spikerush (*Eleocharis* spp.). Fire may be a significant determinant of the vegetation patterns as sawgrass is fire tolerant in the absence of flooding (Herndon et al., 1991, Busch et al., 1998). Periphyton may be a common element of the spikerush dominated wet prairies as bladderwort (*Utricularia* spp.) is often subsumed into a thick matt incorporating many forms of algae. Periphyton is absent in most of the dense sawgrass stands as light is limited due to overshadowing. The substrate of Shark Slough is underlain by a layer of calcium carbonate rock. The subsurface limestone is covered with organic peat soils in central Shark Slough and marl in the peripheral, shorter hydroperiod ones (Busch et al., 1998).

Raccoon Point, BICY

Raccoon Point, BICY is composed of a matrix of cypress (*Taxodium* spp.) domes, contiguous cypress prairies, and Florida slash pine (*Pinus eliotti* var. *densa*) stands. The change of topographic relief within this region causes diverse vegetation to be located on a gradient from flooded pools with hydroperiods of 300 days to pine stands with hydroperiods of 50 days (Deuver et al., 1986). The morphology of a cypress dome is similar to a pond in that the sides slope gently to a central pool. However, viewed from the outside, with little knowledge of a cypress dome, one would not guess that the largest and oldest cypress trees were associated with lower elevation areas surrounding a sparsely or unvegetated pool. Many species of understory emergent and submerged aquatic vegetation inhabit the dome. The deposition of peat, unsurprisingly, follows the contours of the dome such that the central pools may contain as much as 2 m. The outlying prairie is often covered with marl or sand over a protruding limestone base.

East Slough, ENP

East Slough is composed of open expanses of wet prairie which may remain flooded for up to 8 months a year. The region is interspersed with marshes and small cypress forests which may remain flooded for longer period of time depending upon elevation. We sampled open prairie was composed mostly of drought tolerant species. The substrate was typically areas of exposed limestone within a matrix of a thin marl and shallow peat depositions.

Table M-1. Sample locations with associated hydroperiod and substrate.

Site	Hydroperiod (Length of inundation)	Substrate
Rocky Glades	< 9 mo.	marl, limestone
Shark Slough	10-12 mo.	organic peat
East Slough	6-8 mo.	sandy marl
BCNP cypress stands	6-8 mo.	organic/ sandy marl with cypress knobs

Sampling design:

Four locations were chosen to study the distributions in ENP and BICY. The first location, Rocky Glades, was determined to be too heterogenous to the other three to provide comparison through throw trapping. Thus, it was dropped from the sampling design. The other three locations, Raccoon Point, Shark Slough and East Slough were sampled by throw traps. In two locations, Shark Slough and Raccoon Point, we sampled two habitat types within one location. In Shark Slough we sampled spikerush (*Eleocharis* spp.) and sawgrass (*Cladium jamaicense*) dominated habitats, in Raccoon Point we sampled cypress domes and contiguous cypress prairies, and in East Slough we sampled a single habitat type, wet prairie (Table M-1). In March 1996 we initiated the sampling regime by collecting five throw trap samples at three plots of five habitat types in the three locations which equaled 75 throw traps per sampling event (Table M-2). After one field season, we decided to increase the sampling effort to seven throw trap samples, in four plots, of five habitat types, in three locations which equaled 140 throw trap samples per sampling event. We maintained the latter effort throughout the remainder of the study except in those times and locations that did not permit it.

The March 1997 sampling event was reduced in effort in Raccoon Point and East Slough. Because the plots in the Raccoon Point prairie/dome complexes were dry, we could not sample crayfish within them. Still, we sampled outside of the marked plots in the flooded sections of the domes.

During the same period, samples in East Slough were abbreviated to four throw traps per plot due to dry conditions reducing access to the study plots. Because the cost incurred by helicopter rental reduced field time, the four throw traps were coupled with a burrow survey of the plot to determine burrow density.

Table M-2. Sampling schedule in 1996 and 1997.

Site	Date	lots	P	Throw traps/ plot
Shark Slough Spikerush Sawgrass	3/96		3	7
East Slough	3/96		3	7
Raccoon Point Cypress domes Cypress prairie	3/96		3	7
Shark Slough Spikerush Sawgrass	7/96, 11/96, 3/97, 7/97, 12/97		4	7
East Slough	7/96, 11/96		4	7
Raccoon Point Cypress domes Cypress prairie	7/96, 11/96, 7/97, 11/97		4	7
East Slough	3/97		4	4
Raccoon Point Cypress domes Cypress prairie	3/97		3 0	7 0

Throw trap methods

Throw trapping was used to entrap a section of substrate by a frame and mesh device covering approximately 1m². The device was constructed of a cube of copper tubing around which was stretched a mesh exterior. The top and bottom sections of the cube remained open with the bottom resting on the substrate and the top providing an aperture to remove the entrapped animals with seines and dip nets. The swamp substrate was sampled by 'throwing' (which may be more correctly described as 'placing' depending upon the surrounding flora) the trap upon the area to be sampled and quickly pressing the bottom into the sediment. Once the randomly determined sample location was entrapped, we measured water depth, water temperature, vegetation species composition, shoot density, and estimated areal coverage of vegetation and periphyton (a floating complex of algae and plant material). The vegetation and periphyton coverage were classified in 25% intervals before clearing the trap of periphyton.

Sex, carapace length, and in the case of ovigerous females, fecundity was measured in the field; further, an assessment was made on the reproductive stage of the individual in hand. Due to the fact that male procambarids display secondary sexual characteristics including enlarged chelae and ischial hooks when in a reproductively active state ([Hobbs, 1991 #11], we were able to characterize males as form I (reproductively active) or form II (inactive). Although females typically do not display similar secondary sexual characteristics, we attempted to label females as mature or immature based on the shape of their annulus ventralis (seminal receptacle) and the presence of glair gland activity (glair glands, which are located between the third and fourth pereopods in females produce a mutilaginous substance that attaches eggs to pleopods). However, female maturity was ultimately defined by the size of ovigerous females. After measurement, crayfish were returned to the same location from which they were sampled.

Because a second species of crayfish was identified in July 1996 [Hendrix, 1999 #268] crayfish were not identified to species until November 1996. Initial identifications were attempted in Everglades Park with the use of Hobbs (1942) key. In June of 1996 form I males were collected from Shark Slough and Raccoon Point and analyzed by Dr. Richard Franz of the Florida Museum of Natural History in Gainesville, FL. After identification was confirmed by Dr. Franz, animals were identified in the field by coloration.

Sampling burrows:

During March 1997, we sampled burrows in Raccoon Point and East Slough to determine the inhabitants of burrows that were prevalent in the study plots. Burrow density was estimated by a 50m linear transect with 25m in the dome and 25m in the prairie habitats. A single observer paced the transect and identified burrows. Concurrently, an associate placed flagging tape on the identified burrow, which was excavated after the transect had been completed. In March 1997 burrows in prairie/dome complexes a5, 11, and 16 were sampled in Raccoon Point as well as burrows in all four East Slough plots.

Population size structure

Because crayfish may inhabit different habitats due to age [Beingesser, 1985 #16], and reproductive state [Fast, 1973 #259; Stein, 1976 #219], we attempted to divide the population into juvenile and adult components based on size at maturity information. In particular, I wanted to determine if habitat was being used preferentially by a particular species or life history stage.

While cambarids are assumed to molt between form I to form II in an annual cycle (Hobbs, 1942, Payne and Price, 1983), there is some debate regarding the molt from form II to form I once sexual maturity has been attained (Payne, 1978, Taylor, 1985). Still, male form II procambarids were collected at sizes greater than the mean size of form I males. Thus, form II males may be either a juvenile male or a mature male, which is currently in a reproductively inactive form. Non-ovigerous females present a similar problem. Since we did not assess gonadal maturation, we attempted to determine male and female size at maturity by plots of cumulative length-frequency categories. The following methods were applied for form I males and ovigerous females of *P. fallax* and *P. alleni*: 1) all mature animals were classified in 1mm intervals from the minimum size at maturity to the maximum size collected, 2) the previously described distribution was assessed for normality using the Kolmogorov-Smirnov statistic and a Lilliefors significance tests of normality (SPSS, 1998), a cumulative Normal distribution was plotted and probabilities of maturity were assessed for each 1mm size increment. Thus, individuals below the minimum size at maturity (which was determined from field collections) for their given species and sex designation would be categorized as fully juvenile, while individuals within the size range of mature individuals would be assigned a probability of maturity. For example, a male collected at the mean size at maturity would be assigned a probability of maturity of 0.5, while a male larger than the mean size at maturity would be assigned a value greater than 0.5.

Habitat preference

We examined the spatial distribution of particular life history stages of the population as related to habitat type. For this analysis, we used data collected from cypress domes and prairie in Raccoon Point. To detect habitat use by life history stage in Raccoon Point, I used GLIM (Generalized Linear Models in a multifactorial design. Because crayfish density data appear similar to other benthic invertebrate count data (generally Poisson distributed, with clumped distributions and a preponderance of zeros in samples), we assumed a multiplicative effect of error terms (Elliot, 1977) GLIM offers an elegant method of using data distributed in such a fashion by offering a log link, which is roughly equivalent to a log transformation. Because GLIM uses maximum likelihood to obtain parameter estimates in the regression (as opposed to sums of squares` which assume normal error terms), the log link is more effective than transformation with data comprised of many zeros. GLIM produces an estimate of deviance that can be compared to a X^2 distribution. I assumed the data were Poisson distributed and specified a log link.

When we initially chose replicate plots, I selected those dome/prairie complexes which were easily approachable from a service road. Thus, the plot numbers, 3, 11, 16, and a5 were derived from the half-mile markers labelled closest to the complex. The first sampling season, March 1996, consisted of five throw trap samples collected at three plots, 3, 16, and a5. Subsequent sample collections were conducted on four plots as plot 16 was added in July 1996. While we attempted to choose complexes that were similar, a5 seemed dissimilar to the other plots. In particular, the dome was considerably larger than the other three domes and had a well developed, sparsely vegetated, inner pool. These characteristics indicate that this dome was roughly 20 to 30 years older than the smaller domes (rough calculations based on data provided in (Deuver et al., 1986).

Expecting that significant variation could exist in my replicate plots, I constructed an analysis of deviance (ANODEV) table for each sampling date. The ANODEV design consisted

of the independent variables: habitat (dome and prairie), size (adult and juvenile), species (*P. alleni* and *P. fallax*), and plot (plots 3, 11, 16, and a5). Crayfish density was the dependent variable. Variables which are significant descriptors of the variance in crayfish density caused a change in deviance and associated degrees of freedom which were distributed asymptotically as X^2 . The procedure to determine significance of a term is to fit a full model, remove each term (all interactions and main effects), denote the change in deviance and associated change in $n-1$ (n equal to the levels of the factor) degrees of freedom, compare this value to a X^2 table, and determine the significance. Each of the main effects of habitat, species, size, and plot as well as all two way interaction terms were included in the analysis. If differences in plots were observed (either by a significant main effect or significant interaction term), I used contrasts to determine which organization of plots accounted for the greatest change in deviance. This final step allowed me to best describe the differences between domes in the hopes of incorporating statistical complexities into a biological context.

Results and Discussion

Big Cypress Results

Raccoon Point prairie and dome physical parameters indicate that temperatures are similar in each habitat although water depth was always shallower in prairies than domes (Fig BICY-1). We captured 1310 crayfish of both *P. alleni* and *P. fallax* in throw traps over six sampling periods. Because we discovered *P. fallax* in samples during the end of the July 1996 sampling season, only samples collected in November 1996, March 1997, July 1997 and December 1997 were identified with respect to species. The mean density of both species combined is reported for March and July 1996, where the mean density of each species separately is presented for the remaining four sampling periods (Fig BICY-2). Throw traps captured

crayfish greater than 5 mm carapace length (CL) due to the size of the mesh employed in the seine and dip nets. *P. alleni* average density per sampling period ranged from 4.7 m⁻² in November 1996 and July 1997 to 2.6 m⁻² in March 1997 and December 1997. *P. fallax* were relatively constant at ca. 1.25 m⁻² over the four sampling periods in which a two species assemblage was distinguished.

P. alleni life history

P. alleni oviposition occurs in burrows, which we were unfortunately unable to sample. Still, (Rhoades, 1970), was successful in excavating burrows in a southern section of Everglades National Park (which will be referred to as C-111 due to the proximity of the site to a canal of the same name) that were capped with chimneys in shorter hydroperiod locations.

Due to the importance of these excavations, Rhoades (Rhoades, 1970) study will be briefly summarized here. Sex, reproductive state (Form I or II in the case of males and ovigerous or not in females), and size of inhabitants were determined from excavated burrows during the dry season in a short hydroperiod location. All crayfish were identified as *P. alleni*. Water depth was recorded in the adjacent canal throughout the burrowing season.

The fact that the reproductively active portion of the *P. alleni* population burrows during the dry season makes them unavailable to throw trapping. Samples collected during March 1997 were devoid of adults (Fig BICY-3). An increase in the presence of burrows in plots was noted in March 1997, concurrent with loss of water from the surface (Table BICY-1). Rhoades (Rhoades, 1970) collected crayfish in burrows from February through June with the greatest number of crayfish being collected just after water retreated from the surface. This phenomenon is most likely due to their presence in burrows as opposed to predation. If predation was a significant cause of adult loss during this period, we would expect a significant decrease in adult density when the landscape reflooded in July. We did, however, find comparable numbers of adults in the July 1997 as the November 1996 samples. *P. alleni* burrowing and subsequent

movement from domes to burrows occurs as a response to local hydrologic conditions (Table BICY-1); as the dry season progresses the number of burrows increased. The physical parameters that might determine burrowing seasonality are a combination of local rainfall, elevation, local topography, and preceding hydrologic conditions. While the appearance of burrows on the landscape was easily recognized, excavating the inhabitants was another matter entirely.

Results of burrow surveys and excavations revealed few crayfish. In Big Cypress, greater than 70 burrows ranging in external morphology from recently formed chimneys (evidenced by moist spherical pellets), rain altered caps, and open holes were attempted with little success. In total, we collected one female and two form 1 crayfish that were identified as *P. alleni*. The lack of success was due largely to the presence of an impenetrable limestone barrier, located just below the surface and above the termination of the burrow.

Table BICY-1. Burrow samples conducted in Raccoon Point and East Slough. Burrows were estimated by transect counts. Burrows $m^2 = (\text{burrow count}) / [(\text{transect length}) \times (\text{maximum distance from transect line at which a burrow was identified})]$.

Site	Date	Plot	Burrows m^{-2}
Raccoon Point	2/13/97	A5	0.12
Raccoon Point	2/13/97	11(dry dome)	0.54
Raccoon Point	3/13/97	16	0.766
Raccoon Point	3/13/97	A5	2.27
East Slough	3/3/97	2	0.12
East Slough	3/3/97	3	0.33
East Slough	3/3/97	4	0.22

Juvenile *P. alleni* were collected in domes during March 1997. Domes were inhabited by *P. alleni* of both juvenile and adult size in higher densities than the surrounding prairie (Fig

BICY-6, Table BICY-2, BICY-4, and BICY-5) in all seasons in which a comparison of habitats could be attempted. The fact that juveniles remained in domes indicates that non-reproductive portions of the population will remain in habitat that was preferred during other seasons. While it seems obvious that not all animals would burrow, particularly if they were unable to mate, it is unknown whether there are any advantages to remaining in a body of water which would allow aquatic and avian predator access. It is important to note that burrowing does not prevent predation, as the striped swamp snake (*Regina alleni*) is an efficient predator of crayfish within burrows (Franz, 1977, Godley, 1980). Fortunately, we were not faced with identification of this predator in the field during our burrow surveys.

The mean size of form 1 *P. alleni* was 29.3 mm CL, ranging from 19.2 to 38.9 mm CL. The mean size at maturity of females based on burrow excavations by (Rhoades, 1970) was 27.9mm CL ranging in size from 18.2 to 34.4 mm CL. The probability of being mature was distributed as Normal, mean = 29.3, standard deviation = 4.2 for males and as Normal, mean = 27.9, standard deviation = 4.1 for females Fig BICY-5).

In collections of females within burrows from C-111, all females collected in early May were ovigerous (Rhoades, 1970). *P. alleni*, like other procambarids, endures a period in which newly hatched young may attach to the female's pleopods (pers. obs, (Rhoades, 1970). While the duration of attachment may vary depending upon environmental conditions, the hatched young appear to recruit to the population and be sampled by throw trapping (greater than 5 mm CL) by the following summer (Fig BICY-3). In fact, the juvenile peak of $\sim 9 \text{ m}^{-2}$ in July 1997 was the highest juvenile density during the study period. Peaks in procambarid juvenile abundance are common following reflooding, for example *P. clarkii*, juvenile abundance increases after flooding aquaculture ponds (Romaine and Lutz, 1989).

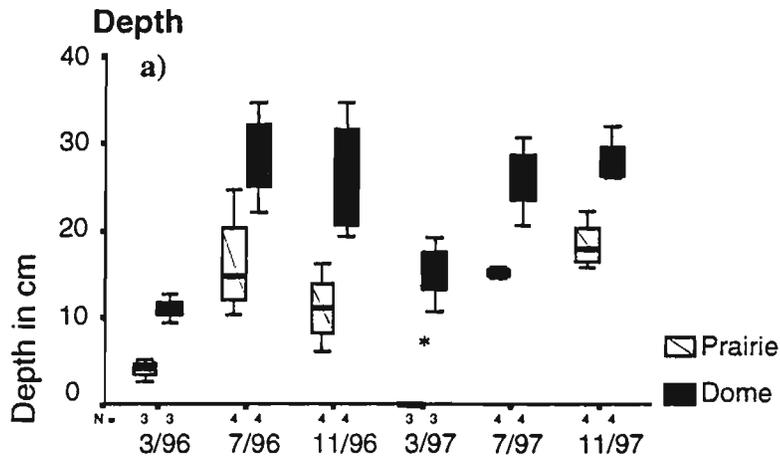
Adult density increased from July 1997 to December 1997 which is most likely a result of maturation by juveniles over the summer into adults by the fall/winter (Fig BICY-3). . As spring progressed, we would expect decreased adult abundance in throw traps as the season

transitioned from the wet summer/fall to the dry winter/spring and *P. alleni* were inhabiting burrows. We see this trend in the November 1996 to March 1997 comparison (Fig BICY-3). However in December 1997 the dry season has not yet begun, in fact the depth during December 1997 was slightly higher in prairies than in July 1997. Still, the concurrent increase in adult density and decrease in juvenile density which occurred between July 1997 and December suggests maturation by juveniles to adults as the dry season was approaching.

Dry weight to carapace length regression yielded the following equation (Fig BICY-6):

$$DW = 2 \times 10^{-5}(CL)^{3.3}.$$

The exponential term for *P. alleni* is slightly higher (3.34) than for *P. fallax* (3.21, from section 2 Fig BICY-5) which indicates that *P. alleni* is slightly heavier than *P. fallax* at the same carapace length. The maximum size of *P. alleni* is larger than *P. fallax* and their time to maturity are probably comparable. Thus one would expect the growth rate of *P. alleni* to exceed that of *P. fallax*. While growth rate has not been attempted with any rigor, a preliminary study revealed that *P. fallax* growth rate (0.9 mm molt⁻¹) was less than *P. alleni* (1.34 mm molt⁻¹).



* Depths for 3/97 were not recorded from within plots, but from traps thrown in dome locations which contained standing water.

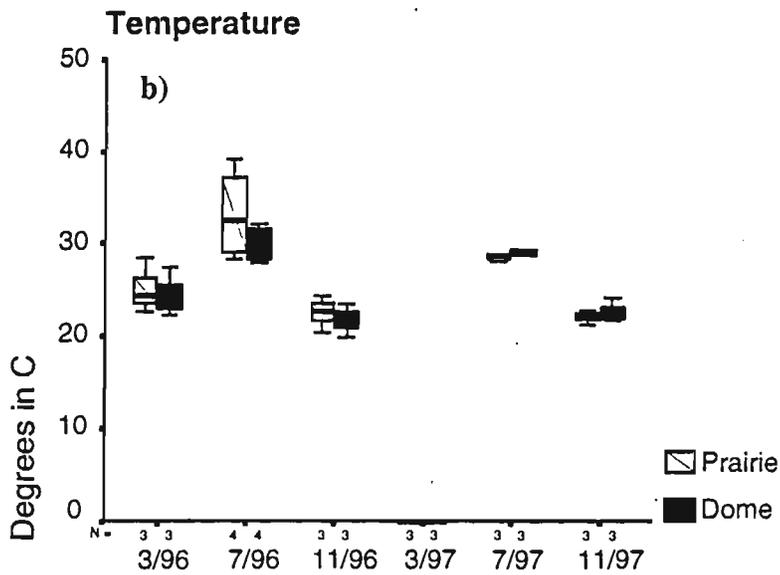


Figure BICY-1. Water depth (a) and temperature (b) in cypress prairie and domes in Raccoon Point, BICY. Box plots represent the second and third quartiles and whiskers represent outliers.

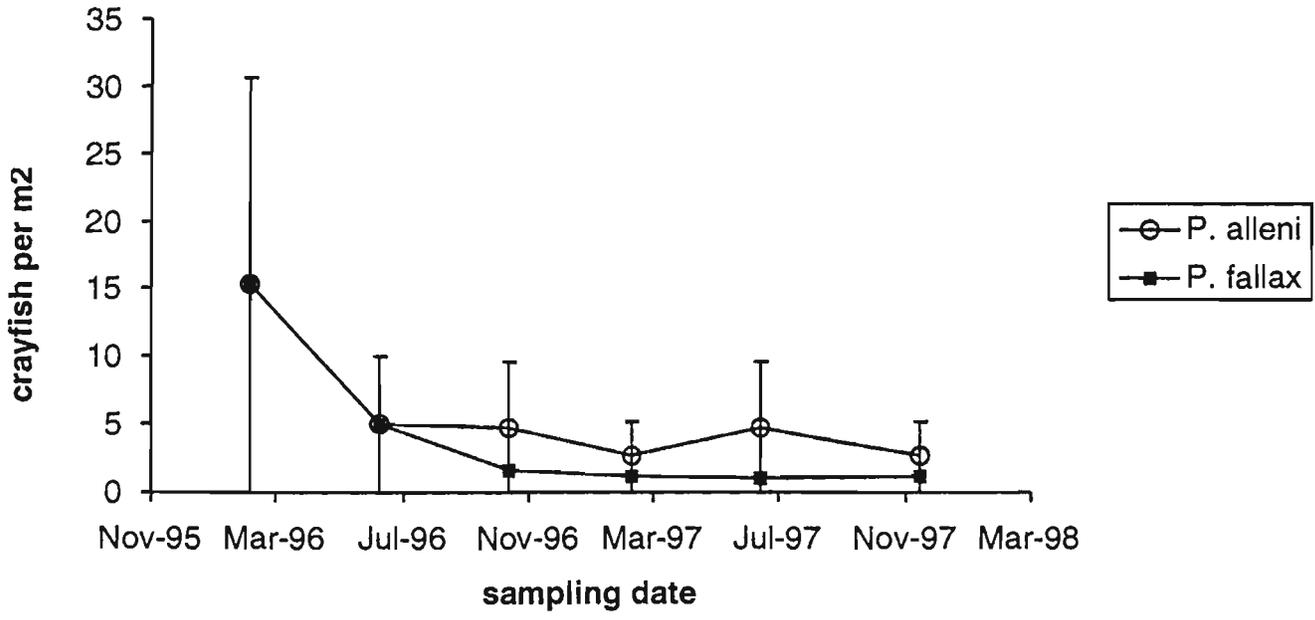


Figure BICY-2. *Procambarus alleni* and *P. fallax* density in Raccoon Point, BICY. Error bars represent 1 standard deviation.

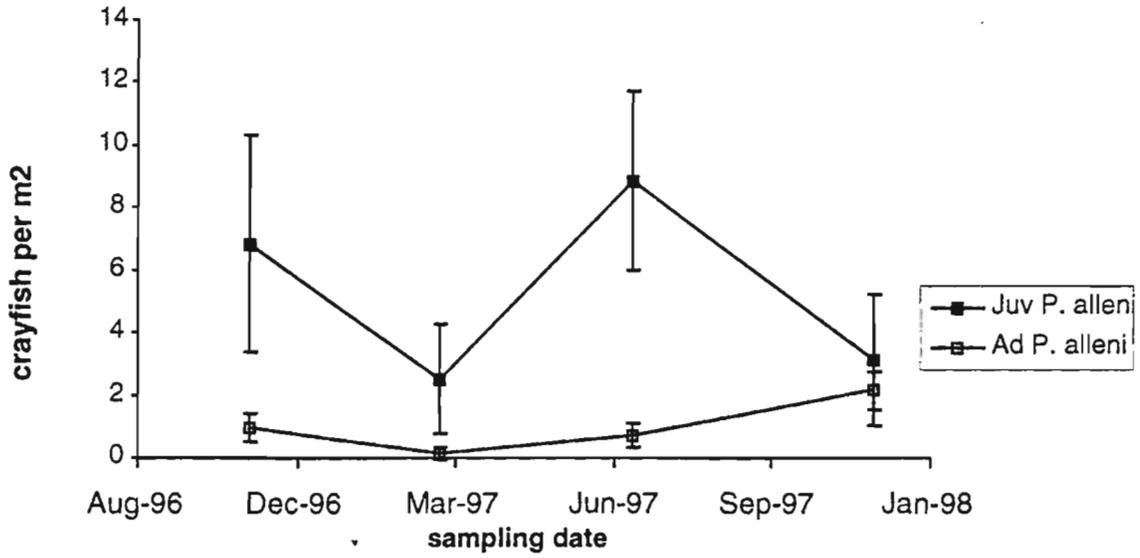


Figure BICY-3. *Procambarus alleni* adult and juvenile density in Raccoon Point, BICY. Error bars represent 1 standard deviation.

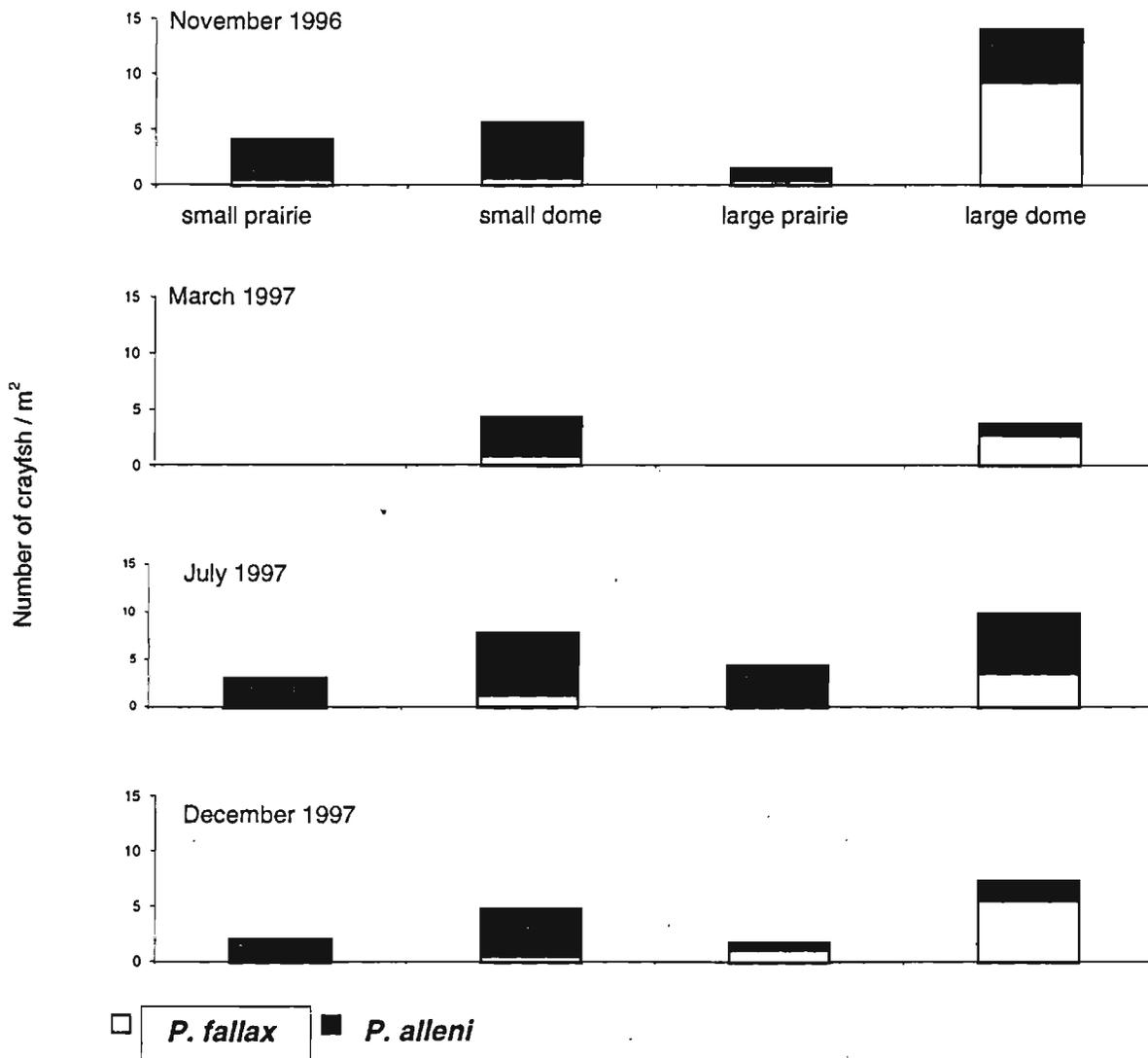


Figure BICY-4. *P. alleni* and *P. fallax* density in large and small cypress complexes. Large domes contained significantly more *P. fallax* in November 1996 and December 1997 while *P. alleni* dominated smaller domes and associated prairies in all months.

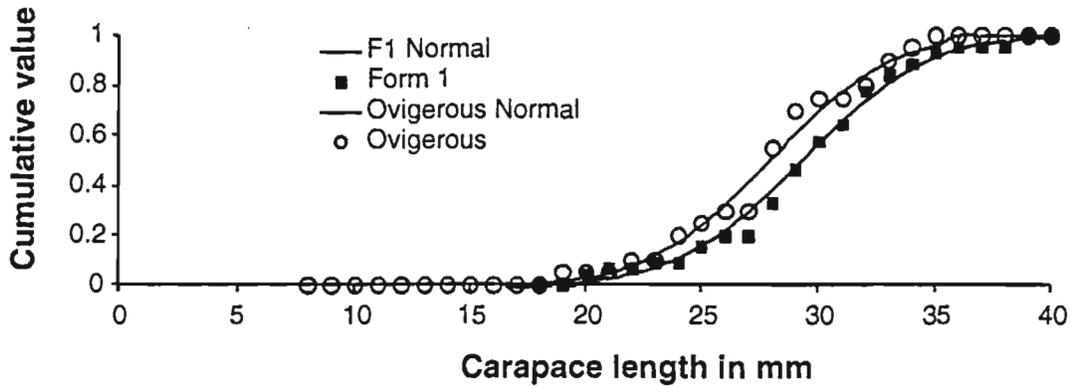


Figure BICY-5. *P. alleni* male and female size at maturity. Curves represent cumulative Normal fits to length frequency histograms of Form I males and ovigerous females. Mean size at maturity (MSAM) is at the 50% cumulative value.

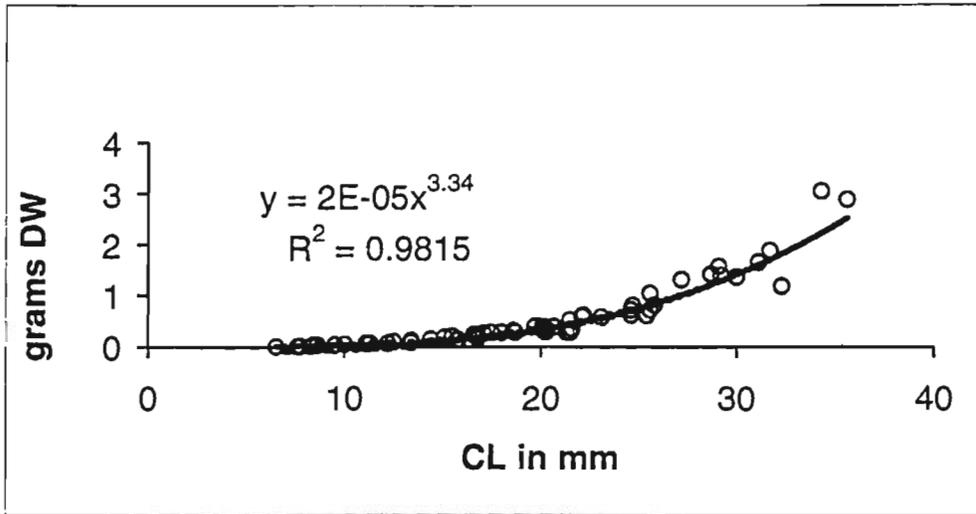


Figure BICY-6. Carapace length (CL) to dry weight (DW) regression for *P. alleni*.

Species and habitat relationships

When domes and prairies were flooded, crayfish were collected in higher densities, regardless of species, in domes (Tables BICY-2, -3, -6, Fig BICY-4). In all seasons there were more juveniles than adults, regardless of species. There were significantly more *P. alleni* than *P. fallax* at all sampling dates except March 1997 (Fig BICY-4, Tables BICY-2 to BICY-5). Average *P. alleni* juvenile density peaked in July 1997 and average *P. fallax* juvenile density climaxed in November 1996 due to a high average density of 9.5 crayfish m⁻² in dome a5. *P. alleni* adult density increased from a low of 0.11 crayfish m⁻² in March 1997 to a high of 2.14 crayfish m⁻² in December 1997.

Domes appeared to be different in age, size and crayfish species composition (Tables BICY-2, -5; -6 Fig BICY-4). The difference in species composition of domes was evident in two months, November 1996 and December 1997; plot a5 was dominated by *P. fallax* where the other three domes were dominated by *P. alleni* (Fig BICY-4). The species by plot interaction term which was significant in November 1996 and December 1997 was parceled into the deviance between large and small plots and 2) the deviance within small plots. The significant portion of the deviance in both collection dates was due to differences between small and large plots (Table BICY-2, BICY-6).

Table BICY-2 November 1996 ANODEV table. Significance values, * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.005$. Dev. = deviance which is distributed as X^2 . Plot is composed of two levels in which plots 3, 11, and 16 were combined as a "small prairie/dome complex" and plot a5 as a "large dome/prairie" complex.

Season	Variable	Dev.	d.f.	sig
November 1996	Habitat	6.55	1	**
	Size	31.41	1	***
	Species	7.46	1	**
	Plot	5.68	3	
	(Large vs small)	(2.12)	(1)	
	(Within small)	(3.56)	(2)	
	Habitat x Species	2.28	1	
	Habitat x Size	3.03	1	
	Habitat x Plot	4.67	3	
	(Large vs small)	(3.07)	(1)	
	(Within small)	(1.60)	(2)	
	Species x Size	0.655	1	
	Species x Plot	10.22	3	**
	(Large vs small)	(10.11)	(1)	***
	(Within small domes)	(0.11)	(2)	
	Size x Plot	2.40	3	
	(Large vs small)	(0.12)	(1)	
	(Within small domes)	(2.28)	(2)	
	Error	6.80	13	
	Total _{corr}	81.16	31	

Table BICY-3 March 1997 ANODEV table. Significance values, * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.005$. Dev. = deviance which is distributed as X^2 . Plot is composed of two levels in which plots 3, 11, and 16 were combined as a "small prairie/dome complex" and plot a5 as a "large dome/prairie" complex.

Season	Variable	Dev.	d.f.	sig
March 1997	Size	12.37	1	***
	Species	0.97	1	
	Plot	1.23	2	
	(Large vs small)	(0.05)	(1)	
	(Within small)	(1.18)	(1)	
	Species x Size	0.01	1	
	Species x Plot	3.40	2	
	(Large vs small)	(3.15)	(1)	
	(Within small domes)	(0.25)	(1)	
	Size x Plot	0.70	2	
	(Large vs small)	(0.09)	(1)	
	(Within small domes)	(0.61)	(1)	
	Error	0.23	2	
	Total _{corr}	18.91	11	

Table BICY-4 July 1997 ANODEV table. Significance values, * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.005$. Dev. = deviance which is distributed as X^2 . Plot is composed of two levels in which plots 3, 11, and 16 were combined as a "small prairie/dome complex" and plot a5 as a "large dome/prairie" complex.

Season	Variable	Dev.	d.f.	sig
July 1997	Habitat	8.70	1	***
	Size	37.32	1	***
	Species	21.44	1	***
	Plot	5.29	3	
	(Large vs small)	(.67)	(1)	
	(Within small)	(4.62)	(2)	
	Habitat x Species	2.48	1	
	Habitat x Size	1.70	1	
	Habitat x Plot	2.31	3	
	(Large vs small)	(.24)	(1)	
	(Within small)	(2.17)	(2)	
	Species x Size	0.02	1	
	Species x Plot	1.95	3	
	(Large vs small)	(1.32)	(1)	
	(Within small domes)	(0.63)	(2)	
	Size x Plot	0.77	3	
	(Large vs small)	(0.09)	(1)	
	(Within small domes)	(0.68)	(2)	
	Error	1.99	13	
	Total _{corr}	83.97	31	

Table BICY-5. December 1997 ANODEV table. Significance values, * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.005$. Dev. = deviance which is distributed as X^2 . Plot is composed of two levels in which plots 3, 11, and 16 were combined as a "small prairie/dome complex" and plot a5 as a "large dome/prairie" complex.

Season	Variable	Dev.	d.f.	sig
December 1997	Habitat	6.64	1	**
	Size	4.55	1	*
	Species	5.54	1	*
	Plot	1.11	3	
	(Large vs small)	(0.47)	(1)	
	(Within small)	(0.64)	(2)	
	Habitat x Species	1.67	1	
	Habitat x Size	5.88	1	*
	Habitat x Plot	0.16	3	
	(Large vs small)	(0.06)	(1)	
	(Within small)	(0.10)	(2)	
	Species x Size	5.17	1	*
	Species x Plot	12.41	3	***
	(Large vs small)	(11.96)	(1)	***
	(Within small domes)	(0.44)	(2)	
	Size x Plot	1.72	3	
	(Large vs small)	(0.44)	(1)	
	(Within small domes)	(1.28)	(2)	
	Error	1.05	13	
	Total _{corr}	45.90	31	

Table BICY-6. Table of dome differences

Parameter	Plot 3	Plot 11	Plot 16	Plot A5
Area inundated in March 1997	~10 m ²	0	-12m ²	~150 m ²
Size of dome	~ 1554m ²	~2594m ²	~6877m ²	~22,496 m ²

P. fallax in BICY

Finding a second species of crayfish initiated a critical evaluation of the habitats being sampled. The prevalence of water during the dry season is a possible method by which *P. fallax* remains in this facet of the available habitats in Raccoon Point. The fact that this species has been found in long hydroperiod sites in other locations, such as Shark Slough, and in those similarly flooded habitats within Raccoon Point, indicates that the species is representative of longer hydroperiod conditions. In particular, the dominance of *P. fallax* in the dome/prairie complex of plot a5 contrasted with the other sampled plots. *P. fallax* were captured throughout all seasons in higher densities in plot a5 than in the other dome/prairie complexes (Fig BICY-4) that were dominated by *P. alleni*. Dome a5 is a larger complex that maintained a greater expanse of water during the drydown in March 1997 (Table BICY-6).

Although the methods by which *P. fallax* constructs burrows is unknown, as we did not collect *P. fallax* in burrows. (Hobbs, 1942) states that he found them in simple, shallow burrows, however *P. fallax* was more prevalent in continually flooded habitats than ephemeral pools and ditches. Although it is unknown how *P. fallax* responds to drydowns, it appears that they are distributed on the landscape in those locations in which water disappears from the surface infrequently.

East Slough

Both *P. alleni* and *P. fallax* were captured in East Slough. As a dual species crayfish assemblage was not determined until after the July 1996 sampling event, identification to species

was initiated in November 1996. In all sampling events, significantly more *P. alleni* were collected by throw trapping in the study plots than *P. fallax* (Figure ES-1, Table ES-1). Average density of *P. alleni* and *P. fallax* were 3.95 and 0.48 crayfish m⁻², respectively. Still, fluctuations were evident (Fig ES-1). In particular, *P. fallax* was not captured from the study plots during July 1997, perhaps as a consequence of the drydown of the previous spring. Densities of *P. fallax* rebounded slightly, however, in December 1997. No significant change in density was apparent for either species from November 1996 to December 1997 (ANODEV X² test statistic = 6.73, 3 d.f., 0.1 > p > 0.05 for *P. alleni* and test statistic = 6.18, 3 d.f., p > 0.1 for *P. fallax*).

No crayfish were captured in the burrow surveys of East Slough. However, burrow chimneys were evident indicating that *P. alleni* had constructed them. The density data during wet periods corroborates this observation. The density of burrows increased in plots located further away from the slough (Table BICY-1) where plot four was the furthest and two the closest to the slough. No burrow surveys were conducted in plot 1 because water still remained on the surface and burrows were not apparent.

East Slough is dominated by *P. alleni*. In particular times the species composition is wholly *P. alleni*. The fact that this is an intermediate hydroperiod location in which sections become dry during the spring and winter indicates that *P. fallax* does not survive as well in other locations.

Table ES-1. ANODEV of East Slough sampling events in which a Poisson distribution was specified and mean values per plot were log linked using GLIM. Sig. values , * = p < 0.05, ** = p < 0.01, *** = p < 0.005. Dev. = deviance which is distributed as X^2 .

Season	Variable	Dev.	d.f.	sig
November 1996	Species	14.13	1	***
	Error	2.66	6	
	Total	16.79	7	
March 1997	Species	8.95	1	***
	Error	4.87	6	
	Total	13.82	7	
July 1997	Species	17.23	1	***
	Error	2.35	6	
	Total	19.58	7	
December 1997	Species	17.08	1	***
	Error	1.55	6	
	Total	18.63	7	

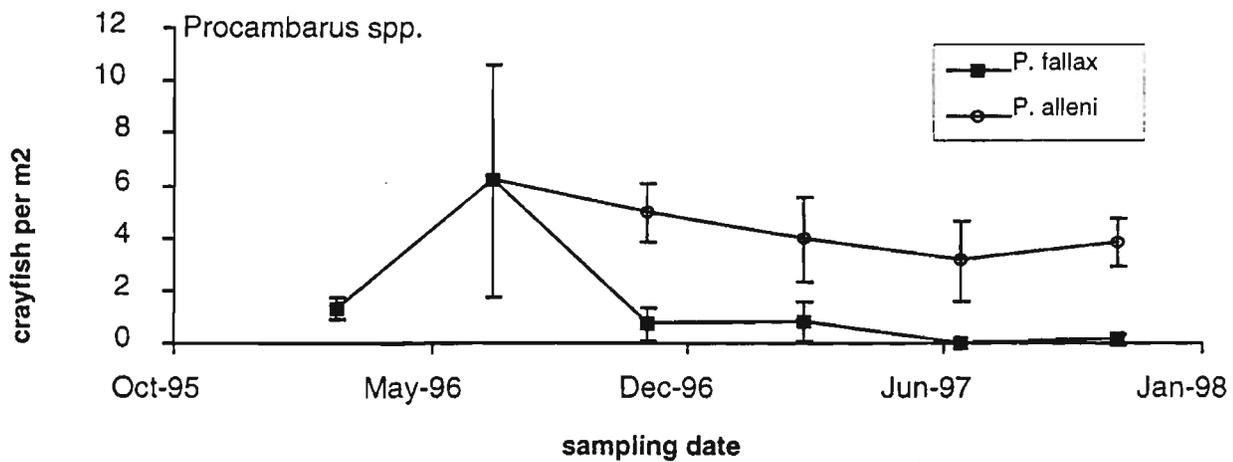


Figure ES-1. *Procambarus fallax* and *P. alleni* density in East Slough. Both species were combined in March and July 1996 samples. Error bars represent one standard deviation.

Crayfish density and foraging ibis

Ibis were observed in feeding assemblages in all study sites. The availability of foraging opportunities appears to be limited by the local hydrology that either permits or excludes ibis. Both excessively high water and the lack of water prevent foraging. Although ibis have been observed feeding on fiddler crabs (*Uca* spp.) that were located in burrows (Bildstein, 1983), this behavior has not been observed for crayfish. Thus, assuming that ibis are foraging in locations that are flooded, they may be excluded from locations that are too deep. It appears that a phenology of habitat availability due to drying conditions and annual hydrology occurs through the nesting season. Habitats suited for foraging early in the season are depleted of prey as these locations dry. Longer hydroperiod sites then become important as the dry season progresses (Frederick and Callopy, 1989). Due to the nature of this drying seasonality, we might also expect a phenology of ibis consuming crayfish prey. Shorter hydroperiod marshes would be composed of *P. alleni* primarily, while intermediate hydroperiod locations would include both species. In those years where the dry season progressed to an extent that long hydroperiod marshes were used, *P. fallax* would dominate the prey assemblage late in the dry season. While there has been no investigation into the species composition of prey taken by ibis, this may be a useful study in the future to determine restrictions on ibis nesting. Further, some information may be gleaned by constructing a crayfish biomass model that defines each species distribution based on hydrologic requirements. Given particular drying scenarios, ibis foraging could be predicted by available prey concentrations. The composition of these prey assemblages would also be known and thus the hypothesis could be tested as being plausible. Still, the requirement for verification via ibis gut or bollus (regurgitant fed to nestlings) would be required.

The discovery of *P. fallax*, unknown to reside in the Florida Everglades prior to this study, has raised additional questions regarding crayfish use of habitat and the importance of crayfish to ibis nesting success. The mechanisms responsible for observed patterns in crayfish distribution are unknown and thus difficult to model. The degree of competition between the two

species, expressed through aggression or resource limitations is similarly undocumented. Finally, the importance of crayfish as a resource to nesting ibis, particularly given distinct responses to drydowns during the nesting season, is unknown. While finding a second species of crayfish has helped to explain the wide use of habitats by crayfish, the significance of this dual species assemblage has yet to be understood.

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Literature review

Everglades Ecosystem

Everglades Hydrology

Drainage of the Everglades began in 1888 with the construction of canals leading from Lake Okeechobee to the Gulf of Mexico. By 1927 five canals had been constructed which lead from Lake Okeechobee to the Atlantic Coast (Tebeau, 1974). Following a hurricane in 1928, flooding of Lake Okeechobee instigated a reduction in lake levels through the afore mentioned canals and the construction of a 30 foot levee surrounding the southern part of the lake (Allison, 1948 as cited in Light and Dineen (1994). A hurricane in 1947, and the subsequent flooding that ensued, indicated that the Everglades watershed needed to be managed with a more complete understanding of the system, thus the Central and Southern Florida Project for Flood Control and Other Purposes was created in 1948.

From 1952 to 1965 four major projects were undertaken to provide flood protection for the burgeoning regions of south Florida. The projects used a combination of levees, canals, water retention areas, and pumping stations to provide flood protection for the Everglades Agricultural Area (EAA), flood protection for the growing metropolises along the eastern coast of Florida, and water retention areas for drinking water and for Everglades National Park. Since 1965, an additional goal of the Central and Southern Florida Project for Flood Control and Other Purposes, which became the South Florida Water Management District (SFWMD), was to provide water in the quantity and quality that ensured the diversity and ecological health of Everglades National Park.

In the 1940's Parker (Parker, 1974) estimated that the water table had been reduced by six feet; the estimate was based on loss of peat due to oxidation and encroachment of salt water due to reduced inland hydraulic pressure. The existence of freshwater springs, which percolated

through the oolitic limestone of Biscayne Bay, was supported by ship logs describing rewatering stops for coastal travel in the region in the 1800's (Tebeau, 1974) and by computer simulated recreations of historical groundwater (Fenema et al., 1994). However, freshwater springs are no longer present in Biscayne Bay. While it may be argued that the loss in water depth could be attributed to changes in rainfall or evaporation rates (Parker, 1974), the primary input and output of the Everglades watershed, respectively, the rainfall and evaporation rates were similar for 1940-1946 as for the period from 1914 to 1939 (Thomas, 1974).

By the mid 1960's the incredible effectiveness with which the Army Corps of Engineers had provided flood protection was evident in the landscape. The sugar industry was booming in the EAA due to rich muck soils and guaranteed flood protection. Unfortunately, ENP which is situated on the downstream end of the engineered structures, was experiencing the lowest hydrologic inputs in the history of its existence. Altered flow to Shark Slough due to the construction of a canal and spillways along Tamiami trail provided water to only half the slough (Light and Dineen, 1994). Water levels in Taylor Slough dropped significantly after the construction of L-31 (W) in 1968 (Rose et al., 1981). Yet as a sign that the water management was still largely unbalanced, the Atlantic Ocean received over one trillion gallons of fresh water from 1980-1989 in comparison to 190 billion for Shark Slough and 30 billion for Taylor slough (Light and Dineen, 1994).

The temporal manipulations of management schedules in the 1960's overemphasized the seasonality of water level in Shark Slough, making the dry season drier through reduced flow and the wet season wetter through dumping of excess water from Conservation Area 3A (Fenema et al., 1994). Alternative water delivery schedules have included: 1) an open gate system by which Shark Slough was allowed to equilibrate with Water Conservation Area 3A (Flow through plan, 1983-1985) and 2) environmentally moderated flow in which releases to Shark Slough are based on weather conditions in the northern sections of the watershed (Rainfall plan, 1985-present) (Light and Dineen, 1994).

Because quantitative hydrologic records do not exist prior to 1940, attempts have been made to theoretically and mathematically recreate historic hydrology (Walters et al., 1992, Fenema et al., 1994). Surface and ground water recreations have elucidated significant differences between the current, plumbed, system (managed) and a theoretical landscape, lacking in canals, levees, water retention areas, and pumping stations (natural). Several important distinctions become apparent in the comparison of a natural and managed system: first, the managed system has a sharp reduction in overland flow throughout the entire system, second, the flow through ENP is concentrated west of its natural trajectory, and third, the flow through the western channel is approximately half of the natural flow which would have reached ENP (Walters et al., 1992, Fenema et al., 1994). In short, the natural ENP would be wetter and broader, and drought events within lower Shark Slough would occur significantly less frequently (Walters et al., 1992).

Effects on vegetation

Wetland habitat types of the Everglades are maintained largely through hydroperiod (duration of inundation) [Gunderson, 1994 #224]. Initial investigations into categorizing habitats within ENP resulted in the distinction of tree islands, sawgrass, wet prairie, and aquatic slough, in order of shortest hydroperiod (rarely flooded) to longest hydroperiod (permanently or semi-permanently flooded) (Davis, 1943, Loveless, 1959). Additional categories of habitat types include willow heads, cypress forests, pond apple forests, and bayhead forests (Gunderson, 1994).

In studies of Everglades vegetation response to hydrology, indicator species are often used to facilitate analysis of habitat types. Sawgrass, *Cladium jamaicense*, is an obvious indicator of sawgrass stands (David, 1996, Jordan et al., 1997). Sawgrass is a drought and fire tolerant species with limited tolerance to flooding (Herndon et al., 1991) which is specific to elevations greater than ca. 2.2 m above sea level (David, 1996). Beak rush, *Rhynchospora tracyi* has been

used as an indicator of wet prairie (Jordan et al., 1997). Beak rush may recolonize a periodically flooded substrate such as wet prairie by building a seed bank which then sprouts upon water retreat (Greening and Gerritsen, 1987). Finally, water lily, *Nymphaea odorata*, is an indicator of slough (David, 1996, Jordan et al., 1997). Water lily is flood resistant and drought susceptible (David, 1996), thus indicating the location of prolonged flooding.

Vegetation response to altered hydrology is dependent upon scale of disturbance, growth rate, and colonization rate of major vegetation types within the habitat (Gunderson, 1994). Studies operating on short time scales of two to ten years have not been successful in exposing change in wetland plant composition due to hydrology (Wood and Tanner, 1990, Jordan et al., 1997) however, a comparison of vegetation patterns spanning 20 years indicated a shift from wet prairie to sawgrass communities over a span of altered hydrology (Davis et al., 1994). The effects of nutrient additions upon vegetation, however, appear in a much shorter time frame. The replacement of sawgrass by cattail (*Typha domingensis*) in northern Everglades marshes has been identified remotely and through mesocosm studies (Newman et al., 1996).

Hydrology and aquatic fauna

Small fish assemblages, on the other hand, responded to hydrology on the order of seven years within wet prairies of the Southern Everglades (Loftus and Eklund, 1994). The rapid life cycle of small marsh fishes provides the ability to respond quickly to changes in hydrology (Haake and Dean, 1983) as cited in (Loftus and Eklund, 1994). Although Kushlan (Kushlan, 1976) stated that Everglades fish communities shift from a small, live-bearing, omnivorous fish assemblage to a large, predatory, piscivorous assemblage during prolonged flooding, Loftus and Eklund (1994) found no support for this theory. Further, they found that both large fish and small fish alike increased in abundance during a drought free period from 1977-1985. Finally, Loftus and Eklund (1994) stated that the strongest abiotic determinant of species composition in a given year is the severity of the dry season in the previous year.

Studies comparing the significantly altered wet prairies of eastern Shark Slough to less impacted regions of central Shark Slough indicated a difference in fish species composition and abundance (Loftus et al., 1992). In the Rocklands region, located in southeast Shark Slough, altered hydroperiod removed dry season refugia through loss in water depth (Loftus et al., 1992). Because of altered hydromanagement, water depths declined from 21 to 56 cm in the wet season and 24 to 35 cm in the dry season. The cumulative effect of reduced water depth caused the area to dry out one month earlier, effectively removing the habitat as a possible foraging area for nesting wading birds (Loftus et al., 1992). The construction of L67, which divided northern Shark Slough into a western catchment for ENP water deliver and an eastern section responsible for maintaining reduced water levels to nearby residences, caused a change in the biota associated with the region (Loftus et al., 1990). The inability of the altered hydroperiod, Northeast Shark Slough site to match the central Slough, in terms of species composition and relative abundance, was due to changes in the underlying soil from peat to calcitic marl (Loftus et al., 1990). The changes in hydrology of eastern Shark Slough has long term implications as substrate alteration due to hydropattern reconfiguration may take decades to restore (Gunderson, 1994).

Wading birds are a conspicuous and politically charged element of the Everglades landscape. Of the wading birds that visit the Everglades each year, white ibis constitute from 55 to 85 percent of the total population (Ogden, 1994). The decreasing presence of white ibis (Ogden, 1994) on the landscape has led some researchers to pose mechanisms by which wading bird populations have been declining.

While alternative explanations have been posed such as shifted nesting habitat(Ogden, 1994) and toxicity due to mercury uptake (Frederick pers. comm.), reduced prey availability appears to be a consistent theory proposed for wading bird declines (Bancroft et al., 1994, Frederick and Spaulding, 1994, Ogden, 1994). In a comparison of wading bird abundance taken from two time periods, 1931-1946 and 1974-1989, the maximum number of white ibis nesting in south-central Everglades dropped from an estimate of ca. 200,000 to 29,000 (Ogden, 1994).

Concurrent with this decline was the implementation of hydromanagement for flood control in the same region (Light and Dineen, 1994). Exploring the development of ibis nestlings from hatching to fledging can expose the relationship of crayfish to ibis.

The seasonality of white ibis nesting is tied closely to availability of aquatic prey. White ibis are tactile feeders that ingest a wide variety of prey, however they are particularly well suited to consume terrestrial, marine, and fresh-water invertebrates (Bildstein, 1984). In brackish or marine environments in South Carolina, which are similar to the mangrove regions of western ENP that supported large rookeries of white ibis in the 1930's (Bancroft, 1989) adult and juvenile white ibis forage on fiddler crabs (*Uca* spp.) (Bildstein, 1984). Still, during development the nestlings have not formed salt glands, which rid the body of excess salt due to ingesting marine derived prey (Johnston and Bildstein, 1990). At this stage in development the nestlings must be supplied with freshwater prey. The most common forage item during this critical stage of development is crayfish.

Kushlan and Kushlan (1975) first described the presence of crayfish in white ibis stomachs collected from ENP. In water conservation area 3A and ENP, Frederick (Frederick and Callopy, 1989) found that years in which nests fledged young, contained a high proportion of crayfish exoskeleton, yet in years where nests failed, the boluses were composed of dark fluid with mud and insects as primary components.

Crayfish ecology

Florida crayfish history

Immigrating crayfish during the early Pleistocene (Hobbs 1942) probably provided the diversity of crayfish species currently found in Florida. Although freshwater crayfish are related to marine lobsters, the locations at which ancestral crayfish wandered into brackish water and ultimately made their residence in the accompanying streams are unknown. While it seems

apparent that Astacids and Cambarids both originated from an ancestral marine stock, two theories attempt to describe the geographic locations of these forays and therefore centers of radial divergence of the Astacoidea.

An initial theory, presented by Ortman (Ortmann, 1905), states that the first crayfish stock originated in Sino-Australia during the lower Cretaceous. During the upper Cretaceous an additional stock migrated to western North America via a land bridge, ultimately residing Mexico. Subsequently, the subfamily Cambarinae was derived from the populations located in Mexico during the Lower Tertiary and spread eastward throughout North America (Ortmann, 1905). A center of radiation was established near the base of the Appalachian Mountains, and this stock provided the source from which *Procambarus* originated (Ortmann, 1905).

Hobbs (Hobbs, 1988) offers an alternative explanation in which the ancestral crayfish to *Procambarus* originated in southeast North America. The holdfast of this theory is anchored in life history traits of the subfamily, Cambarinae, which are represented by a more derived condition than other subfamilies of the family Cambaridae (the reader should note that the family is Cambaridae and the subfamily is Cambarinae and the author will attempt to clarify this distinction whenever possible). All members of the Cambaridae have cyclic dimorphism in males (the presence of a reproductively active and inactive morphotype) and a seminal receptacle in females; qualities ascribed only to the Cambaridae. The sub-family, Cambarinae, is the only family in which species have established themselves in the majority of available habitats (Hobbs, 1988). For example, members of the subfamily Cambarinae have evolved to endure the entirety of their life cycle within the confines of burrows (e.g. Fitzpatrick, 1975; Hobbs, 1942) and caves (Hobbs, 1988). Further, the only location in which troglobytic (cave) crayfish have been found is in the Northern Florida, Alabama, Georgia, Indiana, and Mississippi indicating a hub of adaptive radiation located near this region (Hobbs, 1988). Troglobytic species represent a more evolutionarily advanced form, as they are often distinct morphologically (Hobbs, 1942, Hobbs, 1988) and metabolically (Dickson and Franz, 1979) from the "standard" crayfish bodyplan.

While the author is unaware of a study to address the probable locations of adaptation from marine to freshwater environments, it seems that the conclusions made by Hobbs (Hobbs, 1984) are valid.

The genus *Procambarus*, which contains the greatest number of species (143) of any crayfish genus (Hobbs, 1988), inhabits a wide variety of habitats including burrows, lentic and lotic waters, and caves. While their range extends from Wisconsin throughout the Atlantic and Gulf coasts of the United States and Central America, the center of their radiation lies in southeastern United States (Hobbs, 1984). While Florida maintains populations of six genera, only *Procambarus* can be found statewide (Hobbs, 1942). Still, no single species maintains a distribution that covers the entirety of Florida (Franz and Franz, 1990).

The two species of interest to this thesis, *Procambarus alleni* and *P. fallax*, most likely immigrated to Florida from Georgia and Alabama during the early Pleistocene (Hobbs, 1942). Due to the wide distributions of *P. alleni* and *P. fallax* it is difficult to discern which pathway in particular was utilized. With the continual rise and fall of sea level throughout the Pleistocene, several opportunities were available to migrating crayfish. It is hypothesized that *P. alleni* became established prior to *P. fallax* by advancing south during an opening of the Florida Straights prior to *P. fallax* (Hobbs, 1942). Indeed, they are members of distinct subgenus within the classification of Florida crayfish presented by Franz (Franz and Franz, 1990); *P. fallax* is a member of the subgenus *Ortmannicus* while *P. alleni* is a member of the *Leconticambarus* subgenus.

P. alleni and *P. fallax* research to date

The Everglades crayfish (*Procambarus alleni*) has been the topic of several investigations since it was described by Faxon (Faxon, 1884). Hobbs (Hobbs, 1942) collected *P. alleni* in lakes, marshes, drainage canals, and cypress stands. Several additional unpublished

reports and published investigations, which provided further insight into the life history of *P. alleni*, are briefly summarized here. Rhoads (1970) described basic life history, reproductive seasonality, and fecundity in crayfish from the southeastern area of the Everglades. Crayfish were excavated from burrows to obtain data on sex ratio, size-related fecundity, male morphology, and length-weight relationships. In an unpublished pilot study, Conover (1972) sampled *P. alleni* from several habitat types during January 1972. *P. alleni* was found in permanent ponds, temporary ponds, and prairie habitat that spanned salinities from 3.0 to 18 ppt. Kushlan and Kushlan (1979) reported on *P. alleni* sampled in Everglades National Park using mesh-and-frame pull traps from 1966 to 1972. The researchers concluded that water-level fluctuation led to increased crayfish biomass and density, presumably via decreased predation upon *P. alleni*. However, Loftus and Eklund (1994) found that pull traps bias collection data due to the unnatural conditions they provide (by forming water collecting depressions in an elevation sensitive substrate). Thus, conclusions made by Kushlan and Kushlan (1979) were erroneous. Evidence that *P. alleni* prefers highly vegetated habitats was provided by Jordan in both field (Jordan et al., 1996a) and laboratory (Jordan et al., 1996b) environments.

In the Rocky Glades region of Everglades National Park, *P. alleni* may provide the greatest biomass of any aquatic fauna as they have been collected in aggregations up to 100 crayfish per m² (Loftus, personal communication, Everglades National Park, Florida)! While this density was observed during an early summer recruitment event and may represent a short peak in abundance, Jordan (Jordan et al., 1996a) recorded a peak density of 27 g per m² (28 per m²) in the northern sloughs of the Everglades watershed and Taborsky (Taborsky, 1982) found *P. alleni* in culture ponds at densities up to 150 g wet weight per m².

Because crayfish can assimilate detritus into protein in one trophic step (Momot, 1984), they are efficient energy links to higher trophic levels (Lorman and Magnuson, 1978). In Everglades National Park (ENP), many predators have been shown to ingest *P. alleni*, including occasional consumers such as the snook (*Centropomus undecimalis*), American egret

(*Casmerodius alba*), raccoon (*Procyon lotor*), opossum (*Didelphis virginiana*), otter (*Lutra canadensis*) (Rhoads, 1970), snail kite (*Rostrahamus sociabilis*) (Bennets et al, 1994), and consumers dependent on *P. alleni* for a substantial portion of their diet including largemouth bass (*Micropterus salmoides*), warmouth (*Lepomis gulosus*), eastern glossy ibis (*Plegadis flacinellus*), American bittern (*Botaurus lentiginosus*), white ibis (*Eudocimus alba*), pied billed grebe (*Podilymbus podiceps*) and little blue heron (*Egretta caerulea*) (Rhoads, 1970; Gunderson and Loftus 1993). While *P. alleni* is consumed almost exclusively by several species of wading birds, little is known about the biology and ecology of this species. Robertson and Frederick (1994) stated that "As a dramatic example [of the poor understanding of the ecology of aquatic prey animals], next to nothing is known about the only species of crayfish (*P. alleni*) in the Everglades, which is a central food item for most wading birds and many fishes, anurans and reptiles."

Hobbs (1942) provides the first and only characterization of *P. fallax* since its initial description (Hagen, 1870). *P. fallax* has been collected throughout most of the Florida panhandle, bordered on the north by Georgia and on the south by canal structures leading from Tampa Bay to Lake Okeechobee (Hobbs, 1942). Prior to this study, Palm Beach County formed the southern extent of its range. The species is typically found in heavily vegetated microhabitats, which provide water for most of the year (Hobbs, 1942). *P. fallax* was collected in Flagler, Citrus, Hillsborough, Sumter and Seminole counties sympatrically with several species, including *P. alleni*, in flooded ditches. However, during the dry season, when *P. alleni* was collected from burrows in the dry ditch, *P. fallax* was captured in contiguous streams (Hobbs, 1942).

Trophic importance of crayfish

Trophic cascade theory has been applied to freshwater systems in an attempt to understand, model, and predict the outcome of perturbations to a system (Carpenter et al., 1987, Carpenter and Kitchell, 1992). While it may be argued that primary productivity determines the total available food in a system and therefore the structure of higher trophic levels (bottom-up), most attempts to classify crayfish within the confines of a trophic cascade construction have assumed that the highest trophic level (top-down) is responsible for shaping the community (Hanson et al., 1990, Lodge et al., 1994, Hill and Lodge, 1995). The method by which species are placed into a trophic level typically follows a study of gut content analysis or behavioral observations of foraging. If species one consumes species two, two consumes three, three consumes four, and so on, we would expect that an increase in species one (assuming we are following a simplistic, top-down approach) will likewise cause a decrease in two and four and an increase in three. Similarly species two would be expected to increase if there was some removal of species one (such as fishing pressure or a die off due to changes in physical conditions), although species three would be expected to decrease while four would increase. Returning to our initial conditions, a decrease in abundance of species two due to predation by species one is a direct effect, but the increase in three (due to the reduced abundance of species two) is considered an indirect effect of predation by species one. Interactions within a single trophic level due to competition may also be significant indirect effects e.g. (Capelli and Munjal, 1982, Lodge et al., 1986, Hill et al., 1993, Hill and Lodge, 1995), particularly as species may have particular behavioral traits (such as aggression, or avoidance) which are heightened during competition for resources. Further, alteration of substrate on which other species rely (for example, alteration of macrophyte communities such that epiphyte abundance is reduced) is an additional indirect effect that impacts members of the community. Thus the determination of a species' location within a trophic web is determined firstly by those species it consumes and those species that consume it, and secondly by manipulation of habitat on which other species rely for their survival.

Unfortunately, crayfish do not conform to the trophic cascade theory gracefully. Crayfish are omnivores (O'Brien, 1995, Whitley and Rabeni, 1997) that alter the trophic level below them directly and indirectly (Diehl, 1995). Further, placing them into a trophic level based on gut contents analysis is complicated by attempting to classify the finely masticated remains of a crayfish pyloric stomach. Largely due to the presence of unidentifiable organic material in the gut, detritus was assumed to be a large constituent of the diet with animal material (Saffran and Barton, 1993, Ilheu and Bernardo, 1995, O'Brien, 1995) and conspecifics (Mason, 1975 as cited in Lodge, 1994) a minor component. However, with the use of stable isotope analysis and a review of the physiological requirements for growth of crayfish (Momot, 1995), it appears that animal prey may constitute 30 to 50% of their production due to consumption of animal tissue directly (Whitley and Rabeni, 1997). This value is approximately a fourfold increase in the contribution to production than previously recorded (Mason, 1975, Momot et al., 1978). Thus the trophic placement of crayfish throughout the last two decades needs revisiting. In reexamining the elements of a crayfish diet and the residence time within the gut, it is clear that future studies will have to incorporate an estimate of differential assimilation of prey items (Whitley and Rabeni, 1997).

As omnivores, crayfish typically do not impact the community in which they reside in a defined, detectable fashion. Still, in some systems they are perhaps *the species* responsible for structuring the community. The majority of trophic dynamic studies in the Cambarinae family have been conducted on *Orconectes rusticus*, *O. virilis*, and *O. immunis*. These species inhabit lake littoral zones throughout the central United States from Tennessee to Wisconsin, USA. The presence of crayfish in littoral zones have been found to reduce snail abundance (Hanson et al., 1990; Lodge et al., 1994), reduce macrophyte shoot density (Lodge and Lorman, 1987; Chambers et al., 1990; Lodge et al., 1994), and increase periphyton abundance. Although macrophyte shoot density has been reduced in studies involving trophic cascade investigations, much of this loss is due to non-consumptive damage of the macrophytes (Lodge et al., 1994; Hill and Lodge, 1995).

Still, crayfish may structure the macro-invertebrate community directly through predation (Whitledge and Rabeni, 1997) or indirectly through restructuring the algal (Creed, 1994) and macrophyte (Flint and Goldman, 1975; Chambers et al.; 1990) community. Due to their ability to significantly structure particular environments, namely those lacking large predatory fishes, they have been termed keystone species (Hart, 1992; Matthews et al. 1993; Creed, 1994).

In those systems dominated by higher vertebrates, such as predatory fishes, the trophic interactions of fish, crayfish, macroinvertebrates, and macrophytes may be difficult to discern. Still, littoral food web studies, in which crayfish predators such as Largemouth bass (*Micropterus salmoides*) were used to inhibit crayfish predatory effects (listed above), resulted in reduced macrophyte removal and a non-significant increase in gastropod abundance (Hill and Lodge, 1995).

While the content of crayfish stomachs may cause some confusion in the construction of a trophic web, the impact of crayfish on the benthic community is significant; crayfish are often the largest contributor to freshwater benthos both in number and biomass (Mason, 1963, Momot et al., 1978, Rabeni, 1992, Saffran and Barton, 1993). In oligotrophic lakes, crayfish may be the most abundant macroinvertebrates due to the lack of a phytoplankton/zooplankton assemblage to support higher trophic levels (Momot et al., 1978). In lotic environments crayfish may also be significant. In a Pacific Northwest lentic system *Pacifasticus trowbridgii* comprised 30% of the benthic biomass (Mason, 1963). Because of the contribution to the afore mentioned systems, determining the forces which structure the distributions of cambarinae and their preferences for habitats within broader ecotones is paramount.

Abiotic determinants of habitat selection

Crayfish are found in most aquatic environments in southeastern United States (Hobbs, 1984). Because the cambarinae represent a more derived group and have colonized a diverse array of habitats, habitat preference may be used as an indicator of abiotic and biotic elements of

the landscape. Lodge and Hill (Lodge and Hill, 1994) present several abiotic and biotic elements responsible for observed species distributions in cool-water crayfishes (mostly of the genus *Orconectes*, *Cambarus*, and *Pacifasticus*). While procambarids generally are not cool-water crayfishes, most have been studied in natural conditions as opposed to farming ponds. Thus, these studies focus on the factors responsible for habitat preference and associated life-history characteristics (such as thermal preference, growth, size at maturity, etc.) associated with natural populations. The list of abiotic factors provided by Lodge and Hill (1994) include: temperature, calcium, pH, dissolved oxygen, and salinity while the list of biotic factors are composed of: diet, inter- and intraspecific competition, and predation. To the list of abiotic factors I would add desiccation as it may prove more noteworthy in a shallow, seasonally flooded wetland such as the Florida Everglades than in cool-water lakes. Also, given the confusion surrounding a typical crayfish diet, the limited ability to discern the contents, and the fact that the subject was covered in the previous section, little more will be added to the topic.

Temperature in southern latitudes may limit the period of growth for procambarids. *Procambarus clarkii* in the northern end of its range will be active during the summer and quiescent during the winter, whereas in the southern part of its range the opposite seasonal pattern has been observed (Penn, 1943). In *P. spiculfer* the fastest growth rates were observed in the spring with subsequent reduction in growth during the summer (Taylor, 1990). Further, Caine (1978) stated that, "...in Florida, the high temperatures of the habitats may be more limiting than the low temperatures." Thus, summer months in which water temperatures may often reach greater than 35°C may limit growth in procambarid populations in subtropical latitudes.

Calcium concentration (Ca^{++}) is important to crayfish due to the physical construction of their exoskeleton (Lowery, 1988). During ecdysis, crayfish resorb approximately 10% of the required calcium needed to harden their post-molt exoskeleton in the form of gastroliths (Greenaway, 1985). Thus, the remaining 90% must be absorbed from the surrounding environment. Calcium concentration has been hypothesized to act in a threshold fashion, in

which bodies of water below 5 mg/L (Lowery, 1988) for *Austropotambius* (family: Astacidae) and ca. 2.5 mg/L (Capelli and Magnuson, 1983) for *Orconectes* (subfamily: Cambarinae) did not contain crayfish of each genera.

Calcium concentration is closely associated with pH, as pH limits the amount of available Ca^{++} in the water (Lowery, 1988). Thus, pH also follows a similar response curve as Ca^{++} , in which infrequently molting crayfish (e.g. adults) may be able to tolerate lower pH than frequently molting life stages (e.g. juveniles). In *Orconectes virilis* adults were able to tolerate pH of 4 while in intermolt, however molting adults were unable to absorb calcium at pH less than 5.75 (Malley, 1980).

Dissolved oxygen (DO) concentrations, particularly in burrowing species, can be a misleading value from which to determine habitat suitability. Crayfish may moisten the gills and respire through a thin layer of water remaining on the gill surface (Huner and Barr, 1980). Often the water found in the depths of burrows are deceptively low, if one assumes the crayfish lives submerged in this habitat. For example, Grow and Merchant (Grow and Merchant, 1980) found mean DO concentrations close to 1% for *Cambarus diogenes diogenes*, too low to sustain life if the crayfish were submerged; as expected, crayfish observed in the laboratory were usually located in the air/water interface.

Salinity range of crayfish may vary by species and location. *Procambarus clarkii* has been found in salinities up to 5 ppt (Hogger, 1988), where *P. alleni* has been collected in salinities as high as 18 ppt (Conover and Reid, 1972).

While few studies have addressed desiccation rates in crayfishes, it seems a worthwhile topic, particularly given the seasonal variability of surface water in the Everglades. Several procambarids from northwestern Florida were found to have differential responses to dry down. When tested in laboratory mesocosms, responses ranged from walking until death to burrowing immediately upon loss of surfacial water (Caine, 1978). In general those species, which were collected from the field beneath temporary refuge such as rocks or other substrate, were unable to

survive the desiccation experiments. The observed walking behavior of these species was perhaps an attempt to search for refuge within the confines of the lab aquaria (Caine, 1978).

Biotic determinants of habitat selection

Interspecific competition in sympatric populations of crayfishes has been most thoroughly documented in *Orconectes* spp. (Lodge et al., 1986, Olsen et al., 1991, Hazlett et al., 1992, Hill et al., 1993, Hill and Lodge, 1994). Although much of the energy has been focused on alterations in habitat due to a congeneric invader, *O. rusticus*, these studies represent the most comprehensive analysis of interspecific and intraspecific induced substrate preference. *O. rusticus*, an introduced species from Missouri has been successful in replacing *O. propinquus* and *O. virilis* in Wisconsin lakes (Capelli and Munjal, 1982, Hill et al., 1993, Hill and Lodge, 1994). Studies have been completed to determine the behavioral interaction between the three species and between a predator and the three species (Garvey et al., 1994, Hill and Lodge, 1994). In a survey of Wisconsin lakes, Capelli and Magnuson (Capelli and Magnuson, 1983) determined that the region had been invaded by *O. rusticus* in the period after 1932. Further, *O. rusticus* presence was correlated to human activity in 67 surveyed lakes indicating that humans (presumably through use for bait) were instrumental in contributing to the observed distribution of this exotic species. In mesocosms, Hill and Lodge (1994) determined that cobble was the preferred substrate by all three species, yet when all three congeners were competing for substrate, *O. rusticus* was found disproportionately more often in cobble. In laboratory aquaria Hazlett et al. (Hazlett et al., 1992) observed that *O. propinquus* and *O. virilis*, which were conditioned to *O. rusticus* presence, were subordinate to *O. rusticus* of the same size. While no biotic factors were discovered to explain species composition (Capelli and Magnuson, 1983), aggressiveness (Hazlett et al., 1992, Hill and Lodge, 1994), growth rate (Hill et al., 1993), and selective predation by smallmouth bass [DiDonato, 1993 #215; Garvey, 1994 #216] were all found to be responsible for shaping the observed habitat usage by congeners.

Interspecific competition in somewhat more established populations, (i.e. those that are not involved in the known invasion of an exotic into a niche previously held by an endemic species) while less thorough in their scope of analysis, offer insight into resource partitioning in communities which are perhaps more stable (Penn and Fitzpatrick, 1963, Bovbjerg, 1970, Rabeni, 1985). Populations may be found in distinct regions with areas of overlap along contiguous borders in their distributions (Bovbjerg, 1970, Rabeni, 1985) or the species may be segregated throughout the entirety of their joint distribution with no overlap (Penn and Fitzpatrick, 1963, Flynn and Hobbs, 1984).

Evidence of sympatric populations indicates that combinations of abiotic habitat requirements and biotic interactions allow the sharing of resources. Sympatric populations of *O. luteus* and *O. punctimanus* were maintained in Jacks Fork, Missouri through ontogenetic shifts in resource use by the dominant species, *O. punctimanus* (Rabeni, 1985). Because *O. punctimanus* restricted its distribution to preferred habitat based on life history stage (in the shallows as juveniles and in deeper, large-cobble substrates as adults), peripheral habitat was available to *O. luteus*. Thus, the two species coexisted within the same stream with *O. punctimanus* as the habitat specialist and *O. luteus* as the accommodating generalist.

Still, the collection of crayfish species in contiguous locations does not indicate a sympatric relationship. Although both *O. immunis* and *O. virilis* were collected simultaneously in a small section of the Little Sioux River, Ohio, burrowing behavior, tolerance to low DO, and differential aggressiveness were responsible for the largely segregated distribution (Bovbjerg, 1970). In an attempt to determine if substrate lithology (glaciated versus unglaciated) predicted historically distinct distributions of *O. sanbornii sanbornii* and *O. rusticus* in southern Ohio, parapatric (alternating allopatric) populations were discovered, in which competitive exclusion was hypothesized as the method responsible for the observed distributions (Flynn and Hobbs, 1984).

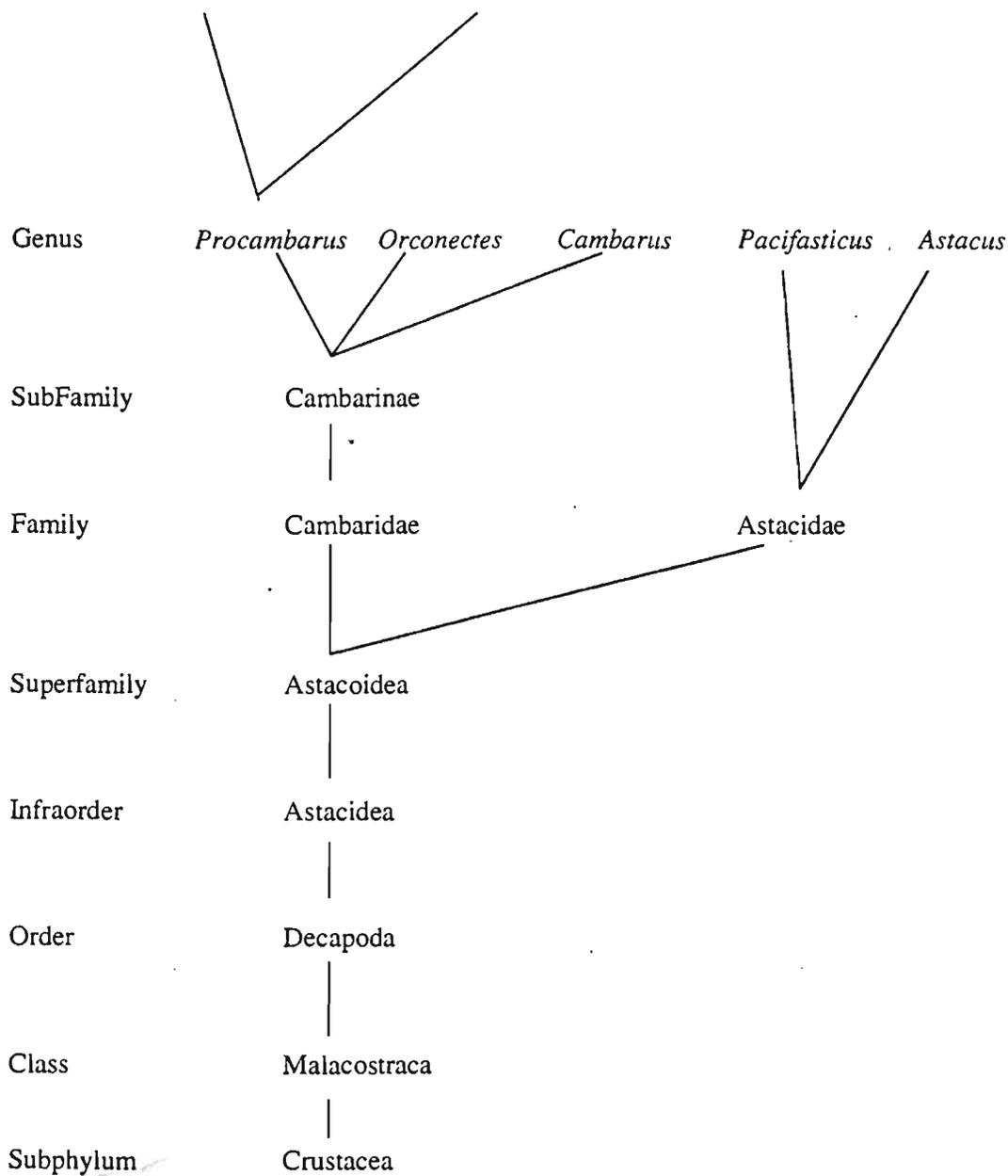
Biotic mechanisms responsible for non-overlapping distributions or distinct habitat preference include differential growth rate providing a predation refuge, behavioral modifications in the presence of predatory fish (i.e. aggressiveness and flight response), and displacing congeners from physical refuge (DiDonato and Lodge, 1993, Garvey et al., 1994, Hill and Lodge, 1994). If offered a variation in size of crayfish prey, smallmouth bass prefer to ingest small crayfish (Stein, 1977, DiDonato and Lodge, 1993). Thus, species with relatively faster growth rates reduce the window of vulnerability to predation, reaching a size refuge before their sympatric congeners. Crayfish typically alter behavior in the presence of fish in an effort to reduce predation (Hill and Lodge, 1994), yet the range of responses differs between species. In the case of *O. rusticus* replacing *O. propinquus* and *O. virilis*, *O. virilis* swam more frequently and was less aggressive towards smallmouth bass than the other two species (Garvey et al., 1994). These behavioral responses made *O. virilis* the preferred prey, though *O. virilis* was 3 mm larger in predation trials than the other two species (Garvey et al., 1994). Refuge provides a method of avoiding predation (Stein and Magnuson, 1976), however species which are forced out of refuge by congeners are more likely to be consumed by predatory fishes (DiDonato and Lodge, 1993, Garvey et al., 1994). Predation by fishes certainly contributes to the observed species distribution, and in the case of replacement of *O. virilis* by *O. rusticus*, exacerbated the effects of niche invasion.

Intraspecific competition may structure the observed population structure within habitats. Young-of-the-year are displaced by adults and occupy less desirable temperature ranges (Peck, 1985), shelters (Alberstadt et al., 1995), and stream depths (Beingesser and Copp, 1985). Within a particular age class, individual recognition and the establishment of dominance hierarchies may structure habitat use. Dominance hierarchies have been identified in *P. clarkii* (Copp, 1984), *C. shufeldtii* (Lowe, 1956), and *P. alleni* (Bovbjerg, 1956). Additionally, fishes may structure the distribution of life history stages by habitat (Stein and Magnuson, 1976). Recently molted individuals, juveniles, form I males, and ovigerous females were preferentially consumed in that

order on a uniform substrate, however, given substrate preference, predation rates dropped for the same life-history stages (Stein, 1977).

Figure 1:

Species *Procambarus fallax* *Procambarus alleni*



The naming of genus, families, subfamilies, superfamilies, etc. was lifted directly from Hobbs (Hobbs, 1988), and no effort has been made by the author to dispute this naming convention. It is presented in somewhat abbreviated form in figure 1.

How did Crayfish get to Florida?

The diversity of crayfish species currently found in Florida was probably provided by immigrating crayfish during the early Pleistocene (Hobbs 1942). Although freshwater crayfish are related to marine lobsters, the locations at which ancestral crayfish wandered into brackish water and ultimately made their residence in the accompanying streams are unknown. While it seems apparent that Astacids and Cambarids both originated from an ancestral marine stock, two theories attempt to describe the geographic locations of these forays and therefore centers of radial divergence of the Astacoidea.

An initial theory, presented by Ortman (Ortmann, 1905), states that the first crayfish stock originated in Sino-Australia during the lower Cretaceous. During the upper Cretaceous an additional stock migrated to western North America via a land bridge, ultimately residing Mexico. Subsequently, the subfamily Cambarinae was derived from the populations located in Mexico during the Lower Tertiary and spread eastward throughout North America (Ortmann, 1905). A center of radiation was established near the base of the Appalachian mountains, and this stock provided the source from which *Procambarus* originated (Ortmann, 1905).

Hobbs (Hobbs, 1988) offers an alternative explanation in which the ancestral crayfish to *Procambarus* originated in southeast North America. The holdfast of this theory is anchored in life history traits of the subfamily, Cambarinae, which are represented by a more derived condition than other subfamilies of the family Cambaridae (the reader should note that the family is Cambaridae and the subfamily is Cambarinae and the author will attempt to clarify this distinction whenever possible). All members of the Cambaridae have cyclic dimorphism in males (the presence of a reproductively active and inactive morphotype) and a seminal receptacle in females; qualities ascribed only to the Cambaridae. The sub-family, Cambarinae, is the only family in which species have established themselves in the majority of available habitats (Hobbs,

1988). For example, members of the subfamily Cambarinae have evolved to endure the entirety of their life cycle within the confines of burrows (e.g. (Fitzpatrick, 1975); (Hobbs, 1942) and caves (Hobbs, 1988). Further, the only location in which troglobitic (cave) crayfish have been found is in the Northern Florida, Alabama, Georgia, Indiana, and Mississippi indicating a hub of adaptive radiation located near this region (Hobbs, 1988). Troglobitic species represent a more evolutionarily advanced form as they are often distinct morphologically (Hobbs, 1942, Hobbs, 1988) and metabolically (Dickson and Franz, 1979) from the “standard” crayfish bodyplan. While the author is unaware of a study to address the probable locations of adaptation from marine to freshwater environments, it seems that the conclusions made by Hobbs [Hobbs, 1984 #153] are valid.

The genus *Procambarus*, which contains the greatest number of species (143) of any crayfish genus (Hobbs, 1988), inhabits a wide variety of habitats including burrows, lentic and lotic waters, and caves. While their range extends from Wisconsin throughout the Atlantic and Gulf coasts of the United States and Central America, the center of their radiation lies in southeastern United States (Hobbs, 1984). While Florida maintains populations of six genera, only *Procambarus* can be found statewide (Hobbs, 1942). Still, no single species maintains a distribution that covers the entirety of Florida (Franz and Franz, 1990).

The two species of interest to this thesis, *Procambarus alleni* and *P. fallax*, most likely immigrated to Florida from Georgia and Alabama during the early Pleistocene (Hobbs, 1942). Due to the wide distributions of *P. alleni* and *P. fallax* it is difficult to discern which pathway in particular was utilized. With the continual rise and fall of sea level throughout the Pleistocene, several opportunities were available to migrating crayfish. It is hypothesized that *P. alleni* became established prior to *P. fallax* by advancing south during an opening of the Florida Straights prior to *P. fallax* (Hobbs, 1942). Indeed, they are members of distinct subgenus within the classification of Florida crayfish presented by Franz (Franz and Franz, 1990); *P. fallax* is a

member of the subgenus *Ortmannicus* while *P. alleni* is a member of the *Leonticambarus* subgenus.

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