for

Debby, Helen, Kathy, and Lizzie

Thanks for helping me to keep it all in perspective
ACKNOWLEDGMENTS

This research would not have been possible without the support of many persons, foremost being those stalwart souls that accompanied me into the marsh and (almost) never questioned the probability of their safe return. Special thanks go to Sean Coyne, Howard Jelks, Jane Jimeian, John Chick, and the many volunteers from the Arthur R. Marshall Loxahatchee National Wildlife Refuge. Additionally, the Refuge staff provided invaluable logistical support and endless comic relief. Laboratory work and experimental studies were carried out with the assistance of Mark Bartolini, Claudia DeLeon, Angela McCreary, Paula Patterson, and Heather Soulen. I appreciate the lab space and logistical support provided by Quinton White and Jacksonville University during the final phase of the this project. Howard Jelks, John Chick, and Kim Babbitt kept the light burning via stimulating arguments and consumption of fermented grains. The light was focused by my advisory committee: Lauren Chapman, Carter Gilbert, Buzz Holling, Wiley Kitchens, and Frank Nordlie. I especially appreciate the support of my doctoral co-advisors, Carter Gilbert and Wiley Kitchens.

This research was supported by the American Museum of Natural History, St. Johns River and South Florida Water Management Districts, U.S. Fish and Wildlife Service, and U.S. Environmental Protection Agency. Boats and vehicles were provided by Wiley Kitchens and the Florida Cooperative Fish and Wildlife Research Unit. Barbara Fesler, Franklin Percival, and the students and staff of the Coop Unit made my tenure at UF successful.

Christine and the rest of my family made all of this possible. And of course, special canine thanks go to Spot, Speck, and Rover for not eating or befouling any draft of this dissertation.
TABLE OF CONTENTS

ACKNOWLEDGMENTS ...................................................................................................................... iii

LIST OF TABLES ........................................................................................................................... vi

LIST OF FIGURES ........................................................................................................................ viii

ABSTRACT ................................................................................................................................... x

CHAPTERS

1 INTRODUCTION .......................................................................................................................... 1
   Overview .......................................................................................................................................... 1
   Dissertation Layout ......................................................................................................................... 13

2 HABITAT STRUCTURE AND PLANT SPECIES COMPOSITION IN A NORTHERN EVERGLADES WETLAND MOSAIC .............................................................. 15
   Introduction .................................................................................................................................... 15
   Study Area and Methods ................................................................................................................. 16
   Results .......................................................................................................................................... 20
   Discussion ..................................................................................................................................... 22

3 HABITAT USE BY THE PRAWN PALAEMONETES PALUDOSUS AND THE CRAYFISH PROCAMBARUS ALLENI IN A NORTHERN EVERGLADES WETLAND MOSAIC ........................................................................... 32
   Introduction .................................................................................................................................... 32
   Study Area and Methods ................................................................................................................. 35
   Results .......................................................................................................................................... 40
   Discussion ..................................................................................................................................... 43
   Summary ...................................................................................................................................... 50

4 POPULATION- AND ASSEMBLAGE-LEVEL RESPONSES OF MARSH FISHES IN A NORTHERN EVERGLADES WETLAND LANDSCAPE ........................................................................................................ 57
   Introduction .................................................................................................................................... 57
   Study Area and Methods ................................................................................................................. 61
   Results .......................................................................................................................................... 67
   Discussion ..................................................................................................................................... 72
   Summary ...................................................................................................................................... 78
## LIST OF TABLES

<table>
<thead>
<tr>
<th>Table</th>
<th>Description</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>2.1</td>
<td>Mean relative abundance (%) and frequency occurrence (%) of plant types in sloughs, wet prairies, and sawgrass stands within the Refuge</td>
<td>27</td>
</tr>
<tr>
<td>2.2</td>
<td>Effects of habitat, month, habitat x month, and area (nested within month) on habitat structure and plant relative abundance in the Refuge</td>
<td>28</td>
</tr>
<tr>
<td>3.1</td>
<td>Effects of habitat, month, habitat x month, and area (nested within month) on abundance of prawn and crayfish in the Refuge</td>
<td>51</td>
</tr>
<tr>
<td>3.2</td>
<td>Partial correlations between abundance of decapod crustaceans and habitat structural features within wet prairies, sloughs, and sawgrass stands</td>
<td>52</td>
</tr>
<tr>
<td>3.3</td>
<td>Number and percentage (in parentheses) of sites classified correctly (diagonal) and incorrectly (off-diagonals) with respect to habitat type</td>
<td>52</td>
</tr>
<tr>
<td>4.1</td>
<td>Absolute (#) and relative abundance (%) of fishes collected with throw traps in the Refuge between February 1990 and July 1992</td>
<td>41</td>
</tr>
<tr>
<td>4.2</td>
<td>Effects of habitat, month, habitat x month, and area (nested within month) on the abundance of nine numerically dominant species, total fish abundance, and species richness in the Refuge</td>
<td>81</td>
</tr>
<tr>
<td>4.3</td>
<td>Number and percentage (in parentheses) of sites classified correctly (diagonal) and incorrectly (off-diagonals) with respect to habitat type</td>
<td>83</td>
</tr>
<tr>
<td>4.4</td>
<td>Results of partial correlations between species pairs after removing variation associated with the spatiotemporal sampling hierarchy (see text for details)</td>
<td>83</td>
</tr>
<tr>
<td>5.1</td>
<td>Analysis of variance testing for the effects of predator presence, habitat complexity, and their interaction on the number of crayfish surviving after five days</td>
<td>100</td>
</tr>
<tr>
<td>7.1</td>
<td>Mean density (individuals/m²) of potential predators and prey fishes collected from sloughs (including alligator holes), wet prairies, and sawgrass stands during non-drought periods (i.e., May 1992 excluded)</td>
<td>128</td>
</tr>
<tr>
<td>7.2</td>
<td>Analysis of variance results testing for effects of block, habitat complexity, predator type, and their interactions on arcsin-transformed survivorship of flagfish (top) and mosquitofish (bottom) at Day 2 of the experiment</td>
<td>129</td>
</tr>
</tbody>
</table>
7.3 Analysis of variance results testing for effects of block, habitat complexity, predator type, and their interactions on arcsin-transformed survivorship of flagfish (top) and mosquitofish (bottom) at Day 7 of the experiment ..............130
## LIST OF FIGURES

<table>
<thead>
<tr>
<th>Figure</th>
<th>Description</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>2.1</td>
<td>Map of lower Florida showing existing management compartments. The shaded area is the Arthur R. Marshall Loxahatchee National Wildlife Refuge (Water Conservation Area 1)</td>
<td>29</td>
</tr>
<tr>
<td>2.2</td>
<td>Mean (+ 1 SE) water depth, canopy height, and dry plant biomass in sloughs, wet prairies, and sawgrass stands of the Refuge</td>
<td>30</td>
</tr>
<tr>
<td>2.3</td>
<td>Seasonal variation in mean (± 1 SE) water depth in sloughs, wet prairies, and sawgrass stands of the Refuge</td>
<td>31</td>
</tr>
<tr>
<td>3.1</td>
<td>Mean (+ 1 SE) number of prawn (top) and crayfish (bottom) per square meter of wet prairie, slough, and sawgrass habitats comprising the Refuge</td>
<td>53</td>
</tr>
<tr>
<td>3.2</td>
<td>Seasonal variation in mean (± 1SE) number of prawn (top) and crayfish (bottom) collected per meter square of wet prairie, slough, and sawgrass habitats comprising the Refuge</td>
<td>54</td>
</tr>
<tr>
<td>3.3</td>
<td>Seasonal variation in mean water depth within wet prairie, slough, and sawgrass habitats comprising the Refuge</td>
<td>55</td>
</tr>
<tr>
<td>3.4</td>
<td>Mean number of prawn (top) and crayfish (bottom) collected per meter square of slough habitat before, during, and after the marsh drawdown of May 1992</td>
<td>56</td>
</tr>
<tr>
<td>4.1</td>
<td>Mean (+ 1 SE) number of fishes per square meter of wet prairie, slough, and sawgrass habitats comprising the Refuge</td>
<td>84</td>
</tr>
<tr>
<td>4.2</td>
<td>Seasonal variation in mean (± 1 SE) number of fishes per square meter of wet prairie, slough, and sawgrass habitats comprising the Refuge</td>
<td>85</td>
</tr>
<tr>
<td>4.3</td>
<td>Mean number of fishes collected per meter square of slough habitat before, during, and after the marsh drawdown of May 1992</td>
<td>86</td>
</tr>
<tr>
<td>4.4</td>
<td>Dominance-diversity curves for different Refuge habitats (top), and seasonal variation in mean (± 1 SE) number of species per collection site (bottom)</td>
<td>87</td>
</tr>
<tr>
<td>4.5</td>
<td>Location (i.e., multivariate least-squares means) of nine dominant fishes in community space as revealed by discriminant function analysis</td>
<td>88</td>
</tr>
<tr>
<td>4.6</td>
<td>Temporal variation in water depth, dry plant biomass, canopy height, dissolved oxygen, conductivity, and total fish abundance within four Refuge habitats</td>
<td>89</td>
</tr>
</tbody>
</table>
5.1 Proportion of crayfish (means + 1 SE) occupying vegetated and open sand portions of behavioral tanks during the day and night. ................................. 101

5.2 Numbers of crayfish (means + 1 SE) surviving after five days as a function of predator presence (open bars) or absence (closed bars) and habitat complexity. ................................. 102

6.1 Mean (+ 1 SE) survivorship of the flagfish *Jordanella floridanae* in the presence and absence of naiads of the predatory insect *Anax junius* ......................... 109

7.1 Mean (+ 1 SE) survivorship of flagfish (top) and mosquitofish (bottom) on Day 2 in relation to predator type and habitat complexity ......................... 131

7.2 Mean (+ 1 SE) survivorship of flagfish (top) and mosquitofish (bottom) on Day 7 in relation to predator type and habitat complexity ......................... 132

7.3 Mean (+ 1 SE) selectivity for mosquitofish on Day 2 (top) and Day 7 (bottom) of the experiment ................................................................. 133

7.3 Diurnal variation in dissolved oxygen levels in sloughs, wet prairies, and sawgrass stands in the Refuge ................................................................. 134
Abstract of Dissertation Presented to the Graduate School of the University of Florida in Partial Fulfillment of the Requirements for the Degree Doctor of Philosophy

SPATIAL ECOLOGY OF DECAPODS AND FISHES IN A NORTHERN EVERGLADES WETLAND MOSAIC

By

Carroll Frank Jordan, Jr.

December, 1996

Chairman: Carter Gilbert
Major Department: Zoology

I carried out descriptive field studies and laboratory experiments to examine the spatial ecology of decapod crustaceans and fishes within the mosaic of sloughs, wet prairies, and sawgrass stands comprising the Arthur R. Marshall Loxahatchee Wildlife Refuge in the northern Everglades. My primary objective was to test the premise that the northern Everglades landscape is organized and maintained by a hierarchy of processes that operate across a range of spatial and temporal scales. I found considerable support for this premise and conclude that the abundance of decapods and fishes at any given location within the northern Everglades landscape is the product of a hierarchy of processes operating across local (i.e., among adjacent habitats), regional (i.e., among widely-separated locations), and seasonal (i.e., among sampling months) scales.

I characterized the habitat mosaic and quantified patterns of habitat use of decapods and fishes across the Refuge landscape. I found persistent local differences in plant species composition and habitat structure among habitats, whereas regional differences were less pronounced. In contrast, regional differences in edaphic-hydrologic conditions generated
considerable variability in decapod and fish abundance. Local factors were also important to decapods and fishes, because most taxa were distributed among habitats nonrandomly. Patterns of habitat use were influenced strongly by seasonal variation in water levels, especially during a severe marsh drawdown in May 1992. Finally, there was evidence that decapod and fish assemblage structure varied among habitats.

My experiments focused on the role that habitat complexity plays in mediating predator-prey coexistence, and on the relative importance of predatory arthropods (i.e., aquatic insects, crayfish) and vertebrates (i.e., largemouth bass) to small prey fishes along a habitat gradient. Crayfish appeared to affect habitat use and survival of prawns. Increased habitat complexity inhibited vertebrate foraging efficiency, but facilitated arthropod foraging efficiency. Ubiquitous arthropods may play an important role in regulating populations of small fishes in marsh systems such as the northern Everglades. In conclusion, I propose that a general model of assemblage regulation in wetland systems should not be based solely on hydrology, but should also incorporate the direct and indirect effects of predators and habitat complexity.
CHAPTER 1  
INTRODUCTION

Overview

Population and community ecologists invest considerable resources into determining the distribution and abundance of vagile organisms within landscapes, usually to test specific hypotheses about their spatial ecology (Wiens 1989a). For example, comparisons are made of the abundance of fishes in beaver ponds and adjacent streams (Schlosser 1995), dung beetles in clear-cut and virgin stands of forest (Klein 1989), or passerine birds within different regions of a shrubsteppe landscape (Wiens et al. 1987). The proximate goal of this often laborious endeavor is to discern underlying spatial patterns in how organisms are distributed. Ultimately, however, ecologists use their knowledge of an organism’s spatial ecology to understand how a variety of biotic and abiotic processes interact to structure populations and communities (Holt 1987, Wiens 1989b, 1989c, Rosenzweig 1991). That is, ecologists work to identify the ecological and evolutionary processes responsible for variation observed in an organism’s distribution and abundance at a variety of spatial scales (Peters 1991), including within habitats (i.e., microhabitat scale), among adjacent habitats (i.e., local scale), and among widely-separated locations (i.e., landscape scale). The relative importance of organizing processes is likely to vary across the scales of this spatial hierarchy (Allen and Starr 1982, O’Neill et al. 1986, Wiens 1989c).

Discerning spatial patterns in population abundance and identifying the processes responsible for these patterns has proved to be a daunting challenge for ecologists studying the decapod crustaceans and fishes of the seasonally dynamic Everglades. These organisms encounter a mosaic of sloughs and alligator holes, wet prairies, and sawgrass stands that differ with respect to plant species composition, habitat complexity, and
hydroperiod (Loveless 1959). Additionally, decapods and fishes are exposed to gradients in hydroperiod, frequency and intensity of fire, and nutrient enrichment that extend across the Everglades landscape (Richardson et al. 1990, Davis 1994, Davis et al. 1994, Gunderson 1994). Finally, seasonal cycles of flooding and drought lead to expansion and contraction of inundated marsh surface, which may force aquatic macrofauna to periodically move between shallower and deeper habitats.

Previous studies of decapods and fishes living in the freshwater marshes of the Everglades have not quantified patterns of habitat use, how habitat use varies over a large spatial extent, or how habitat use changes in response to seasonal expansion and contraction of the marsh surface. Rather, previous research has focused almost exclusively on long-term changes in macrofaunal abundance and community structure, with special reference to the effects of altered hydrologic conditions (Kushlan 1976, 1980, Kushlan and Kushlan 1979, 1980, Loftus and Eklund 1994). Furthermore, most of this research was restricted to the emergent wet prairies of the southern Everglades. Finally, no published research has directly (i.e., experimentally) examined the mechanisms (e.g., predation) responsible for the distribution and abundance of decapods and fishes. My doctoral research was undertaken to address some of these gaps in our knowledge of the Everglades ecosystem. Specifically, I wanted to characterize decapod and fish communities of the northern Everglades, to determine patterns of habitat use over a large spatial scale, and to determine if these patterns were affected by seasonal changes in hydrologic conditions. Additionally, I wanted to examine how predation and habitat complexity could interact with hydroperiod to affect the distribution and abundance of decapods and fishes within a northern Everglades habitat mosaic. In this chapter, I selectively review literature that stimulated my research interests and shaped the design of my field and experimental studies. I then outline the layout of this dissertation and preview the individual research topics comprising each successive chapter.
The Aquatic Macrofauna

The Everglades supports a variety of aquatic macrofauna, and many of these organisms play important roles in marsh food webs by transforming primary production and detritus into forms usable by higher trophic groups such as wading birds, snail kites, and alligators. From a numerical and functional perspective, decapod crustaceans and small (*<100* mm standard length) fishes are the most important members of the aquatic macrofauna (Gunderson and Loftus 1993, Robertson and Frederick 1994) and were therefore selected for study. Other important taxa include the apple snail (*Pomacea paludosa*), fishing spider (*Dolomedes triton*), larval anurans (*Pseudacris gryllus* and *Rana grylio*), creeping water bugs (*Pellocoris femoratus*), and larval dragonflies of the families Aeshnidae and Libellulidae (Kushlan 1975, Gunderson and Loftus 1993, Jordan et al. 1994, Rader 1994).

The prawn *Palaemonetes paludosus* and the crayfish *Procambarus alleni* are the only decapod crustaceans inhabiting the freshwater marshes of the Everglades. *Palaemonetes paludosus* is found in fresh waters throughout Atlantic and Gulf Coast states, whereas *Procambarus alleni* is endemic to southern Florida. These species occupy a diversity of aquatic habitats and they feed primarily on detritus and microalgae (Gunderson and Loftus 1993). The numerically important fishes of the northern Everglades belong to the families Poeciliidae (mosquitofish: *Gambusia holbrooki*; least killifish: *Heterandria formosa*; sailfin molly: *Poecilia latipinna*), Fundulidae (golden topminnow: *Fundulus chrysotus*; bluefin killifish: *Lucania goodei*), Cyprinodontidae (flagfish: *Jordanella floridae*), Elassomatidae (Everglades pygmy sunfish: *Elassoma evergladei*), and Centrarchidae (bluespotted sunfish: *Enneacanthus gloriosus*; sunfishes: *Lepomis* spp.). Important predatory fishes include Florida gar (*Lepisosteus platyrhincus*), bowfin (*Amia calva*), warmouth (*Chaenobryttus gulosus*), and largemouth bass (*Micropterus salmoides floridanus*). Although several predatory species of cichlid fishes have become established
in the network of drainage canals dissecting the south Florida landscape, they are rarely encountered in interior marsh habitats (Loftus and Kushlan 1987, Wiechman 1987).

The Everglades ichthyofauna is not particularly diverse and contains no endemic species (Loftus and Kushlan 1987); rather, most species are represented throughout Florida and are derived from temperate freshwater families. However, there is some morphologic and genetic evidence for population subdivision (Johnson 1975, Gilbert 1987, Trexler 1988; F. Jordan, unpublished protein electrophoresis data). For example, male mosquitofish from a northern Everglades population mature earlier and at a smaller size than males from a population living in North Carolina (D. Campton and F. Jordan, unpublished quantitative genetic data). In general, fishes that are successful in the Everglades share many life history traits characteristic of opportunistic species, including tolerance of adverse physical conditions (e.g., high temperatures, low dissolved oxygen levels, drought), short life spans, young age at first reproduction, and nearly continuous reproduction (Loftus and Kushlan 1987). From a functional perspective, most small fishes of the Everglades are omnivorous, with a few strict herbivores (e.g., sailfin mollies) and carnivores (e.g., pygmy sunfish).

As mentioned previously, there are considerable gaps in our understanding of the spatial ecology of decapods and fishes within the Everglades. For example, how does macrofaunal abundance vary across the landscape, among adjacent habitats, and within habitats? Furthermore, how does seasonal variation in hydrology affect patterns of habitat use? Finally, what abiotic and biotic processes determine the distribution and abundance of Everglades macrofauna?

**Distribution across a Landscape**

Freshwater marshes of the historic Everglades stretched continuously from the southern shores of Lake Okeechobee to the mangrove forests of northern Florida Bay. Vast expanses (≈50%) of these marshes have been drained for agriculture and the remaining wetland landscape has been partitioned into compartments that are presently
managed for flood control, water storage, and wildlife management and conservation (Light and Dineen 1994). The northern remnant of the historic Everglades is managed jointly by the U.S. Fish and Wildlife Service and the South Florida Water Management District as the Arthur R. Marshall Loxahatchee National Wildlife Refuge (hereafter the Refuge) and Water Conservation Area 1, respectively. Hydrologic, nutrient enrichment, and other physicochemical gradients occur across this marsh landscape (Richardson et al. 1990), and these gradients strongly influence the structure of periphyton and macrophyte communities (Richardson et al. 1990, Browder et al. 1994, Davis 1994, Newman et al. 1996). Increased nutrient loading and prolonged hydroperiods have also resulted in greatly elevated abundance of fishes within the virtual monoculture of cattails that has developed in the southern end of the Refuge (see Chapter 4). It is unknown how aquatic macrofauna have responded within interior marshes, which have experienced little to modest nutrient loading and alteration of hydroperiod. There is abundant evidence that aquatic macrofauna are sensitive to landscape-level variation in biotic and abiotic conditions (e.g., Tonn and Magnuson 1982, Tonn et al. 1990, Schlosser 1991, 1995). For example, the intensity of competition and predation varies among locations within a landscape, resulting in differences in growth and survival of aquatic macrofauna (Smith 1983, Petranka 1984, Travis and Trexler 1986, Fraser et al. 1995).

How can nutrient and hydrologic gradients affect the abundance of aquatic macrofauna across the Refuge landscape? First, the historic Everglades was a very low nutrient (oligotrophic) system (Davis 1994), and bottom-up control of food web structure was likely the rule (Loftus et al. 1986, Gunderson and Loftus 1993, Browder et al. 1994). Increases in nutrient loading likely cascade through the marsh food web and result in increased primary and secondary productivity (Goodyear et al. 1972, Melack 1976, Kautz 1980, Lancaster and Drenner 1990, Diana et al. 1991), especially near canals (Richardson et al. 1990, Browder et al. 1994). Local increases in productivity can affect much of the Refuge landscape because many fishes (and decapods to a lesser degree) are capable of
dispersing widely, thereby generating source-sink demographic structure (Pulliam 1988). Nutrient enrichment can also affect the structure of aquatic macrofaunal communities. For example, species that can exploit increased production of blue-green algae may have an advantage over species that cannot efficiently process this food source (Browder et al. 1994).

Altered hydrologic conditions across the Refuge landscape directly and indirectly affect aquatic macrofauna. Prolonged hydroperiods (i.e., few droughts) result in enhanced survival and production of larger, drought-sensitive species such as Florida gar, bowfin, and largemouth bass (Kushlan 1976, 1980, Wiechman 1987, Loftus and Eklund 1994). Therefore, larger predatory fishes are likely to be more abundant in deeper portions of the Refuge landscape, especially near to perimeter canals. Contrary to the earlier conclusions of Kushlan (1976, 1980) and Kushlan and Kushlan (1979, 1980), it also appears that decapods and small fishes are either positively influenced or unaffected by prolonged hydroperiod (Loftus et al. 1986, Loftus and Eklund 1994). Long-hydroperiod marshes accumulate more detritus (Loftus et al. 1990), which results in increased food resources (i.e., detritus and detritivorous invertebrates) for fishes and decapods (Loftus and Kushlan 1987, Gunderson and Loftus 1993). Perhaps more importantly, and as noted by Loftus and Eklund (1994), “Fishes do best where there is water!” It now appears that much of the Everglades landscape experienced longer hydroperiods and less frequent marsh drawdowns (Walters et al. 1992, Fennema et al. 1994) than recent management policies had suggested were necessary for normal ecosystem function (e.g., Kushlan 1987). More research is needed to determine how aquatic macrofaunal abundance varies among locations within the Refuge landscape, and to determine the relative importance of landscape-level processes with respect to the distribution of decapods and fishes.
Distribution among Habitats

The Everglades landscape presents vagile decapods and fishes with a mosaic of habitats that differ with respect to habitat structure, hydroperiod (i.e., duration of inundation), and plant species composition. This habitat mosaic provides a wide spectrum of opportunities and risks for decapods and fishes because each habitat type will have a characteristic array of physical conditions, food resources, parasites, predators, and competitors (Wiens 1976, Jordan et al. 1996a, 1996b). Macrofaunal species will respond differently to these opportunities and risks (Gleason 1926, Wiens 1976, Holling 1992), resulting in differences in habitat-specific rates of production, survival, and movement (emigration and immigration). In other words, species-specific patterns of habitat use can profoundly affect population demographics and community structure within heterogeneous landscapes (Holt 1987, Pulliam 1988, Danielson 1991, Pulliam and Danielson 1991, Rosenzweig 1991, Dunning et al. 1995, Holt et al. 1995), including the Everglades (Smith and Vrieze 1979, DeAngelis and White 1994, Jordan et al. 1994).

The mosaic of sloughs and alligator holes, wet prairies, and sawgrass stands comprising the northern Everglades is used by most of the decapods and fishes that are found in the southern Everglades (Dineen 1974, 1984, Loftus and Kushlan 1987, Wiechman 1987). Previous studies indicate that many of these (and other) aquatic macrofauna are not distributed randomly among available habitat types within the freshwater marshes of southern Florida (Jordan et al. 1994, 1996a, In review a, b, Chick and McIvor 1995, Jordan and Babbitt In review a, b). For example, crayfish were more abundant in densely-vegetated wet prairies than in structurally-simple sloughs of the Blue Cypress Marsh Conservation Area (Jordan et al. 1996a), which is a portion of the St. Johns River upper basin that resembles the Everglades with respect to its plant communities (Lowe 1986). In contrast, prawn, mosquitofish, least killifish, and bluefin killifish tended to be more abundant in sloughs than in wet prairies within the Blue Cypress Marsh Conservation Area (Jordan et al. In review a, b).
Patterns of habitat use by decapods and fishes are primarily driven by local processes, such as differences in the risk of predation and availability of prey among adjacent habitats (reviewed by Orth et al. 1984, Gotceitas and Colgan 1989, Heck and Crowder 1991). Macrofaunal abundance is typically highest in the most densely vegetated habitat available (e.g., Rozas and Odum 1987, Killgore et al. 1989, Savino and Stein 1989, Ferrell and Bell 1991, Sogard and Able 1991, Jordan et al. 1996b), likely because these habitats provide the greatest amount of cover from predators and the greatest amount of prey. Water depth is also an important component of habit use decisions, with prey exposed to avian predators preferring deeper habitats (e.g., Power 1984, Harvey and Stewart 1991) and prey exposed to aquatic predators often avoiding deeper habitats (e.g., McIvor and Odum 1988, DeVries 1990). Everglades macrofauna may find themselves between a “rock and a hard place” since they are exposed to piscine predators in deeper sloughs and alligator holes, whereas they encounter avian and arthropod predators in the shallower wet prairies and sawgrass stands. Although it has been postulated that predatory fishes depress the abundance of Everglades macrofauna (Kushlan 1976, 1980, Kushlan and Kushlan 1979, 1980), there is no experimental evidence to support a model of top-down control. More research is needed to determine how aquatic macrofaunal abundance varies among adjacent habitats and to determine the relative importance of local processes (e.g., predation, oxygen levels) with respect to the distribution of decapods and fishes.

Distribution within Habitats

Differences in habitat use can vary across landscapes, especially when these landscapes have been heavily modified. For example, the relative importance of slough and wet prairie habitats to decapods and fishes differs among the marsh compartments comprising the upper basin of the St. Johns River (Jordan and Babbitt In review a, b). One reason that habitat use varies across a landscape is that microhabitat structure differs from location to location, and aquatic macrofauna respond to these differences. Plant community
composition, plant biomass, canopy structure, and water depth vary not only among habitats, but also within habitats (i.e., at the microhabitat level). Fishes and decapods tend to orient towards dense patches of vegetation within a habitat, and macrofaunal abundance is strongly correlated with microhabitat complexity (Stoner 1980, 1983, Bell and Westoby 1986a, 1986b, 1986c, Gotceitas and Colgan 1987, Worthington and Westoby 1991). The same concerns (i.e., predation risk, prey availability) that motivate preferences for different habitat types also motivate preferences for location within a single habitat type. That is, prey abundance generally increases with increasing microhabitat complexity (Stoner 1980, 1983, Savino et al. 1992), whereas predator foraging efficiency generally decreases with increasing microhabitat complexity (Crowder and Cooper 1979, 1982, Stoner 1983, Savino and Stein 1982, Tomcko et al. 1984, Schramm and Zale 1985, Diehl 1988, Gotceitas and Colgan 1989, Gotceitas 1990). Jordan et al. (1996a) found that crayfish abundance was positively correlated with plant biomass in wet prairies and negatively correlated with water depth in sloughs of the Blue Cypress Marsh Conservation Area. They postulated that observed patterns of microhabitat use reflected behavioral preferences for “safer” areas that provided more cover or reduced encounter rates with predatory fishes. More research is needed to determine how aquatic macrofaunal abundance varies within habitats and to determine the relative importance of microhabitat processes with respect to the distribution of decapods and fishes.

**Seasonal and Long-Term Changes in Distribution**

Seasonal and annual variation in hydrologic conditions is the dominant driving force in the Everglades ecosystem (DeAngelis and White 1994). Accordingly, most studies of aquatic macrofauna have focused on the effects of hydroperiod (Kushlan 1976, 1980, Kushlan and Kushlan 1979, 1980, Loftus and Eklund 1994). Prawn abundance changes strongly in response to seasonal changes in water levels, indicating that this species colonizes newly inundated marsh surface and then retreats into deeper sloughs and alligator
holes as water levels drop (Kushlan and Kushlan 1980, Jordan et al. In review a). In contrast, crayfish abundance is less affected by seasonal changes in hydrology, likely because this species excavates burrows during drought periods (Kushlan and Kushlan 1979, Jordan et al. 1996a). Everglades fishes are incapable of burrowing and therefore move into sloughs and alligator holes during drought periods (Dineen 1974, 1984, Kushlan 1974a, 1974b, 1976, 1980, Loftus and Kushlan 1987). Therefore, responses to seasonal variation in hydrologic conditions are species specific. Moreover, it appears that the relative importance of habitats can vary with seasonal and annual fluctuations of water levels. Although sloughs and alligator holes comprise a relatively small amount of marsh area, they can be critical to the continued survival of most aquatic macrofauna during droughts in the Everglades (Craighead 1968, Kushlan 1974a, 1974b). More research is needed to determine how the relative importance of habitats varies in response to seasonal changes in water levels.

Models of pre-drainage hydrology indicate that much of the historic Everglades experienced longer hydroperiods and seasonal droughts were rare (Walters et al. 1992, Fennema et al. 1994). Therefore, hydroperiod did not likely have strong direct effects on the success of aquatic macrofauna. As mentioned previously, it appears that protracted hydroperiods positively influence both prey and predator fish populations (Loftus and Eklund 1994). Given this relationship, why did earlier studies find that the abundance of decapods and small-sized fishes decreased with protracted hydroperiod (Kushlan 1976, 1980, Kushlan and Kushlan 1979, 1980)? The pull-trap method that Kushlan and his colleagues used to collect aquatic macrofauna modified the habitat being sampled, such that it changed from a structurally-complex wet prairie into a structurally-simple slough or alligator hole (Loftus and Eklund 1994). Because predatory fishes tend to congregate in deeper sloughs and alligator holes (Dineen 1974, 1984, Loftus and Kushlan 1987), the shift towards a predator-dominated community that Kushlan (1976, 1980) described may actually reflect a sorting of species into their preferred habitats (Loftus and Eklund 1994).
Both predator and prey populations grow and certainly interact during periods of prolonged inundation (Loftus and Eklund 1994), which typified pre-drainage hydrologic conditions. However, decapods and small fishes likely persist with their predators by moving into structurally-complex habitats, such as wet prairies and sawgrass stands, where predatory fishes are less abundant (Dineen 1974, 1984, Loftus and Kushlan 1987) and cannot forage efficiently (Heck and Crowder 1991). On the other hand, small fishes may increase their exposure to a myriad of predatory arthropods and wading birds by moving into wet prairies and sawgrass stands (Jordan et al. 1994, 1996a, Rader 1994). Predator community composition varies predictably along a depth-structure gradient in aquatic systems, with arthropods predominating in shallower, structurally-complex habitats, and predatory fishes predominating in deeper, structurally-simple habitats (Werner and McPeek 1994). It is unclear whether arthropods can be significant predators of marsh fishes. Furthermore, it is unclear how increased habitat complexity affects the foraging efficiency of arthropod predators feeding on vagile prey (Heck and Crowder 1991). More research is needed to determine how hydrology, habitat complexity, and predation interact to structure populations and communities of aquatic macrofauna in the Everglades.

**Sampling Aquatic Macrofauna in a Seasonally Variable Landscape**

In the preceding sections, I discussed how aquatic macrofauna of the Everglades may be affected by a variety of biotic and abiotic factors that operate at a variety of spatial (and temporal) scales (DeAngelis and White 1994, Holling et al. 1994). The primary challenge of my field research was to devise a sampling program that could provide both narrow resolution (several meters) and broad extent (several kilometers). In other words, I wanted to collect field data that could be used to quantify the distribution and abundance of decapods and fishes across a range of spatial scales. In contrast, most researchers tend to focus on patterns and processes observable at a single level of the spatial hierarchy. Unfortunately, studies performed at a single spatial scale may misjudge the relative
importance of local or landscape processes, or, perhaps more insidiously, miss important interactions between patterns and processes operating at different scales (O’Neill et al. 1986, Wiens 1989c).

Given the above concerns and the logistical constraints typically confronting field ecologists, what is the most efficient approach to studying the abundance and distribution of aquatic macrofauna within the habitat mosaic comprising the Refuge? There probably is not a “right” or “best” way to incorporate multiple spatial scales into a single ecological study (Andrew and Mapstone 1987). However, ecologists interested in research across spatial scales would benefit greatly by incorporating the population geneticist’s hierarchical sampling perspective into the design of their own field studies. The population geneticist first reviews the known distribution of an organism, and then incorporates spatial scales of interest into a hierarchical sampling program (Hartl and Clark 1989). For example, a population geneticist studying a stream fish would quantify genetic variation among individuals within local sites, among sites within streams, among streams within drainages, and among drainages (e.g., Campton and Utter 1987). This hierarchy of variation would then be analyzed using analysis of variance to test the null hypothesis of no population genetic structure (Wright 1978). Deviations from this null model at any level of the sampling hierarchy (along with the amount of variance explained) indicates the scale(s) at which important processes (e.g., genetic drift, assortative mating, behavioral or geographical isolation) are occurring (Hartl and Clark 1989).

The same hierarchical sampling design and statistical techniques can be used to quantify variation in population abundance and test hypotheses about the spatial ecology of different study organisms. Perhaps more importantly, the amount of variation explained at each level of a sampling hierarchy can be used as a heuristic measure of how important the processes operating at each spatial scale are in determining the abundance and distribution of these organisms. Of course, not all questions concerning spatial ecology will have conveniently defined scales to design studies around. Individual researchers need to
understand the natural history of their study organisms and be familiar with the fundamentals of sampling design in order to design ecologically relevant and statistically powerful studies (Hairston 1989). Fortunately, the natural heterogeneity of landscapes can be used to design studies (Dutilleul 1993). Selection of widely-spaced sampling locations will incorporate landscape-scale effects, and selection of adjacent habitats within each sampling location will incorporate local scale effects. Microhabitat scale variation can be assessed by collecting replicate samples from within each habitat and sampling location combination. Finally, seasonal and annual effects can be assessed by repeated sampling through seasons and successive years. I incorporated this hierarchical approach into my field studies so that I could characterize the aquatic macrofauna of the Refuge at several spatial scales. I then performed experiments to examine the relationship between habitat complexity and predation under constant water levels. I focused on predation as an organizing process because it can affect the distribution and abundance of decapods and fishes across the range of spatial scales that I examined with my field studies.

**Dissertation Layout**

The goal of my field research was to characterize seasonal variation in the spatial ecology of decapods and fishes within the Refuge. I described the Refuge and the mosaic of sloughs, wet prairies, and sawgrass stands to determine whether differences in water depth, canopy structure, plant biomass, and plant community structure were persistent over a large spatial scale (Chapter 2). Decapods (Chapter 3) and fishes (Chapter 4) were sampled to determine how population abundance and community structure varied within habitats, among habitats (sloughs, wet prairies, sawgrass stands), and among locations within this wetland landscape.

The goal of my experimental research was to determine how habitat complexity affected survival of aquatic macrofauna exposed to different arthropod and vertebrate predators under constant water levels. I first examined the importance of increasing habitat...
complexity on survival of crayfish exposed to predatory largemouth bass (Chapter 5). I then determined how increased habitat complexity affected survival of flagfish exposed to predatory dragonfly naiads (Chapter 6). Finally, I determined how habitat complexity affected the survival of flagfish and mosquitofish exposed to either arthropod (crayfish, dragonfly naiads) or vertebrate (largemouth bass) predators (Chapter 7). These experiments also indirectly examined the potential significance of arthropod predators (Chapters 5 and 7), the influence of ambient dissolved oxygen levels on the survival of aquatic macrofauna and some of their predators (Chapters 6 and 7), and the importance of size-structured interactions on coexistence of juvenile and adult decapods (Chapter 6). Chapters 2-7 are summarized and integrated to demonstrate how hydrology, habitat complexity, and predation interact to structure macrofaunal communities within wetland landscapes such as the Everglades (Chapter 8).
CHAPTER 2
HABITAT STRUCTURE AND PLANT SPECIES COMPOSITION
IN A NORTHERN EVERGLADES WETLAND MOSAIC

Introduction

The historic Everglades ecosystem stretched from the southern end of Lake Okeechobee to the mangrove forests of Florida Bay and encompassed about 1 million ha of freshwater wetland habitat. Construction of canals and levees to accommodate agriculture and urbanization resulted in a 50% areal reduction in the Everglades landscape during the last century (Kushlan 1990). Today, the Everglades ecosystem is a highly compartmentalized landscape that has suffered landscape fragmentation, alteration of historical hydrologic conditions, and nutrient enrichment. Although anthropogenic changes are pervasive, much of the remaining Everglades ecosystem is relatively intact and retains the mosaic nature of the historic marsh landscape. Sloughs (including alligator holes), emergent wet prairies, sawgrass stands, and tree islands are interspersed with one another over much of the Everglades landscape and provide a diversity of aquatic habitats (Loveless 1959, Gunderson 1994).

Loveless (1959) provided a qualitative analysis of the structure and plant species composition of these habitats within the central Everglades (Water Conservation Areas 1 and 2), along with an elegant description of the natural history of the Everglades ecosystem in general. The structure and plant species composition of aquatic habitats comprising the southern Everglades (Everglades National Park) have also been well studied (see review in Gunderson 1994). However, little effort has focused on characterizing the aquatic habitat mosaic of the northern Everglades. Differences in hydrologic conditions, fire and nutrient regimes, and substrate conditions have led to the generation of a habitat mosaic that is
distinct from other management compartments within the Everglades landscape (Goodrick 1974, Richardson et al. 1990, Pope 1991).

This study examined the structure and plant species composition of the dominant aquatic habitats comprising the Arthur R. Marshall Loxahatchee National Wildlife Refuge, which forms the northern remnant of the Everglades ecosystem. Total plant biomass, canopy height, water depth, and the relative abundance of plant species in adjacent sloughs (including alligator holes), wet prairies, and sawgrass stands were compared over a 30-month period. This study complements previous studies of plant communities in the northern Everglades that focused on 1) ordination and delineation of habitat classes (Pope 1991) and 2) analysis of patterns of habitat degradation and loss (Richardson et al. 1990). Where these earlier studies examined habitat variation at the landscape level using spatially extensive data, the present study examined habitat variation on both a small (i.e., among habitats within an area) and large scale (i.e., among areas across the landscape) using a combination of spatially extensive and intensive data. Moreover, this study focused on \textit{a priori}-defined habitats that are important to aquatic macrofauna (e.g., Loftus and Kushlan 1987, Gunderson and Loftus 1993, Jordan et al. 1994, 1996a) to provide the basis for a better understanding of the functional relationships between these organisms and their habitats.

Study Area and Methods

Study Area

The Arthur R. Marshall Loxahatchee National Wildlife Refuge (hereafter the Refuge) is a 57,234-hectare impounded marsh system that is operated as Water Conservation Area 1 by the South Florida Water Management District (see Figure 2.1). As part of its role in the vast south Florida water routing system, the Refuge is encircled by a deep-water canal and dike system that drains an approximately equal area of the Everglades Agricultural Area (Richardson et al. 1990, Fennema et al. 1994). Unfortunately, water
derived from the Everglades Agricultural Area is enriched with phosphorus, nitrogen, and other contaminants that profoundly affect Refuge habitats near pumping stations and perimeter canals. This water is not distributed evenly across the Refuge landscape because topographic variation in the underlying peat results in a gradient of increasing depth and longer hydroperiod along the north-south axis of the Refuge (and, to a lesser degree, from the interior marshes to peripheral canals). Furthermore, the perimeter canal and dike system has intensified this hydrologic gradient through increased drainage in the northern end and increased “ponding” of water behind dikes in the southern end of the Refuge.

Nutrient enrichment and alterations in hydrology have resulted in profound changes to the habitat mosaic comprising the Refuge (Richardson et al. 1990, Davis 1994, Davis et al. 1994). The pre-drainage Refuge landscape was comprised of emergent wet prairies, sawgrass stands, sloughs (including alligator holes), and elongate tree islands overlying a deep bed of peat. Recent studies, including spatially extensive ground surveys and spectral analysis of satellite imagery, have resulted in the delineation of 18 habitat classes (Richardson et al. 1990, Pope 1991). This increased resolution of habitats does not simply reflect improvements in study design, censusing techniques, and statistical ordination procedures. Rather, new classes such as cattail, open water, and willow tree islands have become predominant in disturbed areas that are near canals and are therefore subject to increased nutrient loading and protracted hydroperiods. In comparison, interior marshes have seen an increase in sawgrass (Davis et al. 1994) and red bay-dahoon holly-wax myrtle tree islands (Richardson et al. 1990), likely due to altered hydrology. It is unknown how structure (e.g., plant biomass, canopy height) and plant species composition in sloughs (including alligator holes), wet prairies, and sawgrass stands have responded to alterations in nutrient loading and modified hydroperiod.
Sampling Methods

Water depth, canopy height, plant biomass, and plant species composition were measured in conjunction with a study of the aquatic macrofauna of the Refuge (Jordan et al. 1994, Chapters 3 and 4). An aluminum throw trap (100 x 100 x 75 cm; see Chick et al. 1992 for details) was deployed into the desired habitat and pressed firmly into the substrate. Water depth (peat surface to water surface) and canopy height (peat surface to tip of stems) were then measured to the nearest centimeter at three points within the throw trap and these values were averaged. Living plants were identified and their relative coverage was visually estimated in 5% increments. Periodically (17 of 24 sampling events), above-ground vegetation (living and dead) was removed from within the trap, returned to the laboratory for drying (60°C), and weighed to the nearest gram to determine plant biomass.

Habitat characterizations were performed approximately monthly between February 1990 and July 1992 (24 sampling events). Additionally, plant species composition data were collected between October 1990 and July 1992 (17 sampling events). During each sampling period, six areas (statistical blocks) were randomly selected for sampling using a grid map of the Refuge and a random number table. Some portions of the Refuge were avoided because they were closed to airboat travel or because excessive woody vegetation limited access. Within each area, one site each of sawgrass, wet prairie, and slough habitat was sampled as encountered. All three habitats could be found in proximity to one another, except in the northern, drier half of the Refuge where slough habitat was less common. The areal extent of these three habitats within the Refuge is approximately 1% sloughs (including alligator holes), 40% wet prairies, and 36% sawgrass (Richardson et al. 1990). Alligator holes were common in the drier portion of the Refuge and were similar to sloughs based upon vegetation composition and habitat structure (Gunderson and Loftus 1993). Further, alligator holes frequently formed large networks that resembled contiguous slough habitat. Therefore, sampling was performed in alligator holes whenever sloughs could not be located. Sloughs (including alligator holes), wet prairies, and sawgrass stands were
located as close to one another as possible without sampling in ecotones. Within each of these habitats, three throw traps (subsamples) were haphazardly collected. Therefore, 54 samples of plant and habitat structure data (6 areas x 3 habitats x 3 subsamples) were collected during each sampling event. Subsamples were averaged for each date and location in order to avoid pseudoreplication at the habitat level (*sensu* Hurlbert 1984). This stratified random design with blocking was used 1) to minimize airboat damage to vegetation associated with repetitive sampling of fixed positions and 2) to maximize spatial coverage of the Refuge.

**Data Analyses**

Three complementary approaches were used to analyze the above habitat structure and plant species composition data. First, analyses of variance were used to determine the effects of month, area (nested within month), habitat, and the habitat x month interaction on water depth, canopy height, plant biomass, and the relative abundance of sawgrass, water lily, bladderwort, and numerically dominant sedges (*Eleocharis* and *Rhynchospora*). These analyses examined how habitat structure varied at a small spatial scale (i.e., among habitats within an area), at a large spatial scale (i.e., among areas within the landscape), and at a temporal scale that encompassed several seasonal cycles (i.e., among months). Month and area were treated as random effects in these analyses, whereas habitat was treated as a fixed effect. Area was treated as a statistical block because each habitat type was sampled within each area. Furthermore, area was nested in months because a different set of six areas was selected for each sampling period. Habitat structure data were log$_{10}$-transformed and relative abundance (%) data were arcsin-transformed prior to analysis. However, figures include untransformed data because conclusions did not differ from those produced by transformed data. Least-squares means were used to test for differences among means when a fixed effect (i.e., habitat) was significant. Next, discriminant function analysis was used to determine how well habitat structure, plant species composition (six most abundant
taxa only), and both of these sets of data combined classified sites (i.e., each habitat x area x month combination) with respect to habitat type. For this analysis, multivariate models were created using habitat as an independent variable and vectors of habitat structure and/or plant species composition data as dependent variables. Finally, a nonparametric correlation test (Kendall’s tau) was used to determine concordance of plant species ranks between habitat types. This analysis quantified the similarity of plant community composition between pairs of habitat types. Statistical procedures followed Winer et al. (1991), Milliken and Johnson (1992), and Sokal and Rohlf (1995).

Results

Sloughs, wet prairies, and sawgrass stands were distinct habitats with respect to water depth, canopy height, and plant biomass (Table 2.1 and Figure 2.2). Sloughs were relatively deep, supported little plant biomass, and had minimal canopies. In contrast, sawgrass stands were relatively shallow, supported substantial plant biomass, and had well-developed canopies. Wet prairies were intermediate to sloughs and sawgrass stands with respect to water depth, plant biomass, and canopy stature. Therefore, sloughs, wet prairies, and sawgrass stands comprised gradients of increasing habitat complexity and decreasing hydroperiod within the Refuge. Overall, habitat type accounted for much of the variation (Table 2.2) observed in water depth (22%), canopy height (51%), and plant biomass (66%).

Differences in habitat structure were strongly associated with differences in the relative abundance of dominant species (Table 2.1). Deeper sloughs were dominated (88%) by floating vegetation (i.e., *Nymphaea, Utricularia*), intermediate wet prairies were dominated (79%) by short sedges (i.e., *Rhynchospora, Eleocharis*), and shallower sawgrass stands were dominated (93%) by tall culms of *Cladium*. Habitat type accounted for most of the variation observed in the relative abundance of sawgrass (95%), water lily (77%), bladderwort (28%), and short sedges (88%).
Although much of the variation observed in water depth, canopy height, and plant biomass was accounted for at the habitat level, there was also variation in habitat structure at the landscape level (Table 2.2). For example, 17% of the variation in water depth was attributable to differences among Areas within the Refuge. Area accounted for less of the variation observed in canopy height (10%) and plant biomass (7%).

The relative abundance of most of the dominant plant species tended to be consistent among areas in the Refuge as evidenced by no significant area effects (Table 2.2). However, area accounted for a considerable amount (22%) of the variation observed in the relative abundance of *Utricularia*. That is, bladderwort comprised a larger proportion of plant communities in the southern, deeper end of the Refuge. Partial correlation analyses indicate that this shift in abundance was likely due to water depth effects (partial r=0.534, p<0.0001) rather than latitude effects per se (partial r=0.038, p>0.05).

Water levels varied considerably during the study period (Figure 2.3) and sampling month accounted for 42% of the variation observed in water depth (Table 2.2). The Refuge remained inundated for most of 1991, whereas there was a typical seasonal drawdown during the spring of 1992. In contrast to water depth, canopy height and plant biomass varied little during the study, and month accounted for little of the variation observed in these variables (Table 2.2). Similarly, the relative abundance of dominant plant species varied little during the study (Table 2.2).

The univariate analyses above indicate that the relative abundance of dominant plant species differed considerably among habitat types. Similarly, linear combinations (i.e., community vectors) of relative abundance data for the six dominant plant taxa were strongly separated in multivariate space. Sloughs, wet prairies, and sawgrass stands were correctly classified (via discriminant function analysis) in 95%, 99%, and 100% of the samples, respectively. After inclusion of habitat structure data (i.e., water depth, canopy height, plant biomass), classification rates of sloughs and wet prairies improved to 97% and 100%, respectively. Misclassification of slough and wet prairie sites was due to similarities in
plant community structure (including all taxa in Table 2.1) between these two habitats (Kendall’s tau = 0.5611, p = 0.0015). In comparison, sawgrass stands showed little concordance of plant species ranks with either sloughs (Kendall’s tau = 0.0410, p = 0.8176) or wet prairies (Kendall’s tau = 0.1320, p = 0.4475). Finally, data on habitat structure alone generated excellent classification rates for sloughs (78%), wet prairies (97%), and sawgrass (92%).

Discussion

Previous researchers have provided qualitative descriptions of the structure and plant species composition of slough, wet prairie, and sawgrass habitats in the central and southern Everglades (e.g., Loveless 1959). Results from this study indicate that these a priori-defined habitats formed a similar mosaic in the northern Everglades. Floating and submerged vegetation (e.g., Utricularia, Nymphaea) predominated in sloughs and alligator holes, emergent sedges (e.g., Rhynchospora, Eleocharis) predominated in wet prairies, and sawgrass stands were virtually monotypic. As noted by Goodrick (1974), there was considerable overlap in species composition between sloughs and wet prairies. However, the relative abundance of plant species varied considerably between these habitats. In fact, relative abundance data for dominant plant taxa provided excellent discrimination between these two habitats.

At the landscape level, there are differences in plant species dominance among management compartments comprising the present-day Everglades (e.g., Wood and Tanner 1990). For example, wet prairies in the Refuge lie upon a deep bed of peat and tend to be dominated by Rhynchospora tracyi and Eleocharis spp. (mostly E. elongata), although Lachnanthes sp. and Xyris sp. can predominate following periods of protracted drought (Goodrick 1974). Eleocharis cellulosa was locally abundant in deeper portions of the Refuge and around the periphery of alligator holes. In contrast, wet prairies in the central and southern Everglades are dominated by E. cellulosa, with R. tracyi and E. elongata being
considerably less abundant (McPherson 1973, Wood and Tanner 1990). The relative importance of different graminoid species within wet prairie communities depends upon antecedent hydrologic conditions, composition of underlying substrate, and composition of local seed banks. In contrast, slough and sawgrass communities are generally dominated by the same species throughout the Everglades landscape, tend to be much less dynamic with respect to species turnover, and tend to have lower species richness (e.g., Wood and Tanner 1990, Gunderson 1994; this study). Higher species richness in wet prairies likely reflects the intermediate nature of this habitat along a disturbance continuum (sensu Connell 1978).

Habitat effects accounted for much of the variation observed in water depth, canopy height, plant biomass, and plant species relative abundance (see Table 2). From a structural perspective, sloughs were relatively deep and structurally simple, sawgrass stands were relatively shallow and structurally complex, and wet prairies were of intermediate depth and habitat complexity. Therefore, these three habitats formed a habitat mosaic varying in hydroperiod and habitat complexity. Qualitative differences in habitat structure and the overall mosaic nature of the Everglades landscape has been noted by previous researchers (e.g., Loveless 1959, McPherson 1973, Goodrick 1974, Wood and Tanner 1990, Gunderson 1994, Jordan et al. 1994). The present study complements earlier research efforts by 1) quantifying structural differences among adjacent habitats, 2) determining how habitat structure and plant relative abundance vary over a large spatial scale, and 3) determining how these habitats vary seasonally.

Description and comparison of sloughs, wet prairies, and sawgrass stands within the Everglades has typically been performed at sites close to hydrologic stations or other structural features (e.g., canals, pump stations). One result of this approach has been to compare these habitats using sites that were separated by large distances, thereby confounding small-scale (i.e., among habitats) and large-scale (i.e., among areas) spatial variation (Dutilleul 1993). For example, Gunderson (1994) noted that large-scale spatial variation has precluded quantitative delineation of soil elevation (= water depth) differences
among habitat classes in the Everglades. The present study overcame this problem by sampling each of the habitats in proximity to one another at sites (i.e., statistical blocks) located across the Refuge landscape. The significance of this finding is that small differences in topography among habitats (especially between wet prairies and sawgrass stands) have been masked and that our ability to determine the relative roles that fire and hydroperiod play in structuring the Everglades landscape has been hampered (e.g., Lowe 1986, Herndon et al. 1991). Future models of vegetation dynamics within the Everglades and similar marsh systems should incorporate these local differences in habitat structure.

Observed differences in habitat structure and plant species composition appear to be persistent across the Refuge landscape, which is surprising given that there can be large differences within and among the management compartments comprising the Everglades (e.g., Wood and Tanner 1990). In fact, little (≈1-10%) of the variation observed in canopy height, plant biomass, and the relative abundance of most plant taxa was attributable to processes operating at the landscape level. In contrast, 17% of the variation observed in water depth was accounted for by the area effect, indicating that water depth varied considerably across the Refuge landscape. Hydrologic gradients occur across the Refuge landscape because of underlying latitudinal variation in peat accretion rates and because of the construction of canals and dikes around the Refuge. These naturally- and anthropogenically-induced gradients have played an important role in shaping the Everglades landscape and have resulted in large-scale conversion of habitats during the past century. For example, Richardson et al. (1990) and Davis (1994) found that the relative abundance of cattail, which is a competitively-dominant species under eutrophic conditions, decreased with increasing distance from nutrient-enriched perimeter canals.

Fortunately, the effects of human modifications have been largely restricted to areas adjacent to nutrient-laden peripheral canals, and plant community composition appeared to be relatively unaffected throughout the remaining, oligotrophic marshes of the Refuge interior (Richardson et al. 1990; this study). For example, the relative abundance of
sawgrass, water lily, and numerically dominant sedges such as *Rhynchospora* and *Eleocharis* were nearly constant across the Refuge landscape (cf., among management compartments). In contrast, the relative abundance of bladderwort varied considerably, likely in response to latitudinal variation in water depth. Floating vegetation (e.g., bladderwort, water lily) appeared to be favored strongly by increased hydroperiod in the Everglades (e.g., Wood and Tanner 1990).

The present study did not examine changes in the areal extent of sloughs, wet prairies, and sawgrass stands within the Refuge landscape, but it does appear that there have been shifts in the relative abundance of these habitats (Richardson et al. 1990, Davis et al. 1994). For example, sawgrass and small tree islands have increased in areal extent due to increased drainage in the northern end of the Refuge and slough communities have expanded somewhat in the southern end due to “ponding” of water behind dikes. Therefore, shifts in the areal coverage of these habitats appear to be due to long-term changes in hydrologic conditions (e.g., McPherson 1973, Richardson et al. 1990, Davis et al. 1994) rather than short-term (i.e., seasonal) effects. This study provided little evidence for short-term changes in the height, biomass, or relative abundance of dominant plant taxa, even though water depths varied considerably during the study period (see Figure 2 and Table 3). Finally, significant habitat x month interactions (Table 3) for water depth, canopy height, and plant biomass indicate that structural differences among habitats changed seasonally, likely in response to autecological differences in growth rate and response to water levels.

This research was performed in conjunction with an analysis of the relative importance of slough, wet prairie, and sawgrass habitats to macroinvertebrates and fishes (Chapters 3 and 4). Quantitative sampling has revealed that aquatic macrofauna are not distributed randomly among available wetland habitats, but rather display species-specific patterns of habitat use. For example, Jordan et al. (1994) found that the fishing spider *Dolomedes triton* is significantly more abundant in structurally-complex sawgrass stands.
The numerically and trophically important crayfish *Procambarus alleni* is much more abundant in wet prairies than in sloughs (Jordan et al. 1996a, Chapter 3). Finally, sawgrass stands appear to support significantly fewer fishes than either wet prairies or sloughs (Loftus and Kushlan 1987, Chapter 4). These and other patterns of habitat use likely reflect behavioral responses to differences in structural complexity and hydroperiod, which are strongly correlated with factors such as food availability, risk of predation, and physiological conditions (e.g., Wiens 1976, Jordan et al. 1996b). The present study shows that differences in habitat structure and plant species composition are consistent across the Refuge landscape. Therefore, local patterns of differential habitat use may translate up to the landscape level and affect population demographics (e.g., Pulliam 1988) and community organization (e.g., Rosenzweig 1991). In conclusion, the complex habitat mosaic comprising the Refuge landscape provides the ecological template upon which individuals, populations, and communities interact. Understanding the nature of this template is critical to the successful management and conservation of macroinvertebrates, fishes, and their predators (e.g., alligators, wading birds).
Table 2.1. Mean relative abundance (%) and frequency occurrence (%) of plant types in sloughs, wet prairies, and sawgrass stands within the Refuge. Scientific names and taxonomic authorities follow Godfrey and Wooten (1979). Asterisks denote taxa used in discriminant function analyses.

<table>
<thead>
<tr>
<th></th>
<th>Slough</th>
<th>Wet prairie</th>
<th>Sawgrass</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>mean</td>
<td>freq</td>
<td>mean</td>
</tr>
<tr>
<td><em>Cladium jamaicense</em> Crantz</td>
<td>0.9</td>
<td>2.2</td>
<td>0.2</td>
</tr>
<tr>
<td><em>Eleocharis</em> spp.</td>
<td>0.8</td>
<td>7.7</td>
<td>14.3</td>
</tr>
<tr>
<td><em>Eleocharis cellulosa</em> Torr</td>
<td>2.9</td>
<td>8.3</td>
<td>11.4</td>
</tr>
<tr>
<td><em>Eriocaulon compressum</em> Lam.</td>
<td>0.0</td>
<td>0.3</td>
<td>1.0</td>
</tr>
<tr>
<td><em>Hypericum</em> sp.</td>
<td>0.0</td>
<td>0.0</td>
<td>0.0</td>
</tr>
<tr>
<td><em>Nymphaea odorata</em> Ait.</td>
<td>67.9</td>
<td>95.7</td>
<td>6.5</td>
</tr>
<tr>
<td><em>Nymphoides aquatica</em> Kuntze</td>
<td>0.1</td>
<td>0.6</td>
<td>0.1</td>
</tr>
<tr>
<td><em>Panicum hemitomon</em> Schult.</td>
<td>1.9</td>
<td>13.9</td>
<td>1.7</td>
</tr>
<tr>
<td><em>Peltandra virginica</em> (L.)</td>
<td>0.0</td>
<td>0.0</td>
<td>0.0</td>
</tr>
<tr>
<td><em>Pontederia cordata</em> L.</td>
<td>0.3</td>
<td>1.5</td>
<td>0.4</td>
</tr>
<tr>
<td><em>Rhynchospora inundata</em> Fern.</td>
<td>0.5</td>
<td>4.0</td>
<td>0.7</td>
</tr>
<tr>
<td><em>Rhynchospora tracyi</em> Britt.</td>
<td>3.2</td>
<td>14.8</td>
<td>52.5</td>
</tr>
<tr>
<td><em>Sagittaria lancifolia</em> L.</td>
<td>0.0</td>
<td>0.0</td>
<td>0.1</td>
</tr>
<tr>
<td><em>Typha</em> spp.</td>
<td>0.5</td>
<td>1.2</td>
<td>0.0</td>
</tr>
<tr>
<td><em>Utricularia</em> spp.</td>
<td>20.6</td>
<td>71.9</td>
<td>8.7</td>
</tr>
<tr>
<td><em>Xyris</em> spp.</td>
<td>0.1</td>
<td>0.6</td>
<td>2.6</td>
</tr>
<tr>
<td>Unidentified fern</td>
<td>0.0</td>
<td>0.0</td>
<td>0.0</td>
</tr>
</tbody>
</table>
Table 2.2. Effects of habitat, month, habitat x month, and area (nested within month) on habitat structure and plant relative abundance in the Refuge.

<table>
<thead>
<tr>
<th>Source</th>
<th>df</th>
<th>SS</th>
<th>F</th>
<th>P</th>
<th>R²</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Log₁₀-transformed water depth</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Month</td>
<td>23</td>
<td>17.6</td>
<td>6.3</td>
<td>0.0001</td>
<td>42.2</td>
</tr>
<tr>
<td>Area (Month)</td>
<td>120</td>
<td>7.1</td>
<td>3.4</td>
<td>0.0001</td>
<td>17.0</td>
</tr>
<tr>
<td>Habitat</td>
<td>2</td>
<td>9.2</td>
<td>58.6</td>
<td>0.0001</td>
<td>22.1</td>
</tr>
<tr>
<td>Habitat x Month</td>
<td>46</td>
<td>3.6</td>
<td>4.6</td>
<td>0.0001</td>
<td>8.7</td>
</tr>
<tr>
<td>Error</td>
<td>240</td>
<td>4.1</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Log₁₀-transformed canopy height</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Month</td>
<td>23</td>
<td>8.0</td>
<td>0.7</td>
<td>0.8377</td>
<td>4.6</td>
</tr>
<tr>
<td>Area (Month)</td>
<td>120</td>
<td>17.8</td>
<td>1.0</td>
<td>0.4655</td>
<td>10.2</td>
</tr>
<tr>
<td>Habitat</td>
<td>2</td>
<td>89.7</td>
<td>88.1</td>
<td>0.0001</td>
<td>51.5</td>
</tr>
<tr>
<td>Habitat x Month</td>
<td>46</td>
<td>23.4</td>
<td>3.5</td>
<td>0.0001</td>
<td>13.4</td>
</tr>
<tr>
<td>Error</td>
<td>240</td>
<td>35.2</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Log₁₀-transformed plant biomass</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Month</td>
<td>16</td>
<td>5.2</td>
<td>1.1</td>
<td>0.3569</td>
<td>6.5</td>
</tr>
<tr>
<td>Area (Month)</td>
<td>85</td>
<td>5.3</td>
<td>1.3</td>
<td>0.0542</td>
<td>6.6</td>
</tr>
<tr>
<td>Habitat</td>
<td>2</td>
<td>53.0</td>
<td>99.2</td>
<td>0.0001</td>
<td>66.3</td>
</tr>
<tr>
<td>Habitat x Month</td>
<td>32</td>
<td>8.5</td>
<td>5.8</td>
<td>0.0001</td>
<td>10.7</td>
</tr>
<tr>
<td>Error</td>
<td>170</td>
<td>7.9</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Arcsin-transformed sawgrass relative abundance</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Month</td>
<td>16</td>
<td>0.5</td>
<td>1.0</td>
<td>0.4396</td>
<td>0.5</td>
</tr>
<tr>
<td>Area (Month)</td>
<td>85</td>
<td>1.8</td>
<td>1.2</td>
<td>0.1482</td>
<td>1.5</td>
</tr>
<tr>
<td>Habitat</td>
<td>2</td>
<td>109.9</td>
<td>1904.8</td>
<td>0.0001</td>
<td>94.7</td>
</tr>
<tr>
<td>Habitat x Month</td>
<td>32</td>
<td>0.9</td>
<td>1.7</td>
<td>0.0201</td>
<td>0.8</td>
</tr>
<tr>
<td>Error</td>
<td>170</td>
<td>2.9</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Arcsin-transformed water lily relative abundance</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Month</td>
<td>16</td>
<td>0.7</td>
<td>1.0</td>
<td>0.4986</td>
<td>1.5</td>
</tr>
<tr>
<td>Area (Month)</td>
<td>85</td>
<td>3.0</td>
<td>1.0</td>
<td>0.5457</td>
<td>6.0</td>
</tr>
<tr>
<td>Habitat</td>
<td>2</td>
<td>38.1</td>
<td>396.7</td>
<td>0.0001</td>
<td>77.0</td>
</tr>
<tr>
<td>Habitat x Month</td>
<td>32</td>
<td>1.5</td>
<td>1.3</td>
<td>0.1257</td>
<td>3.1</td>
</tr>
<tr>
<td>Error</td>
<td>170</td>
<td>6.1</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Arcsin-transformed bladderwort relative abundance</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Month</td>
<td>16</td>
<td>0.6</td>
<td>1.3</td>
<td>0.2477</td>
<td>6.2</td>
</tr>
<tr>
<td>Area (Month)</td>
<td>85</td>
<td>1.9</td>
<td>1.2</td>
<td>0.1837</td>
<td>21.6</td>
</tr>
<tr>
<td>Habitat</td>
<td>2</td>
<td>2.5</td>
<td>55.1</td>
<td>0.0001</td>
<td>27.7</td>
</tr>
<tr>
<td>Habitat x Month</td>
<td>32</td>
<td>0.7</td>
<td>1.2</td>
<td>0.2632</td>
<td>8.0</td>
</tr>
<tr>
<td>Error</td>
<td>170</td>
<td>3.3</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Arcsin-transformed sedge (Eleocharis and Rhynchospora) relative abundance</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Month</td>
<td>16</td>
<td>0.9</td>
<td>1.2</td>
<td>0.2983</td>
<td>1.3</td>
</tr>
<tr>
<td>Area (Month)</td>
<td>85</td>
<td>1.8</td>
<td>1.1</td>
<td>0.3587</td>
<td>2.9</td>
</tr>
<tr>
<td>Habitat</td>
<td>2</td>
<td>55.9</td>
<td>669.8</td>
<td>0.0001</td>
<td>88.2</td>
</tr>
<tr>
<td>Habitat x Month</td>
<td>32</td>
<td>1.3</td>
<td>2.1</td>
<td>0.0018</td>
<td>2.1</td>
</tr>
<tr>
<td>Error</td>
<td>170</td>
<td>3.4</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Figure 2.1. Map of lower Florida showing existing management compartments. The shaded area is the Arthur R. Marshall Loxahatchee National Wildlife Refuge (Water Conservation Area 1).
Figure 2.2. Mean (+ 1 SE) water depth, canopy height, and dry plant biomass in sloughs, wet prairies, and sawgrass stands of the Refuge. Means with different letters are significantly different (least-squares means).
Figure 2.3. Seasonal variation in mean (± 1 SE) water depth in sloughs, wet prairies, and sawgrass stands of the Refuge.
CHAPTER 3

HABITAT USE BY THE PRAWN Palaemonetes paludosus
AND THE CRAYFISH Procambarus alleni IN A
NORTHERN EVERGLADES WETLAND MOSAIC

Introduction

Characterizing the spatial and temporal heterogeneity of natural landscapes is a primary focus of ecologists studying the organization of populations and communities of mobile organisms. Much of this research is based upon the premise that continuous environmental gradients can best explain distribution patterns (Farnsworth and Ellison 1996). For example, a typical study measures the relative abundance of species along one or several environmental gradients (e.g., altitude, nutrient concentration, water depth), correlates matrices of species and environmental data, and then uses a morass of multivariate statistics to divine underlying ecological relationships (Gauch 1982). However, many studies fail to detect strong environmental gradients to account for observed patterns in the distribution and abundance of mobile organisms.

Absence of underlying environmental gradients is consistent with a landscape perspective (Wiens and Milne 1989, Chick and McIvor 1994), which recognizes that landscapes are comprised of mosaics of habitats or patches (Forman and Godran 1986, Urban et al. 1987). Rather than forming continuous gradients, these habitats are often physically distinct from one another and may have sharply defined boundaries. The abundance and relative importance of these habitats will change seasonally and annually as physical conditions across the landscape of interest change (Pickett and White 1981). Importantly, this perspective also recognizes that natural landscapes can have pronounced environmental gradients superimposed on the habitat mosaic. Therefore, the landscape perspective is based on the premise that populations and communities are regulated by processes that operate across a hierarchy of spatial and temporal scales.
In the previous chapter, I demonstrated that the freshwater marshes of the northern Everglades could be profitably viewed as a landscape. This spatially complex marsh system provides aquatic macrofauna with a mosaic of sloughs, alligator holes, wet prairies, and sawgrassstands to use during the course of their life histories. Persistent differences in physical structure and vegetation composition likely result in each of these habitats having characteristic arrays of conditions, resources, predators, and competitors that affect habitat use decisions, population demographics, and community composition (Wiens 1976, Pulliam 1988, Rosenzweig 1991). The abundance and relative importance of these marsh habitats may change in response to short-term (i.e., seasonal) and long-term (i.e., annual) trends in hydrologic conditions (Davis et al. 1994). Finally, this marsh landscape is also characterized by large-scale gradients in factors such as nutrient enrichment and hydroperiod (Richardson et al. 1990), which can affect aquatic macrofaunal populations and communities.

In this and the next chapter, I describe the results of a field study designed to test whether two taxonomic guilds (decapod crustaceans and fishes) respond (behaviorally and/or numerically) to their marsh landscape in a scale-dependent manner. In other words, how is population abundance and guild composition at a given location in the marsh landscape affected by processes operating locally (i.e., within and among habitats), regionally (i.e., among widely-separated locations), and seasonally (i.e., among months). I also use this and the next chapter to describe the basic spatial ecology and temporal dynamics of decapods and fishes within the northern Everglades, which appears to be quite different from the other compartments comprising the greater Everglades ecosystem (see various chapters in Davis and Ogden [1994]). Finally, I use this and subsequent chapters to describe the results of laboratory experiments designed to elucidate processes affecting the abundance and guild composition of decapods and fishes within the Everglades landscape.
The Decapod Crustacean Guild

The prawn \textit{Palaemonetes paludosus} and the crayfish \textit{Procambarus alleni} comprise the decapod guild within the extensive freshwater marshes of the Florida Everglades (Gunderson and Loftus 1993). Both species are important members of the Everglades food web and comprise significant portions of the diets of prominent predators such as wading birds, alligators, swamp snakes, pig frogs, and predatory fishes (Gunderson and Loftus 1993). \textit{Palaemonetes} is an important consumer of detritus and periphyton (Beck and Cowell 1976), whereas the larger \textit{Procambarus} is omnivorous and consumes detritus, periphyton, and other aquatic macrofauna (Gunderson, and Loftus 1993, Hobbs 1993, Browder et al. 1994). Considering their importance to food web structure, surprisingly little is known about the spatial ecology of \textit{Palaemonetes} and \textit{Procambarus} within the freshwater marshes comprising the Everglades (Davis and Ogden 1994), or about how these two species interact with one another (Jordan et al. In review a).

Kushlan and Kushlan (1979, 1980) found that \textit{Palaemonetes} and \textit{Procambarus} were common in wet prairies of the southern Everglades, and suggested that sloughs and alligator holes may be important to \textit{Palaemonetes} and \textit{Procambarus} during seasonal drawdowns. Recently, Jordan et al. (1996a, In review a) examined habitat use by \textit{Palaemonetes} and \textit{Procambarus} in the headwater marshes of the St. Johns River. They found that \textit{Procambarus} was more abundant in wet prairies than in sloughs, whereas \textit{Palaemonetes} was usually more abundant in sloughs than in wet prairies. Unfortunately, no research has quantified the abundance of decapods within sawgrass stands, which cover about half of the Everglades and other wetland landscapes in southern Florida (Lowe 1986, Gunderson 1994). Areally extensive stands of sawgrass may provide excellent habitat for \textit{Palaemonetes} and \textit{Procambarus} because these habitats are not often used by predatory fishes and wading birds (Loftus and Kushlan 1987, Hoffman et al. 1994, Chapter 4). However, \textit{Palaemonetes} and \textit{Procambarus} may become concentrated in local marsh depressions (i.e., sloughs and alligator holes) during seasonal marsh drawdowns, thereby
increasing their exposure to nesting wading birds (Kushlan and Kushlan 1979, 1980, Frederick and Spalding 1994). Finally, the abundance of *Palaemonetes* and *Procambarus* is likely to vary among widely-separated locations due to gradients in topography, hydrology, and nutrient enrichment that often persist across wetland landscapes (Richardson et al. 1990, Davis et al. 1994, Bedford 1996).

**Study Area and Methods**

**Study Area**

Prawn and crayfish were collected in the northern remnant of the Everglades from the 57,234 ha Arthur R. Marshall Loxahatchee National Wildlife Refuge (hereafter the Refuge). The Refuge is encircled by a deep-water canal and dike system that drains an approximately equal area of the Everglades Agricultural Area (Richardson et al. 1990). The Refuge is managed both for the conservation of wildlife resources (U.S. Fish & Wildlife Service) and as part of the vast water routing system in south Florida (South Florida Water Management District). Much of the hydrology and water chemistry of the Refuge is driven by rainwater. However, water derived from the Everglades Agricultural Area and delivered by perimeter canals is enriched with phosphorus, nitrogen, and chloride ions. This water is not distributed evenly across the Refuge landscape because topographic variation in the underlying peat results in a gradient of increasing depth and a longer hydroperiod along the north-south axis of the Refuge. The perimeter canal and dike system has intensified this hydrologic gradient through increased drainage in the northern end and increased “ponding” of water behind dikes in the southern end of the Refuge.

Nutrient enrichment and alterations in hydrology have resulted in profound changes to the habitat mosaic comprising the Refuge (Richardson et al. 1990, Davis 1994, Davis et al. 1994). Historically, the oligotrophic Refuge landscape was comprised of emergent wet prairies, sawgrass stands, sloughs (including alligator holes), and elongate tree islands overlying a deep bed of peat. Stands of cattail (*Typha* spp.) and other opportunistic species
have replaced these habitats in disturbed areas near canals because of increased nutrient loading and protracted hydroperiods (Richardson et al. 1990, Davis 1994, Newman et al. 1996). Plant community changes decline with increasing distance from perimeter canals (Richardson et al. 1990) and interior marshes appear to have retained much of their mosaic nature (Chapter 2). However, ecological function (e.g., primary and secondary production, food web dynamics) may have been compromised within this marsh mosaic. The present study was motivated by concern over the impact of habitat conversion on wetland resources and forms part of a larger ecological characterization of the Refuge. Accordingly, descriptions of the study area, sampling techniques, and analytical approaches are modified from Jelks et al. (1992) and Jordan et al. (1994).

Field Survey

The spatial heterogeneity and temporal variability characteristic of freshwater marshes in southern Florida have proved to be the greatest obstacle to studying aquatic macrofauna (Gunderson and Loftus 1993). However, the mosaic nature of aquatic landscapes can serve as a useful template when designing field surveys (e.g., Wiens and Milne 1989, Chick and McIvor 1994, Jordan et al. 1996a). In the present study, I quantified the abundance of *Palaemonetes* (hereafter prawns) and *Procambarus* (hereafter crayfish) within the mosaic of sloughs (including alligator holes), wet prairies, and sawgrass stands that comprise the northern remnant of the Florida Everglades. Variation in decapod abundance was characterized at several spatial scales (i.e., within habitats, among adjacent habitats, among widely-separated areas), which reflect a hierarchy of population, community, and ecosystem processes operating at different spatial and temporal scales (Allen and Starr 1982, O’Neill et al. 1986, Menge and Olson 1990, Holling 1992, Farnsworth and Ellison 1996).

Prawn and crayfish were collected with an aluminum throw trap (100 x 100 x 75 cm), which provides accurate and reliable density estimates for decapods and fishes
Sampling involved throwing the throw trap into the desired habitat and then pressing it firmly into the substrate. Above-ground plants were identified, counted (relative coverage), uprooted, and rinsed to dislodge any prawn or crayfish. A bar seine with 3.0-mm mesh was then passed through the trap until three consecutive empty sweeps were obtained. Prawn and crayfish were picked carefully from the detritus collected in each sweep of the bar seine and preserved in 10% buffered formalin. Prawn and crayfish were later rinsed and enumerated in the laboratory.

Water depth, canopy height, plant biomass, and plant species composition were also measured in order to characterize the habitat mosaic (Jordan et al. 1994, Chapter 2) and examine relationships between habitat structure and decapod abundance. Habitat data are presented in detail elsewhere (Jordan et al. 1994, Chapter 2). In summary, sloughs were relatively deep, structurally simple, had poorly developed canopies, and were dominated by floating aquatic plants such as bladderwort (*Utricularia*) and water lily (*Nymphaea*). Sawgrass stands were relatively shallow, structurally complex, had well developed canopies, and supported virtual monocultures of *Cladium*. Wet prairies were intermediate in depth, structural complexity, and canopy development. Dominant plant taxa included emergent sedges and grasses (*Rhynchospora, Eleocharis, Panicum*). Although there was some overlap along univariate environmental axes, these three habitats occupied distinct multivariate space with respect to physical structure and plant community composition (Chapter 2).

Sampling was performed approximately monthly between February 1990 and July 1992 (24 sampling events). During each sampling period, six areas (statistical blocks) were randomly selected for sampling using a grid map of the Refuge; however, some portions of the Refuge were avoided because they were closed to airboat travel or because excessive woody vegetation limited access. Within each area, one site each of sawgrass, wet prairie, and slough habitat was sampled as encountered. All three habitats could be found in
proximity to one another except in the northern, drier half of the Refuge, where slough habitat was less common. Alligator holes were substituted in these areas because they were similar to sloughs with respect to vegetation composition and habitat structure (Gunderson and Loftus 1993). The term slough refers to both slough and alligator hole habitats throughout the rest of this paper. Within each habitat, three throw traps (subsamples) were haphazardly collected and average densities of prawn and crayfish were calculated for these three traps.

Decapod abundance and habitat structure (water depth, canopy height, plant biomass) data were log_{10}-transformed prior to analysis; however, graphical results are presented for original data because conclusions were qualitatively similar. Analyses of variance (ANOVAs) were used to determine the effects of month, area (nested in month), habitat, and the habitat x month interaction on the average densities of prawns and crayfish. Specifically, these analyses examined how variation in decapod abundance could be partitioned among several ecologically relevant scales: i.e., among adjacent habitats (local scale), among widely-separated areas (landscape scale), and among months (seasonal scale). Month and area (nested within month) were treated as random effects in these analyses, whereas habitat was treated as a fixed effect. Least-squares means were used to test for differences in decapod abundance among habitats. Discriminant function analysis was used to determine how well prawn and crayfish abundance data correctly classified sites with respect to habitat type. Finally, partial correlation analysis was used to examine relationships between decapod abundance, habitat structure data (water depth, canopy height, plant biomass), and correlates of underlying gradients in nutrient enrichment and hydrology (distance to canal, conductivity, latitude). Additional analyses are described as used. Statistical procedures followed Winer et al. (1991), Milliken and Johnson (1992), and Sokal and Rohlf (1995).
Predation and Behavior Experiment

Although omnivorous, crayfish are extremely aggressive and interact strongly (i.e., competition, intraguild predation, cannibalism) with one another and other aquatic macrofauna (Hobbs 1991, 1993). Aggression in crayfishes and other decapod crustaceans appears to be size-structured (Capelli and Munjal 1982, Butler and Stein 1985, Söderbäck 1991), motivated by competition for access to refugia from predators (Eggleston and Lipcius 1992, Garvey et al. 1994, Beck 1995), and often results in lowered survival of small-sized crayfish via either cannibalism or increased exposure to predators (Caine 1978, Garvey et al. 1994). Since adult Palaemonetes are smaller than most age classes of Procambarus, differences in habitat use between these species may reflect size-structured aggression and community organization (Werner and Gilliam 1984, Ebenman and Persson 1988), especially in complex habitats (Chapters 5 and 7). I tested this hypothesis by exposing crayfish to small and large prawns in simple and complex environments.

Prawns and crayfish were collected from freshwater marshes, transported back to the laboratory, and allowed to acclimate to a 12L:12D light cycle and ≈20°C water temperatures. Crayfish were collected several weeks prior to the experiment and were fed pelleted fish food, whereas prawns were collected 48 h prior to the experiment and were not fed in the laboratory. Groups of three large (mean ± 1 SE: 24 ± 0.5 mm total length, n=15) and three small prawns (17 ± 1 mm total length, n=15) were then transferred into each of 24 opaque plastic tanks (32 x 22 x 17 cm) containing 8 liters of aerated water from the prawn collection site.

Twelve experimental tanks each were randomly assigned to either a complex or simple habitat treatment. Complex habitat was created by covering the bottom of the tank with shredded plastic mesh, which mimicked the thick detritus base found in wet prairies and sawgrass stands (Jordan et al. 1994). No cover was provided in the simple habitat treatment. One crayfish (62 ± 3 mm total length, n=12) was then randomly assigned to each of six bins in both treatments. The experiment was run for 7 days and then the
proportion of prawns remaining (survivorship) was determined for each tank. Survivorship scores were arcsin-transformed and then used as the response variable in a factorial ANOVA testing for the effects of habitat complexity (simple vs. complex) and predators (absent vs. present). Means are presented for the untransformed data because they produced very similar ANOVA results. Finally, a paired t-test was used to compare the vulnerability of small and large prawns.

The effects of crayfish on habitat use by prawns may be mediated through behavioral pathways rather than through direct predation. Therefore, I made behavioral observations in tanks lacking habitat structure on several occasions during the predation experiment. The lighting and physical layout of the laboratory resulted in each tank having a small shaded section, and preliminary observations indicated that both prawns and crayfish oriented towards this section (also see Alberstadt et al. 1995). I exploited this cover-seeking behavior to test whether prawns reduced their use of the shaded section of tanks when exposed to crayfish. I recorded the number of prawns surviving and the number occupying the shaded side of each tank on several occasions and converted these values to a single proportion for each tank. A one-sided, paired t-test was used to compare proportions of prawns on simple and complex sides of tanks that lacked crayfish (n=6), whereas a one-sided, un-paired t-test was used to compare proportions of prawns on simple sides of tanks with and without crayfish (n=12).

Results

Field Survey

A total of 32,212 prawn and 4,364 crayfish were collected during this study (n=1,296 throw traps), yielding average densities of about 25 prawn and 3 crayfish per m². Prawn and crayfish were not distributed equally among habitats (Figure 3.1) and the habitat effect (i.e., local processes) accounted for 14% of the variation observed in abundance of both species (Table 3.1). Prawns were significantly more abundant in sloughs (45 per m²)
than in either wet prairies (21 per m$^2$) or sawgrass stands (8 per m$^2$). In contrast, crayfish were significantly more abundant in structurally complex sawgrass stands (5 per m$^2$) and wet prairies (4 per m$^2$) than in sloughs (1 per m$^2$).

Partial correlation analyses indicated that relationships between decapod abundance and habitat structure (water depth, canopy height, plant biomass) differed among sloughs, wet prairies, and sawgrass stands (Table 3.2). Prawn abundance was positively correlated with water depth in sawgrass stands and canopy height in sloughs, but negatively correlated with water depth and plant biomass in sloughs. Crayfish abundance was positively correlated with canopy height in both sloughs and sawgrass stands.

There was considerable seasonal variability in the abundance of prawn and crayfish (Figure 3.2) and the month effect accounted for 18 and 20%, respectively, of the variation observed in abundance of these species (Table 3.1). Prawn abundance ranged from a low of 5 individuals per m$^2$ in July 1992 to a high of 147 individuals per m$^2$ in May 1992. Crayfish abundance ranged from a low of fewer than 1 individual per m$^2$ in May 1992 to a high of 6 individuals per m$^2$ in March 1992. The distinct life histories of these two species is reflected in their responses to the marsh drawdown of May 1992. Figure 3.3 shows seasonal fluctuation in water levels that occurred during the study period. A seasonal drought occurred in May 1992 and water levels in sawgrass stands and wet prairies were near or below the peat surface across much of the Refuge landscape. However, relatively deep sloughs and alligator holes remained inundated during the drought, providing a local refuge for aquatic macrofauna. Prawns, which were not capable of excavating burrows, congregated in the deeper sloughs and therefore had greatly elevated numbers in May 1992 (Figure 3.4). In contrast, crayfish appeared to burrow beneath the peat surface and avoid sloughs (Figure 3.4). Finally, differences in habitat use for each species depended partly on sampling period (Figure 3.2) and associated seasonal changes in water levels (Figure 3.3). An additional 10 and 12% of the variation observed in prawn and crayfish abundance, respectively, was attributable to the habitat x month interaction (Table 3.1).
A considerable amount of variation observed in abundance of prawn (37%) and crayfish (28%) was attributable to the area effect (i.e., landscape processes; Table 3.1). The Refuge landscape was characterized by underlying gradients in hydrology and nutrient enrichment that could affect the size of decapod populations. Three measures of these gradients are conductivity, distance to perimeter canal, and latitude (Richardson et al. 1990). Partial correlation analyses indicated that prawn abundance was negatively correlated with latitude in both sloughs and wet prairies, suggesting that prawn numbers tended to increase along a north to south gradient of increasing hydroperiod. Crayfish abundance was negatively correlated with conductivity in wet prairies, indicating that crayfish numbers declined with increasing influence of canal-derived waters.

There was some evidence for habitat-specific decapod assemblage structure. First, prawn and crayfish appeared to use wet prairies, sloughs, and sawgrass stands differently (Figure 3.1), although the abundance of both species was positively correlated within sloughs (Table 3.2). Discriminant functions using only prawn and crayfish abundance data classified 58% of the sampling locations correctly with respect to habitat type (Table 3.3), indicating that decapod assemblage structure varied predictably among sloughs, wet prairies, and sawgrass stands. Classification rates varied among sloughs (66%), wet prairies (40%), and sawgrass stands (69%). Although prawn and crayfish overlapped somewhat in their use of the Refuge landscape, these species used available habitats in distinct ways and each habitat was generally characterized by unique decapod assemblage structure.

**Predation and Behavior Experiment**

Small and large prawns did not differ in their survival rates when exposed to crayfish \( t_{11} = 1.149, p = 0.2750 \). Overall, prawn survival rates were 98.5% in the absence of crayfish and 93.1% in the presence of crayfish, indicating a 5% mortality rate due to crayfish predation. However, differences in survival rates between predator and control tanks were not statistically significant \( F_{1,20} = 2.428, p = 0.1349 \). The presence of complex
structure did not affect survival rates of prawn ($F_{1,20}=1.352$, $p=0.2586$). Finally, there was no evidence for an interaction between predator and habitat complexity factors ($F_{1,20}=0.065$, $p=0.8007$).

Predation rates were low in this experiment likely because prawns altered their habitat use in the presence of crayfish. In the absence of crayfish, most prawns (89%) were found on the shaded sides of the simple tanks ($t_{5}=-14.512$, $p<0.0001$). In contrast, the percentage of prawns observed on the shaded sides was 8% lower in simple tanks that contained crayfish ($t_{10}=-1.793$, $p=0.0516$). Most crayfish (96%) occupied the shaded portion of the simple tanks, which appears to have lowered the appeal of this refuge to prawns.

Discussion

Decapod Abundance along a Spatial Hierarchy

The abundance of decapods at any given location is determined by a variety of population, community, and ecosystem processes that operate across a range of spatial and temporal scales (e.g., O’Neill et al. 1986). The present study was designed such that the relative importance of processes operating at local scales (i.e., among adjacent habitats) and landscape scales (i.e., among widely separated areas) could be distinguished and compared. Overall, it appears that landscape-level processes account for most of the variation observed in prawn (37%) and crayfish (28%) abundance.

What kinds of processes could operate over such large expanses of marsh? First, gradients in nutrient enrichment can affect the abundance of decapods through increased production of microalgae (i.e., bottom-up effects), which is an important resource for both prawns and crayfish (Hunt 1952, Beck and Cowell 1976, Browder et al. 1994). Nutrient enrichment is highest along perimeter canals and decreases with increasing distance from canal. However, prawn abundance was unaffected by distance to canals, and crayfish abundance tended to decrease towards canals. Moreover, the abundance of prawns was not
inflated at highly-enriched cattail sites adjacent to canals, and the abundance of crayfish was depressed at these sites (see “Decapod Abundance” section below). Two factors likely offset the potential positive influences of increased primary production. First, the relative abundance of blue-green algae is significantly higher in nutrient enriched sites, and these microalgae appear to have substantially lower nutritive value for decapods (Browder et al. 1994). In contrast, nutrient enrichment appears to have strong bottom-up effects on both herbivorous and carnivorous fishes (Chapter 4), which have greatly elevated densities in cattail sites (see “Decapod Abundance” section below). Therefore, enhanced production of fishes may result in strong top-down (i.e., predator-mediated) effects on production of vulnerable decapod prey (Hobbs 1991, 1993).

Gradients in hydroperiod can also affect large-scale variation in the abundance of decapods (Kushlan and Kushlan 1979, 1980, Loftus et al. 1986, Jordan et al. 1996a). For example, hydroperiod increases along a north-south gradient within the Refuge landscape (Richardson et al. 1990). Populations of most small aquatic organisms appear to respond positively to prolonged inundation within the Everglades (cf., Kushlan 1976) because of increased production of nutritive microalgal taxa (Browder et al. 1994), increased accumulation of detritus (Loftus et al. 1986), and uninterrupted reproduction in the absence of frequent droughts (Loftus and Eklund 1994). Negative correlations between prawn abundance and latitude in both sloughs and wet prairies indicate positive effects of hydroperiod on prawn production. Crayfish were unaffected by hydroperiod effects, likely because they can burrow in response to drought conditions (Kushlan and Kushlan 1979, Jordan et al. 1996a).

Relative water depths vary consistently among sawgrass stands, wet prairies, and sloughs (Chapter 2). Therefore, hydroperiod effects may also be important on a local scale. Indeed, prawn abundance tends to increase along this habitat gradient (i.e., sawgrass < wet prairies < sloughs). However, differences in prawn abundance among habitats may reflect the indirect effects of hydroperiod on predator assemblage composition, rather than the
direct effects of hydroperiod on food resources as described above. Partial correlation analyses indicated that prawn abundance decreased with increasing water depth in sloughs and wet prairies, increased with increasing water depth in sawgrass stands, and decreased with increasing habitat complexity in all habitats. In contrast, the abundance of large predatory fishes is highest in relatively deep habitats, and the abundance of large predatory arthropods (including crayfish) is highest in relatively shallow Everglades habitats (Chapter 7). Therefore, prawns may find themselves between the proverbial “rock and a hard place” with respect to different suites of predators (Chapter 7). Predatory fishes are voracious consumers of prawns (e.g., Hunt 1952), whereas less is known about the voracity of arthropod predators (Chapters 6 and 7; see “Do Prawns and Crayfish Interact?” section below).

Habitat use by crayfish is also influenced by risk of predation (Stein and Magnusson 1976, Stein 1977, Garvey et al. 1994). For example, Jordan et al. (1996a) found that Procambarus abundance was highest in wet prairies within the headwater marshes of the St. Johns River. Jordan et al. postulated that crayfish encountered fewer predatory fishes in complex habitats (Dineen 1974, 1984, Loftus and Kushlan 1987, Chapter 4), and that the foraging efficiency of resident predatory fishes was reduced because of structural interference (Heck and Crowder 1991, Chapter 7). Indeed, subsequent research (Chapter 5) demonstrated that Procambarus preferred complex habitats and that their vulnerability to predatory largemouth bass (Micropterus salmoides floridanus) decreased with increasing habitat complexity. This shift in habitat use may not represent a foraging tradeoff (sensu Werner et al. 1983), because Procambarus appear to have improved foraging efficiency within complex habitats (Chapter 7) due to increased foraging activity in the absence of efficient predators (Werner 1994).

Do Prawns and Crayfish Interact?
Prawns and crayfish used available habitats in different ways. Since crayfish were, on average, ≈850% larger than prawns, I hypothesized that differences in habitat use reflected size-structured interactions between these species. The results of my laboratory experiment indicate that crayfish were not voracious predators of prawns. However, low predation rates partially reflected avoidance behavior (e.g., Lima and Dill 1990, Jordan et al. 1996b), because prawns decreased their use of preferred refugia in the presence of large crayfish. Crayfish aggressively protect refugia and their agonistic behavior generally results in increased vulnerability of smaller crayfish due to increased exposure to predatory fishes (Caine 1978, Garvey et al. 1994). Results of this study suggest that crayfish may have a similar effect on prawns. Prawns may reduce their use of sawgrass stands and dense wet prairies because of exposure to highly aggressive and potentially predatory crayfish. The dearth of predatory fishes in these marsh habitats (Chapters 4 and 7) suggests that shifting to slough habitats may lower the overall vulnerability of crayfish to predation. Finally, although crayfish have a broad diet, they rely most heavily upon microalgae (Browder et al. 1994), which is also the most important trophic resource for prawns in the Everglades (Hunt 1952). Therefore, competition for microalgae may also contribute to habitat segregation by these species, especially in nutrient-starved (i.e., interior) portions of the Refuge. Additional research is needed to untangle the complex relationships between prawns, crayfish, habitat complexity, and large predatory fishes.

Decapod Responses to Variation in Water Levels

A substantial amount of the variation observed in decapod abundance was associated with sampling month and the habitat x month interaction (Table 3.1), indicating that both prawns and crayfish are sensitive to changes in water levels. Prawns tend to move laterally across the marsh surface in response to changing water levels (Kushlan and Kushlan 1980), as evidenced by increases in their numbers in sloughs as waters recede and then decreases in their numbers as water levels rise. For example, prawn numbers in sloughs rose to about
425 per m² during the severe marsh drawdown of May 1992, with one throw trap containing 1,673 prawns! Prawn numbers then dropped to about 13 per m² after the marsh reflooded, likely reflecting a combination of dispersal and drought-related mortality. Crayfish appeared to move both laterally and vertically across the marsh surface when water levels changed. Crayfish moved laterally into sawgrass and wet prairies in the months prior to the May 1992, but did not increase further during May 1992, likely because of vertical movement into the peat substrate. Similarly, Jordan et al. (1996a) found that crayfish numbers increased considerably in wet prairies as water levels dropped, but there was little evidence for concentration into sloughs. Crayfish appear to move out of sloughs during severe drawdowns, likely in response to increased numbers of large predatory fishes and wading birds (Loftus and Kushlan 1987).

Figure 3.4 demonstrates conclusively that prawns and crayfish respond differently to marsh drawdowns. However, the similar amount of variance explained by habitat x month interactions indicates that the abundance of both species changes among habitats seasonally. As mentioned above, decapods are abundant within the Refuge and other wetland systems in southern Florida. However, much of this biomass occurs in habitats (e.g., sawgrass) not readily accessible to wading birds, alligators, large fishes, and other prominent Everglades predators (e.g., Loftus and Kushlan 1987, Frederick and Spalding 1994). The present study shows that prawn availability will increase considerably during marsh drawdowns, whereas crayfish availability may decline across the Refuge during marsh drawdowns due to burrowing.

Decapod Abundance and Macrofaunal Community Composition

Although nutrient enrichment has profoundly affected portions of the Everglades ecosystem (Richardson et al. 1990, Davis 1994), most of this vast landscape remains oligotrophic (Davis 1994). Indeed, most of the data in the present study were obtained from non-enriched interior sites. The overall abundance of prawns (20 per m²) and crayfish (4
per m²) during non-drought periods (i.e., excluding data from May 1992) seems to reflect a nutrient poor system. In contrast, the eutrophic littoral zones of Lake Okeechobee and Hillsborough River (both in southern Florida) support about 275 and 215 prawns per m², respectively (Beck and Cowell 1976, Chick 1992). The potential production of decapods in Everglades marshes is staggering when density estimates are crudely extrapolated to the landscape level. For example, the 57,234 ha Refuge supports about $10^{10}$ prawns ($\approx 1,000$ metric tons) and $10^9$ crayfish ($\approx 1,600$ metric tons)!

Nutrient status is not the only factor limiting the standing stocks of decapods in the marshes of southern Florida. For example, the abundance of prawns (10 per m²) in cattail sites adjacent to peripheral canals was not significantly different from interior sites on the Refuge (contrast: $F_{1,183}=0.9$, $p>0.05$), and the abundance of crayfish (1 per m²) was significantly lower (contrast: $F_{1,183}=10.9$, $p=0.0012$) in peripheral cattail sites (see collection details in Chapter 4). Although these cattail sites have greatly elevated nutrient levels (Richardson et al. 1990), they also support about five times as many fishes as interior sites (Chapter 4). Therefore, strong top-down (i.e., predator-mediated) effects may counteract any positive effects that increased primary production may have on production of prawns and crayfish in this system.

Comparisons of decapod standing stocks across locations is complicated by differences in habitat availability and sampling methodology. Fortunately, several studies have quantified decapod abundance in wet prairie habitats using equivalent sampling gear (Chick et al. 1992). The average abundance of prawns in wet prairies appears to be remarkably similar among widely-separated freshwater marshes in southern Florida: 22 per m² in the upper basin of the St. Johns River (Jordan et al. In press a), 34 per m² in the southern Everglades (Kushlan and Kushlan 1980), 15 per m² in the un-enriched Eleocharis flats of Lake Okeechobee (Chick 1992), and 21 per m² in this study. The higher abundance of prawns observed in the southern Everglades likely reflects a profound sampling bias (Loftus and Eklund 1994) more than any regional difference in production. The abundance
of crayfish in wet prairies appears to vary more among these freshwater marshes: 28 per m² in the upper basin of the St. Johns River (Jordan et al. 1996a), ≈1 per m² in southern Everglades (Kushlan and Kushlan 1979, Loftus et al. 1986), and about 4 per m² in this study. It is unclear why the abundance of crayfish is more variable than the abundance of prawns when examined at this large spatial scale. However, this variation has management and conservation implications for widely dispersing predators (e.g., alligators, wading birds) that rely upon this prey base (Holling 1992, Davis and Ogden 1994, Frederick and Powell 1994, Frederick and Spalding 1994, Mazzotti and Brandt 1994, Ogden 1994).

Composition of the aquatic macrofauna is fairly consistent across marsh systems in southern Florida, with small cyprinodontiform fishes, anuran larvae, prawns, crayfish, apple snails, odonate larvae, coleopteran adults and larvae, and various hemipterans being relatively common. The relative abundance of large arthropods is notable, especially considering how strongly fishes affect the distribution of large arthropods in many aquatic systems (Werner and McPeek 1994). Decapods (23 per m²) were about as abundant as small fishes (22 per m²) in the Refuge. Furthermore, marshes of the upper basin of the St. Johns River supported about 35% more decapods (38 per m²) than small fishes (28 per m²), and supported about 425% more decapod biomass (17 g per m²) than small fish biomass (4 g per m²). Most marsh fishes are of equal or smaller size than their arthropod neighbors, which eliminates the size advantage that fishes typically enjoy in many freshwater systems. Additionally, populations of large predatory fishes are depauperate and largely confined to relatively deep sloughs and alligator holes (Dineen 1974, 1984, Loftus and Kushlan 1987, Chapter 4). Therefore, the effects of these larger fishes is limited largely to deterring use of sloughs by vulnerable taxa. The relative sizes and abundance of small fishes and arthropod predators suggest that the usual predator-prey relationships between these taxa could be reversed (sensu McCormick and Polis 1982, Freeman 1989, Polis et al. 1989). Indeed, small marsh fishes are preyed upon by large arthropod predators, including the crayfish *Procambarus* (Chapter 7). In contrast to predatory fishes, the foraging efficiency of
predatory arthropods is enhanced in structurally complex habitats such as the densely vegetated marshes of southern Florida (Chapter 7).

**Summary**

This study examined variation in decapod abundance and guild composition across a range of spatial and temporal scales. Most of the observed variation resulted from processes operating at the regional or landscape scale. That is, the relative abundance of prawns and crayfish at any given location was determined by factors that affected the entire landscape (e.g., hydrology). Prawns appeared to respond positively to increased hydroperiod, likely because of increased production of microalgal and detrital resources. In contrast, crayfish were largely unaffected by hydrologic gradients, consistent with their flexible foraging ecology. Local (e.g., relative risk of predation) and temporal (i.e., seasonal drawdowns) processes were also important to marsh decapods. Prawns were most abundant in sloughs and wet prairies, whereas crayfish were most abundant in sawgrass stands and wet prairies. Seasonal declines in water levels apparently caused crayfish to burrow vertically into the marsh, whereas prawns were forced to move across the marsh and were concentrated into local depressions (i.e., sloughs and alligator holes) in the marsh. Differences in habitat use and behavioral observations suggest that size-structured interactions may be occurring between prawns and their larger crayfish counterparts.
Table 3.1. Effects of habitat, month, habitat x month, and area (nested within month) on abundance of prawn and crayfish in the Refuge.

$log_{10}$-transformed prawn abundance

<table>
<thead>
<tr>
<th>Source</th>
<th>DF</th>
<th>SS</th>
<th>F</th>
<th>P</th>
<th>$R^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Model</td>
<td>191</td>
<td>125.360</td>
<td>4.792</td>
<td>0.0001</td>
<td>79.2</td>
</tr>
<tr>
<td>Habitat</td>
<td>2</td>
<td>22.228</td>
<td>31.878</td>
<td>0.0221</td>
<td>14.0</td>
</tr>
<tr>
<td>Month</td>
<td>23</td>
<td>29.108</td>
<td>1.821</td>
<td>0.0059</td>
<td>18.4</td>
</tr>
<tr>
<td>Habitat x Month</td>
<td>46</td>
<td>16.038</td>
<td>2.545</td>
<td>0.0001</td>
<td>10.1</td>
</tr>
<tr>
<td>Area (Month)</td>
<td>120</td>
<td>57.987</td>
<td>3.528</td>
<td>0.0001</td>
<td>36.7</td>
</tr>
<tr>
<td>Error</td>
<td>240</td>
<td>12.786</td>
<td>0.053</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

$log_{10}$-transformed crayfish abundance

<table>
<thead>
<tr>
<th>Source</th>
<th>DF</th>
<th>SS</th>
<th>F</th>
<th>P</th>
<th>$R^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Model</td>
<td>191</td>
<td>37.370</td>
<td>3.672</td>
<td>0.0001</td>
<td>74.5</td>
</tr>
<tr>
<td>Habitat</td>
<td>2</td>
<td>7.022</td>
<td>25.671</td>
<td>0.0001</td>
<td>14.0</td>
</tr>
<tr>
<td>Month</td>
<td>23</td>
<td>10.081</td>
<td>2.192</td>
<td>0.0059</td>
<td>20.0</td>
</tr>
<tr>
<td>Habitat x Month</td>
<td>46</td>
<td>6.291</td>
<td>2.567</td>
<td>0.0001</td>
<td>12.5</td>
</tr>
<tr>
<td>Area (Month)</td>
<td>120</td>
<td>13.976</td>
<td>2.186</td>
<td>0.0001</td>
<td>28.0</td>
</tr>
<tr>
<td>Error</td>
<td>240</td>
<td>12.786</td>
<td>0.053</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Table 3.2. Partial correlations between abundance of decapod crustaceans and habitat structural features within wet prairies, sloughs, and sawgrass stands. Underlined values are significant at the p<0.05 level.

<table>
<thead>
<tr>
<th></th>
<th>Prairie</th>
<th>Sawgrass</th>
<th>Slough</th>
</tr>
</thead>
<tbody>
<tr>
<td>prawn abundance</td>
<td>0.138</td>
<td>0.133</td>
<td>0.282</td>
</tr>
<tr>
<td>vs crayfish</td>
<td>-0.520</td>
<td>-0.131</td>
<td>-0.125</td>
</tr>
<tr>
<td>abundance</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>vs plant biomass</td>
<td>-0.181</td>
<td>0.273</td>
<td>-0.263</td>
</tr>
<tr>
<td>vs water depth</td>
<td>0.280</td>
<td>0.012</td>
<td>-0.084</td>
</tr>
<tr>
<td>vs canopy height</td>
<td>0.079</td>
<td>0.147</td>
<td>-0.014</td>
</tr>
<tr>
<td>vs conductivity</td>
<td>-0.383</td>
<td>-0.197</td>
<td>-0.316</td>
</tr>
<tr>
<td>vs latitude</td>
<td>-0.129</td>
<td>0.107</td>
<td>0.130</td>
</tr>
<tr>
<td>vs distance to canal</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th></th>
<th>Prairie</th>
<th>Sawgrass</th>
<th>Slough</th>
</tr>
</thead>
<tbody>
<tr>
<td>crayfish</td>
<td>0.002</td>
<td>-0.053</td>
<td>-0.139</td>
</tr>
<tr>
<td>abundance</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>vs plant biomass</td>
<td>-0.197</td>
<td>0.014</td>
<td>0.102</td>
</tr>
<tr>
<td>vs water depth</td>
<td>0.193</td>
<td>0.401</td>
<td>0.330</td>
</tr>
<tr>
<td>vs canopy height</td>
<td>-0.233</td>
<td>-0.066</td>
<td>-0.038</td>
</tr>
<tr>
<td>vs conductivity</td>
<td>-0.089</td>
<td>0.013</td>
<td>-0.192</td>
</tr>
<tr>
<td>vs latitude</td>
<td>0.163</td>
<td>0.078</td>
<td>-0.012</td>
</tr>
<tr>
<td>vs distance to canal</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Table 3.3. Number and percentage (in parentheses) of sites classified correctly (diagonal) and incorrectly (off-diagonals) with respect to habitat type.

<table>
<thead>
<tr>
<th></th>
<th>Actual Prairie</th>
<th>Actual Sawgrass</th>
<th>Actual Slough</th>
</tr>
</thead>
<tbody>
<tr>
<td>Predicted Prairie</td>
<td>58 (40)</td>
<td>30 (21)</td>
<td>25 (17)</td>
</tr>
<tr>
<td>Predicted Sawgrass</td>
<td>45 (31)</td>
<td>99 (69)</td>
<td>24 (17)</td>
</tr>
<tr>
<td>Predicted Slough</td>
<td>41 (29)</td>
<td>15 (10)</td>
<td>95 (66)</td>
</tr>
</tbody>
</table>
Figure 3.1. Mean (+ 1 SE) number of prawn (top) and crayfish (bottom) per square meter of wet prairie, slough, and sawgrass habitats comprising the Refuge. Means with different letters are significantly different at the $p<0.05$ level.
Figure 3.2. Seasonal variation in mean (± 1 SE) number of prawn (top) and crayfish (bottom) collected per square meter of wet prairie, slough, and sawgrass habitats comprising the Refuge. Data for collections made in May 1992 are shown in Figure 3.4.
Figure 3.3. Seasonal variation in mean water depth within wet prairie, slough, and sawgrass habitats comprising the Refuge. Most sawgrass sites and many prairie sites dried up during May 1992, whereas all slough sites contained water.
Figure 3.4. Mean number of prawn (top) and crayfish (bottom) collected per square meter of slough habitat before, during, and after the marsh drawdown of May 1992.
CHAPTER 4

POPULATION- AND ASSEMBLAGE-LEVEL RESPONSES OF MARSH FISHES IN A NORTHERN EVERGLADES WETLAND MOSAIC

Introduction

The northern Everglades landscape is organized and maintained by a hierarchy of processes that operate across a range of spatial and temporal scales (Holling 1992, DeAngelis and White 1994, Holling et al. 1994). For example, variation in hydroperiod (i.e., frequency and duration of inundation) has a regional (i.e., continuous) component that corresponds to a generally north-south gradient and is mediated through variation in factors such as underlying limestone topography, differential rates of peat accretion and oxidation, overdrainage in the north due to construction of perimeter canals, and “ponding” of water in the south due to construction of levees (Richardson et al. 1990). Variation in hydroperiod also has a local (i.e., patchy) component that reflects local disturbance and is mediated through events such as isolated fires, limestone irregularites, dissolution and collapse of limestone pockets, peat “pop-ups”, and the burrowing activities of alligators (Richardson et al. 1990, Gleason and Stone 1994).

In many respects, hydroperiod can be viewed as the critical organizing feature of the Everglades landscape because it facilitates and constrains the activities of producers and consumers at multiple scales (Holling et al. 1994). For example, I demonstrated that plant species composition and habitat structure reflect both local and regional variation in water depth and hydroperiod (Chapter 2). Plant assemblages appear to be most responsive to variation at the local level (i.e., among adjacent habitats), as evidenced by persistent differences in species composition and habitat structure across the marsh landscape. There is also evidence that regional gradients in hydrology and nutrient enrichment affect habitat structure and plant species composition in the northern Everglades (Richardson et al. 1990,
Seasonal and annual variation in precipitation and evapo-transpiration produces a regime of flooding and fire that promotes habitat heterogeneity (DeAngelis and White 1994). Therefore, the structure and dynamics of the vegetative landscape is determined largely by hydrologic factors acting on local, regional, and seasonal scales (Gunderson 1994).

The primary objective of my dissertation research was to determine whether important consumer groups (i.e., decapod crustaceans and fishes) also exhibited scale-dependent responses to the spatially and temporally heterogeneous Everglades landscape. In other words, how is population abundance and assemblage composition at a given location in the marsh landscape affected by processes operating locally (i.e., within and among habitats), regionally (i.e., among widely-separated locations), and seasonally (i.e., among months)? In the previous chapter, I showed that the abundance of prawns and crayfish did indeed respond to these cross-scale processes. Furthermore, I showed that these species responded in very distinct ways and that differences between the species may reflect both differences in life history traits and intraguild interactions. Finally, I showed that there was habitat-specific decapod assemblage structure. In this chapter, I test whether these findings can be generalized by analyzing abundance data for the small-fish assemblage of the northern Everglades. By using a larger suite of species, I am able to more fully explore the issue of habitat-specific assemblage structure. I use this and the previous chapter to describe the basic spatial ecology and temporal dynamics of decapods and fishes within the northern Everglades, which appears to be quite different from the other compartments comprising the greater Everglades ecosystem (see various chapters in Davis and Ogden [1994]). I also examine the consequences of habitat conversion in the Everglades on the success of small fishes. Finally, I discuss how patterns of habitat use and distribution of small fishes may be related to the distribution and abundance of arthropod and vertebrate predators along hydrologic and habitat-complexity gradients.
The Small-Fish Assemblage

About thirty species of freshwater fishes occur regularly in the marshes of the Florida Everglades (Dineen 1974, 1984, Loftus and Kushlan 1987; scientific and common names of fishes collected during this study are provided in Table 4.1). Small-sized fishes in the families Poeciliidae (3 species), Cyprinodontidae (1 species), Fundulidae (2 species), and Elassomatidae (1 species) are numerically dominant. Additionally, two diminutive species belonging to the relatively speciose family Centrarchidae are modestly abundant. Together, these nine species comprise what I will refer to as the small-fish guild or assemblage.

The ichthyofauna of southern Florida lacks endemics (Gilbert 1987) and occupies a landscape that formed very recently (≈ 5,000 YBP). Therefore, this ichthyofauna is best characterized as a group of rapidly dispersing, opportunistic species rather than as a co-evolved assemblage of species uniquely adapted to the Everglades landscape. That is not to say these species do not interact with one another and that these interactions don’t affect patterns of habitat use and distribution across the Refuge landscape. Indeed, shared individualistic responses can result in habitat-specific assemblage structure (e.g., Gleason 1926, Strong 1983, Capone and Kushlan 1991, Kodric-Brown and Brown 1993).

The ecological success of these fishes is likely due to autecological factors such as ability to tolerate physiologically-stressful conditions (i.e., high water temperatures and low dissolved oxygen levels), opportunistic feeding habits, and a suite of life history traits well-suited for a seasonally dynamic landscape (Kushlan 1974a). In general, these species mature rapidly and at relatively small sizes, have continuous or nearly-continuous spawning, and either produce many small-sized clutches (e.g., mosquitofish, least killifish) or a few large clutches (e.g., pygmy sunfish) each hydrologic year.

Large-bodied fishes are not particularly successful in most Everglades habitats because recruitment cannot offset high mortality rates associated with frequently occurring conditions of hypoxia, intense size-selective predation by wading birds, and drought (e.g.,
inundation result in growth of populations of large-bodied fishes, whereas periods of
protracted drought result in reduction of these populations (Kushlan 1976). When present,
these fishes are largely restricted to deep water refugia such as sloughs and alligator holes
(Dineen 1974, 1984, Loftus and Kushlan 1987). Interestingly, the relative abundance and
(presumably) importance of predatory fishes and arthropods vary predictably along
continuous (landscape level) and dis-continuous (local level) gradients in water depth.
Significantly, the small-fish assemblage appears to be vulnerable to both vertebrate and
arthropod predators (see Discussion section below; Chapters 6 and 7).

Some Caveats and Assumptions

I was interested in testing hypotheses about scale-dependent patterns and processes,
which required some critical choices and assumptions. First, I adopted a landscape
perspective (Wiens and Milne 1990, Chick and McIvor 1994), which allowed me to view the
entire Everglades as a hierarchy of mosaics: i.e., plant stems nested within habitats, habitats
nested within areas, areas nested within water compartments, water compartments nested
within hydrologic basins, etc. Second, I assumed that each distinct level of this spatial
hierarchy corresponded with a distinct group of organizing processes (O’Neill et al. 1986,
decided to focus on local (i.e., among adjacent habitats) and regional (i.e., among widely-
separated areas in the landscape) scales because these are important axes of community
organization in freshwater and marine systems (e.g., Paine and Levin 1981, Schoener 1987,
abundance was a reliable integrator/indicator of aquatic macrofaunal responses, which
obviated the need to assess individual demographic parameters (i.e., birth, death,
immigration, emigration).
Study Area and Methods

The Northern Everglades Marsh Landscape

The following description of the study area is adapted from Jordan et al. (1994) and Chapters 2 and 3. Research was performed in the Arthur R. Marshall Loxahatchee National Wildlife Refuge (hereafter the Refuge), which is the northern remnant of the vast Everglades ecosystem. The 57,234 ha Refuge is encircled by a deep-water canal and dike system that drains an approximately equal area of the Everglades Agricultural Area (Richardson et al. 1990). Much of the hydrology and water chemistry of the Refuge is driven by rainwater, but water derived from the Everglades Agricultural Area and delivered by perimeter canals is enriched with phosphorus, nitrogen, and chloride ions. This water is not distributed evenly across the Refuge landscape because topographic variation in the underlying peat results in a gradient of increasing depth and hydroperiod along the north-south axis of the Refuge. The perimeter canal and dike system has intensified this hydrologic gradient through increased drainage in the northern end and increased “ponding” of water behind dikes in the southern end of the Refuge (Richardson et al. 1990).

Nutrient enrichment and alterations in hydrology have resulted in profound changes to the habitat mosaic comprising the Refuge (Richardson et al. 1990, Davis 1994, Davis et al. 1994). Historically, the oligotrophic Refuge landscape was comprised of emergent wet prairies, sawgrass stands, sloughs (including alligator holes), and elongate tree islands overlying a deep bed of peat. Stands of cattail (*Typha* spp.) and other opportunistic species have replaced these habitats in disturbed areas near canals because of increased nutrient loading and protracted hydroperiods (Richardson et al. 1990, Davis 1994, Newman et al. 1996). Plant community changes decline with increasing distance from perimeter canals (Richardson et al. 1990), and interior marshes appear to have retained much of their mosaic nature (Chapter 2). However, ecological function (e.g., primary and secondary production, food web structure) may have been compromised within this marsh mosaic. The present study was motivated by concern over the impact of habitat conversion on wetland resources.
and forms part of a larger ecological characterization of the Refuge (Jelks et al. 1992, Jordan et al. 1994, Chapter 2).

Field Survey

Fishes were collected with an aluminum throw trap (100 x 100 x 75 cm), which provides accurate and reliable density estimates for the small-sized fishes that predominate in the Refuge (Kushlan 1981, Freeman et al. 1984, Chick et al. 1992, Rozas and Minello In press). The throw trap was thrown into the desired habitat and then pressed firmly into the substrate. Above-ground plants were identified, counted (relative coverage), uprooted, and rinsed to dislodge any fishes. A bar seine with 3.0-mm mesh was then passed through the trap until three consecutive empty sweeps were obtained. Fishes were picked carefully from the detritus collected in each sweep of the bar seine and preserved in 10% buffered formalin. Fishes were later rinsed and enumerated in the laboratory.

Water depth, canopy height, plant biomass, and plant species composition were also measured in order to characterize the habitat mosaic (Jordan et al. 1994, Chapter 2) and examine relationships between habitat structure and fish abundance. Habitat data are presented elsewhere (Jordan et al. 1994, Chapter 2) and only the essential details will be recounted here. In summary, sloughs were relatively deep, structurally simple, had poorly developed canopies, and were dominated by floating aquatic plants such as bladderwort (Utricularia) and water lily (Nymphaea). Sawgrass stands were relatively shallow, structurally complex, had well developed canopies, and supported virtual monocultures of Cladium. Wet prairies were intermediate in depth, structural complexity, and canopy development. Dominant plant taxa included emergent sedges and grasses (e.g., Rhynchospora, Eleocharis, Panicum). Although there was some overlap along univariate environmental axes, these three habitats occupied distinct multivariate space with respect to physical structure and plant community composition (Chapter 2).
Sampling was performed approximately monthly between February 1990 and July 1992 (24 sampling events). During each sampling period, six areas (statistical blocks) were randomly selected for sampling using a grid map of the Refuge; however, some portions of the Refuge were avoided because they were closed to airboat travel or because excessive woody vegetation limited access. Within each area, one site each of sawgrass, wet prairie, and slough habitat was sampled as encountered. All three habitats could be found in proximity to one another except in the northern, drier half of the Refuge, where slough habitat was less common. Alligator holes were substituted in these areas because they were similar to sloughs with respect to vegetation composition and habitat structure (Gunderson and Loftus 1993). The term slough refers to both slough and alligator hole habitats throughout the rest of this paper. Within each habitat, three throw traps (subsamples) were haphazardly collected and average densities of fishes were calculated for these three subsamples.

As mentioned above, extensive habitat conversion has occurred in the southern end of the Refuge due to increased nutrient loading and protracted hydroperiod. Specifically, a virtual monoculture of cattail has replaced ≈2,400 ha of what was once a mosaic of sawgrass stands, wet prairies, and sloughs (Richardson et al. 1994, Davis 1994). In addition to vegetation composition, nutrient-enriched cattail sites are distinct from the interior habitat mosaic as measured by greater water depths, more well-developed canopies, greater accumulations of detritus, more flocculent sediments, increased dominance of blue-green algae, lower dissolved oxygen levels, and changes in macroinvertebrate community composition (Browder et al. 1994, Davis 1994, Chapter 3; see Figure 4.6). It has been hypothesized that these conditions may affect higher trophic levels (e.g., fishes) directly or through altered food web structure (Richardson et al. 1990, Browder et al. 1994, Davis 1994). I tested this hypothesis by comparing the mean abundance of fishes collected at cattail sites with those of interior marsh sites. Throw traps were used to collect fishes from cattail sites during the periods February 1990 (4 sites, 1-3 samples per site), January 1992
(6 sites, 1 sample per site), and March 1992 (6 sites, 1 sample per site). Sampling procedures were identical to those used for interior sites except when the cattail canopy exceeded about 3 meters (=5 sites). For these sites, I carefully clipped cattail culms about 1 meter above the water line, waited about 30 minutes to avoid sampling any fishes attracted to this minimal above-water disturbance, and then deployed the throw trap.

**Data Analysis**

Fish abundance, habitat structure (water depth, canopy height, plant biomass), and landscape data (i.e., conductivity, distance to canal, latitude) were log10-transformed prior to analysis to better conform to parametric assumptions (e.g., homogeneity of variances, normality). Analyses using transformed and nontransformed data produced qualitatively similar results, therefore I generally present results for nontransformed data to simplify interpretation. Statistical procedures generally followed Winer et al. (1991), Milliken and Johnson (1992), and Sokal and Rohlf (1995). Primarily, these data were used to address questions at both the species and community level. I also used subsets of these data to examine the effects of marsh drawdown and cattail invasion on the small-fish assemblage.

Analyses of variance (ANOVAs) were used to determine the effects of month, area (nested in month), habitat, and the habitat x month interaction on the average abundance of each of the nine numerically dominant fishes. Specifically, these analyses examined how variation in fish abundance could be partitioned among several ecologically relevant scales, i.e., among adjacent habitats (local scale), among widely-separated areas (landscape scale), and among months (seasonal scale). Month and area (nested within month) were treated as random effects in these analyses, whereas habitat was treated as a fixed effect. Least-squares means were used to test for differences in fish abundance among habitats. Partial correlation analysis was used to examine relationships between fish abundance, habitat structure data (water depth, canopy height, plant biomass), and correlates of underlying gradients in nutrient enrichment and hydrology (i.e., distance to canal, conductivity, latitude).
During 1992, water levels in much of the Refuge declined to the point that many sawgrass and wet prairie sites went dry, which provided an excellent opportunity to characterize the responses of fishes to a reduction in the availability of inundated marsh surface. I separated 1992 collection data into periods corresponding to Before (January and March), During (May), and After (July) the drying event, and then tested two specific hypotheses by constructing linear contrasts in tandem with the ANOVAs described above. First, I tested whether fishes became concentrated in sloughs as water levels dropped (i.e., Before vs. During contrast). I then tested whether fish populations in sloughs “rebounded” after the marsh surface was re-inundated (Before vs. After contrast). In essence, this contrast asks whether the effects of drought persisted after a hydrologic disturbance.

One of my primary goals was to test the hypothesis that sloughs, wet prairies, and sawgrass stands supported distinct assemblages of fishes. I approached this question in several ways. First, I used the ANOVA model described above to determine the effects of month, area (nested in month), habitat, and the habitat x month interaction on 1) the average abundance of all fishes combined, 2) species richness (i.e., the number of species in each group of three throw traps), and 3) the vector of abundance data for the nine numerically dominant species. The first two analyses were univariate ANOVAs, whereas the third analysis was a multivariate ANOVA that tested for differences in multivariate community space. Species richness was strongly correlated with total fish abundance (r=0.582, p<0.0001); therefore, I included total fish abundance as a covariate in the univariate ANOVA examining species richness. Discriminant function analysis was then used to determine how well the vector of species abundance data classified sites with respect to habitat type. High rates of correct classification indicate some degree of correspondence between fish assemblage composition and the environmental characteristics of each habitat type (i.e., habitat-specific assemblage structure). These data are presented in graphical form to illustrate correspondence between habitats and fish species in multivariate space.
Dominance-diversity curves were produced to illustrate richness and eveness components of fish diversity for each habitat (Magurran 1988). A nonparametric rank test (Kendall’s tau) measured the degree of concordance in fish assemblage structure (using only the nine most abundant taxa) between each habitat type. Low concordance of species ranks would indicate habitat-specific assemblage structure.

Finally, I used partial correlation analyses to measure co-association and the potential strength of interactions between pairs of species (n=36 comparisons) within the small-fish assemblage. Simple correlations indicated that most species were strongly correlated with one another. However, simple correlations not only measure how two species respond to each other, but also how they respond to shared environmental conditions. Therefore, this environmental component should be (statistically) removed prior to assessing interaction strengths (e.g., Norton 1991, Pfister 1995). This was accomplished by re-running the univariate ANOVAs described above after including water depth as a covariate. I included water depth as a covariate because this was the only environmental factor that appeared to affect total fish abundance (see Results section below). Residuals were calculated and saved for each of these ANOVAs, and then I compared the residuals for each species using partial correlations. Residuals represented variation in fish abundance that could not be ascribed to environmental conditions as measured in this study (Norton 1991).

For each cattail site, I calculated means for the following response variables: total fish abundance, water depth, canopy height, dry plant biomass, conductivity, and dissolved oxygen levels. I also calculated means for these response variables at each of the six interior areas (averaging across habitat types) sampled during February 1990, January 1992, and March 1992. Response variables were log10-transformed and then used in two-way ANOVAs to test for the effects of habitat type (cattail vs. interior) and sampling period. I used least-squares means to compare the abundance of fishes in cattail and interior sites during each sampling period.
Results

Species-Level Responses

A total of 33,601 individuals, 14 families, 20 genera, and 23 species were collected from the sloughs, wet prairies, and sawgrass stands of the Refuge (Table 4.1). However, 99% of all fishes collected belonged to only 9 species: *Gambusia holbrooki* > *Heterandria formosa* > *Jordanella floridae* > *Fundulus chrysotus* > *Lucania parva* > *Elassoma evergladei* > *Poecilia latipinna* > *Lepomis punctatus*. Most analyses and inferences will pertain to this guild of small fishes. On average, the Refuge supported 26 fishes per m². Fishes were not distributed evenly among habitats and the habitat effect accounted for 9% of the variation observed in total fish abundance (Table 4.2, Figure 4.1). Sloughs supported higher densities of fishes (42 per m²) than wet prairies (22 per m²), which in turn supported higher densities than sawgrass stands (14 per m²). Collections were made during a marsh drawdown that occurred in May 1992 (see “Effects of a Marsh Drawdown” section below), which could exaggerate differences between sloughs and the other two habitats. However, mean densities were still significantly higher in sloughs (26 per m²) than in wet prairies (22 per m²) or sawgrass stands (15 per m²) after omitting data for May 1992.

Species tended to differ somewhat in their numerical responses to available habitats (Figure 4.1), with the habitat effect accounting for between 2 and 31% of the variation observed in the abundance of individual taxa (Table 4.2). *Gambusia, Lucania, Enneacanthus*, and *Lepomis* were most abundant within sloughs; *Jordanella* and *Poecilia* were most abundant in sloughs and wet prairies; *Heterandria* and *Fundulus* were most abundant in wet prairies; and *Elassoma* was most abundant in wet prairies and sawgrass stands (Figure 4.1). *Gambusia, Lucania, and Lepomis* abundance was greatly depressed in sawgrass stands and wet prairies, whereas *Elassoma* abundance was greatly depressed in sloughs. Most other species were too rare to make inferences about habitat use patterns.
However, *Erimyzon* (n=137) and *Notemigonus* (n=80) were found only in sloughs (logistic analyses indicated these patterns were significant). Additionally, the “sunfish guild” (i.e., lepomine fishes) appeared to be consistently more abundant in sloughs. One obvious (and important) pattern is that larger-bodied species were more abundant in the deeper, structurally-simple sloughs (Table 4.1) than in shallower, structurally-complex wet prairies and sawgrass stands.

Partial correlations between fish abundance and habitat structure data were generally low (i.e., less than ± 0.25), especially considering the large sample sizes. In fact, the only significant partial correlation was between total fish abundance and water depth (r=0.309, p<0.0001).

Perusal of interaction plots in Figure 4.2 and habitat x month interactions in Table 4.2 indicates that habitat use varied considerably among sampling months. The habitat x interaction effect accounted for between 8 and 18% of the variation observed in the abundance of individual taxa (Table 4.2). Much of this interaction was driven by the concentrating effects of the May 1992 marsh drawdown event (see “Effects of Marsh Drawdown” section below). The highest density of fishes (398 per m²) observed in sloughs was during May 1992 (see Figure 4.3). In contrast, the lowest densities of fishes collected in wet prairies (6 fishes per m²) and sawgrass stands (1 fish per m²) were also during May 1992! Finally, the highest density of fishes collected in wet prairies (39 fishes per m²) was during August 1991, whereas the peak month in sawgrass stands (27 fishes per m²) was during July 1990.

Water levels varied considerably during the study period (see Figure 3.3) and probably played a significant role in temporal effects. Indeed, the main effect of month explained a considerable amount (6-27%) of the variation observed in the abundance of individual taxa (Table 4.2). Overall, 23 and 18% of the variation observed in total fish abundance was accounted for by the habitat x month and month effects, respectively (Table 4.2). The temporal dynamics of several individual taxa should be noted (Figure 4.2). First,
*Jordanella* was relatively abundant at the start of the study and then declined rapidly as other fishes slowly dispersed across the Refuge following a severe drought in 1989. In contrast, populations of most other taxa started out rather small and tended to grow during the study period (esp., *Lucania, Heterandria, Enneacanthus*). *Gambusia* was an early colonist in reflooded portions of the marsh and was numerically dominant throughout much of the study period.

Similar to responses observed for decapods (Chapter 3), large amounts (20-35\%) of the variation observed in the abundance of individual taxa was attributable to area effects (Table 4.2). About 22\% of the variation in total fish abundance could be attributed to area effects. Overall, this suggests that factors operating at large scales profoundly influenced fish abundance.

Partial correlations between fish abundance and landscape data (i.e., conductivity, distance to peripheral canal, latitude) were invariably low (i.e., less than ± 0.25) and provided little insight into those factors responsible for the sizeable area effects described above.

**Effects of a Marsh Drawdown**

Water depth and latitude were negatively correlated with one another ($r=-0.351$, $p<0.0001$), indicating that hydroperiod increased towards the southern end of the Refuge. Therefore, it does appear that a hydroperiod gradient occurs across the Refuge landscape. The marsh drawdown afforded a unique glimpse of this north-south hydrologic gradient. Airboat access was “difficult” during this month because most interior wet prairies and sawgrass stands in the northern, drier half of the Refuge did not have surface water! The only inundated areas over large portions of the Refuge were networks of inter-connected alligator holes and occasional sloughs. The overall response of fishes during this drawdown was to move into dry season refugia such as sloughs and alligator holes. Indeed, one isolated alligator hole contained 1,849 fishes per m$^2$ in May 1992! Perusal of Figure
4.3 shows that almost all taxa were concentrated in sloughs during this period, although for some taxa the increase was not statistically significant. Interestingly, the only species that showed a decline during the drying event was the larger-bodied spotted sunfish, which is typically successful in slough habitats (Figure 4.3).

The marsh drawdown also provided an opportunity to determine the effects of a minor drought on resiliency of small fish populations. I could not detect differences in the density of any species between the Before and After drought periods, suggesting that demographic processes (e.g., deaths, emigration) quickly “reset” slough densities.

**Assemblage-Level Responses**

I attacked the question of habitat-specific assemblage structure from multiple angles. First, I looked at how patterns of assemblage structure varied among habitats at the scale of the entire dataset (i.e., disregarding the spatiotemporal sampling hierarchy). Total species richness was higher in sloughs (S=21) than in wet prairies (S=15) and sawgrass stands (15). Only two species (*Lepisosteus platyrhinchus, Clarias batrachus*) were found in sawgrass stands or wet prairies, but not in sloughs. Therefore, the species complements within these former habitats were almost completely nested subsets of what occurred in sloughs (Kodric-Brown and Brown 1993). Figure 4.4 shows dominance-diversity plots for sloughs, wet prairies, and sawgrass stands. These curves show that the allocation of individuals among species (i.e., evenness) is fairly equitable across habitats and confirm that sloughs are more speciose than wet prairies and sawgrass stands. Finally, I used Kendall’s tau to assess concordance of species ranks between sloughs and wet prairies (tau=0.778, p=0.0035), between sloughs and sawgrass stands (tau=0.611, p=0.0218), and between wet prairies and sawgrass stands (tau=0.833, p=0.0018). These values indicate moderate to high concordance and suggest that, at this scale of analysis, there is much similarity in assemblage composition. Therefore, analyses of habitat-specific assemblage structure at this crude scale provide equivocal results.
The second analytical approach I used to examine habitat-specific assemblage structure was to compare the number of species obtained in each set of three throw trap samples. Table 4.2 shows that each level of the spatiotemporal sampling hierarchy affected fish species richness: habitat (8%), month (22%), habitat x month (16%), and area (24%). Least-squares means indicated that all three habitats were significantly different from each other (sloughs > wet prairies > sawgrass stands; see Figure 4.4). Comparison of least-squares means indicated that slough habitats still had significantly higher species richness after adjusting (i.e., rarefying; Magurran 1998) for total fish abundance, but that wet prairies and sawgrass no longer differed from one another with respect to fish species richness. Overall, analyses of species richness data suggest that there is evidence for habitat-specific assemblage structure. Variation in species richness was also considerable at regional and seasonal levels (Table 4.2, Figure 4.4).

By definition, ecological communities are multi-species groups that co-occur in space and time, which suggests that multivariate analysis may provide greater resolution of the habitat-specific assemblage structure question. Multivariate ANOVA indicated that fish-assemblage structure varied among habitat (Wilk’s lambda=0.15, p<0.0001). Inspection of Figure 4.5 indicates that sloughs, wet prairies, and sawgrass stands were clearly isolated in multivariate community space. Moreover, the location of individual taxa in this canonical bivariate plot represents their position in community space, and largely corresponds with the results of univariate tests of habitat use described above. Relatively deep, structurally-simple sloughs were dominated by *Gambusia, Lucania, Enneacanthus*, and *Lepomis*. *Jordanella, Fundulus, Ellasoma*, and *Heterandria* tended to be more common in relatively shallow, densely-vegetated wet prairies and sawgrass stands. *Poecilia* is one of the most patchily distributed fishes in southern Florida, which contributes to its enigmatic position in multivariate community space (Figure 4.5). Species abundance data correctly classified sites with respect to habitat type very well in sloughs (76%) and sawgrass stands (76%), but somewhat less so in wet prairies (56%) (Table 4.3). Overall, multivariate procedures
provide good support for the notion that sloughs, wet prairies, and sawgrass stands were characterized by unique assemblage structure.

Results of pairwise comparisons of species residuals (i.e., abundance data with environmental effects removed) are provided in Table 4.4. Only one out of 36 possible combinations was (weakly) significant, which might have been predicted by chance alone. Therefore, there is little correlative evidence that distribution patterns of these species is determined by strong intraguild interactions.

Comparison of Cattail and Interior Sites

Two-way ANOVAs revealed that water depth, canopy height, dissolved oxygen levels, and conductivity differed between cattail and interior marsh sites (Figure 4.6). More importantly, fish abundance in cattail sites was 3-11 times greater than in interior marsh sites ($F_{1,28} = 18.7, p = 0.0002$). This pattern contrasts markedly with that observed for prawns and crayfish in Chapter 3.

Discussion

Fish Abundance along a Spatial Hierarchy

Ecologists have come to recognize that natural landscapes are spatially and temporally heterogeneous, and that this heterogeneity provides the template upon which demographic and community processes are realized (Levin 1992). Fundamental to this emerging perception of the natural world is an appreciation for the multiple scales at which process and pattern interwine (e.g., 1989a, 1989b, 1989c, Wiens and Milne 1989, Holling 1992). The central challenge to ecologists is to determine which scales are most relevant to their system of interest (Farnsworth and Ellison 1996). In previous research, I used a landscape perspective to demonstrate that water levels, plant species composition, and habitat structure vary at several scales within the northern Everglades (Chapter 2). I have also demonstrated that the abundance of decapod crustaceans is organized along a
spatiotemporal hierarchy (Chapter 3). In the present study, I have shown that the abundance of small fishes at any given location is the product of processes operating at local, regional, and seasonal scales.

On a local level, most small fishes were distributed nonrandomly among adjacent sloughs, wet prairies, and sawgrass stands. Relatively deep, structurally-simple sloughs supported the highest density of fishes, although these habitats occupied a relatively small amount of marsh surface (except during drought conditions). *Gambusia*, *Lucania*, *Enneacanthus*, and *Lepomis* densities were significantly higher in sloughs than in wet prairies or sawgrass stands. Areally extensive wet prairies supported the next highest densities of fishes, including *Heterandria*, *Jordanella*, *Fundulus*, and *Elassoma*. Finally, although supporting fewer fishes, areally extensive sawgrass stands contribute significantly to marsh-wide secondary productivity. Important processes that determine local abundance include physical conditions (e.g., dissolved oxygen levels), resource availability, intensity of competition, and risk of predation (e.g., McIvor and Odum 1988, Jordan et al. 1996b). There were persistent differences in water depth, plant biomass (i.e., habitat complexity), and canopy stature among sloughs, wet prairies, and sawgrass stands (Chapter 2). Predator assemblage composition varies predictably along these gradients, with large predatory fishes predominating in relatively deep, structurally-simple sloughs and predatory arthropods predominating in relatively shallow, structurally-complex wet prairies and sawgrass stands. Therefore, small fishes may find themselves between a “rock and a hard place” with respect to these different types of predators (Chapter 7).

Although there was strong evidence for the importance of local processes, it appeared that regional processes were more important in determining fish abundance. This pattern was also true for decapods (Chapter 3), but not for most dominant plant taxa or habitat structural features (Chapter 2). It appears that landscape-wide variation in water depth and nutrient enrichment may contribute to observed variation in fish abundance. These factors are discussed fully in Chapter 3 and will only be briefly recounted here. First,
gradients in nutrient enrichment can have strong bottom-up effects on small fishes. For example, fish densities were considerably higher in highly eutrophic cattail sites than in oligotrophic interior habitats. Fishes may be more efficient at converting abundant blue-green microalgae into biomass than decapod crustaceans (Chapter 3). Perhaps more importantly, cattail sites are deeper, inundated longer, and relatively close to permanent deep-water refugia in the form of perimeter canals (see below). It is likely that hydrologic conditions and nutrient enrichment interact to affect fish abundance (e.g., Newman et al. 1996). Considerable gaps remain in our understanding of how these factors affect higher trophic groups (Browder et al. 1994, Davis 1994).

Fish Responses to Variation in Water Levels

Fishes and other vagile organisms move about their landscape, encounter a hierarchy of opportunities (and risks), and respond with a hierarchy of behavioral decisions (Lima and Dill 1990, Holling 1992). Of course, opportunities change as the surrounding landscape changes. Perusal of Figure 4.2 and Table 4.2 (i.e., habitat x month interactions) reveals that habitat use patterns varied considerably among sampling periods. During the wet season, sawgrass stands may appear quite attractive to a small fish that is in search of foraging opportunities and avoiding predatory fishes. However, this fish must alter its behavior as water levels recede and conditions (i.e., depth, dissolved oxygen levels, density of competitors and predators) become less tolerable within the sawgrass stand. Therefore, the relative quality of habitats within the Refuge varies seasonally. Although sloughs comprise ~1% of the Refuge landscape during the wet season, they comprise ~100% of the inundated marsh surface during severe droughts! Significantly, each of the habitats comprising the Refuge mosaic may alternate between “source” and “sink” states (sensu Pulliam 1988) through seasonal and annual hydrologic cycles. The demographic potential of habitats may change with location in the Refuge. For example, dry-season refugia may be relatively more important to small fishes in the northern, drier half of the Refuge. It would be a worthwhile
endeavor to couple the demographic models of Pulliam and his colleagues (e.g., Pulliam 1988, Pulliam and Danielson 1991, Pulliam et al. 1992) with a seasonally-dynamic landscape model of the Everglades.

In the previous chapter, I showed that prawns and crayfish differed considerably in their responses to a marsh drawdown. Prawns concentrated in local dry season refugia because they could not burrow into the marsh surface (Kushlan and Kushlan 1980), whereas crayfish apparently burrowed into the peat substrate (Kushlan and Kushlan 1979, Jordan et al. 1996a). Since Everglades fishes do not burrow, I expected that they would respond to a marsh drawdown by concentrating. Indeed, the overall concentration factor in sloughs and alligator holes was 16 fold, which is consistent with previous estimates for marsh systems in southern Florida (Carlson and Duever 1977, Loftus and Kushlan 1987). Densities of both centrarchid species (*Lepomis* and *Enneacanthus*) remained unchanged or even declined somewhat during the drawdown of May 1992. This likely reflects both the low abundance of these species in wet prairies and sawgrass stands prior to the drawdown, and their relatively poor tolerance of the harsh physiological conditions (i.e., high temperatures, low dissolved oxygen levels) that occur in dry season refugia (Kushlan 1974a, 1974b, Loftus and Kushlan 1987).

Most species “rebounded” quickly after the drawdown of 1992, with their densities in sloughs returning to pre-drawdown levels in roughly two months. Of course, “rebounding” involves both mortality during the drawdown (Kuslan 1974) and emigration from crowded sloughs after re-inundation of the surrounding marsh (Loftus and Kushlan 1987). It appears that emigration was significant since the densities of most fishes within wet prairies and sawgrass stands were not significantly different between the Before and After periods. To reiterate, the small-fish assemblage is comprised of a group of opportunistic species that 1) are tolerant of harsh physiological conditions, 2) are capable of rapid dispersal, and 3) possess a suite of life history traits well adapted for life in the
seasonally dynamic marshes of the Florida Everglades (Loftus and Kushlan 1987). There resiliency is not unexpected.

Fish Assemblage Composition

In the previous chapter, I showed that sloughs, wet prairies, and sawgrass stands were characterized by distinct decapod-assemblage structure. This was a somewhat trivial result given that the “assemblage” was comprised of two species! Therefore, I was very interested in using data from the more speciose fish community to address the question of habitat-specific assemblage structure. Sloughs were distinct from wet prairies and sawgrass stands when I examined this question at the level of species richness (i.e., total number of species) or species density (i.e., number of species per unit area). However, I found relatively high concordance of species ranks among sloughs, wet prairies, and sawgrass stands. This suggested that fish assemblage-structure did not vary considerably among habitats!

The data above can be reconciled by noting that fish assemblages in wet prairies and sawgrass stands were nested subsets of the larger slough assemblage. In essence, the nine species comprising the small-fish guild were ubiquitous. For the most part, it was the larger species (e.g., *Lepomis* spp., *Erimyzon*) and more “open-water” species (e.g., *Notemigonus*, *Labidesthes*) that differentiated the slough assemblage. Kodric-Brown and Brown (1993) found a similar pattern of nestedness based on water depth and “openness” in the fish assemblages occupying a system of Australian springs. In general, water depth appears to play an important role in structuring freshwater fish communities, with larger fishes occupying deeper pools and smaller fishes occupying shallower pools (e.g., Power 1984, Schlosser 1987, 1995, Capone and Kushlan 1991, Harvey and Stewart 1991). Interestingly, these studies have revealed that large fishes utilize deeper habitats often to avoid terrestrial and avian predators, whereas smaller fishes utilize shallower habitats to avoid predatory fishes. Similarly, large arthropods avoid deeper habitats to minimize exposure to predatory
fishes (Werner and McPeek 1994). The end result of these predator-mediated behavioral cascades is that small fishes increase their exposure to large arthropods! I propose that large arthropods may play an important role in regulating populations of small-size fishes in heavily vegetated marsh systems such as the northern Everglades (see Chapters 6 and 7).

Assemblage data are multivariate by definition; therefore, it is logical to examine the question of habitat-specific assemblage structure using multivariate tools. Multivariate ANOVA and discriminant function analysis indicated that sloughs, wet prairies, and sawgrass stands occupied distinct locations in multivariate community space. Two relatively distinct groups of species emerged (slough species and wet prairie/sawgrass species), although these groups could be predicted based on their individual responses to the habitats censused (sensu Gleason 1926). Strong covariation in abundance between species pairs would provide indirect support for habitat-specific structure. However, partial-correlation analysis provided little evidence that species were interacting strongly. Therefore, I conclude that 1) individual species had distinct patterns of habitat use, 2) habitats could be distinguished by different groups of species, and 3) these differences reflected the sorting out of species based on autecological factors rather than synecological factors. This individualistic view (Gleason 1926, Strong 1983) is consistent with the spatiotemporal heterogeneity of the northern Everglades landscape; i.e., hydrology, habitat complexity, physiological conditions (e.g., oxygen levels), and predation probably interact to maintain fish populations at levels too low for competition to be an important process except during “ecological crunches.”

Fish Abundance in Cattail and Interior Sites

As mentioned earlier, this research was motivated by a concern over the effects of habitat conversion on wildlife resources. Resource managers were especially concerned that the replacement of ≈2,400 ha of marsh mosaic by a virtual monoculture of cattail would adversely affect aquatic prey communities. Low dissolved oxygen levels, significant
accumulations of detritus, dense mats of blue-green algae, dense canopy development, and alteration of invertebrate prey communities were identified as mechanisms possibly limiting to fishes (e.g., Browder et al. 1994, Davis 1994). Indeed, these stands of cattail look rather inhospitable when standing on the banks of perimeter levees or flying overhead in an airplane. However, from the perspective of the small-fish assemblage, it appears that cattail provides a rather viable habitat. Fish densities were \( \approx 4-5 \) times greater in cattail stands than in the interior habitat matrix. Three factors likely drive this increased abundance. First, nutrient enrichment may lead to significant bottom-up effects in cattail stands. Browder et al. (1994) postulated that blue-green algae, which dominate in eutrophic sites, are of lower nutritive value than other microalgal taxa. However, critical experiments have not been performed to evaluate this hypothesis. Second, cattail stands are also characterized by longer, less variable hydroperiods (Richardson et al. 1990). Therefore, reproduction may not be interrupted by seasonal and annual variation in water levels. The final and perhaps most parsimonious explanation is that cattail stands comprise part of the vast littoral zone associated with the deep-water canal system surrounding the Refuge. In essence, the canal system functions as a linear lake that supports a diverse assemblage of fishes (Wiechman 1987), which in turn rely upon the littoral zone for production of prey resources and nursery habitat for juveniles.

Summary

This study examined variation in fish abundance and assemblage composition across a range of spatial and temporal scales. Fishes exhibited scale-dependent responses to the spatiotemporal sampling hierarchy. Regional processes appeared to be most important in regulating population abundance, although local and seasonal factors were also important. Sloughs supported the most species, the highest species density, and the greatest densities of fishes. Most species exhibited nonrandom habitat use, and these patterns of habitat use translated into habitat-specific assemblage structure. However, there was little
correlative evidence for strong association among species pairs. Most species concentrated into sloughs during the marsh drawdown of May 1992, with the larger species generally showing the smallest increases. Fish densities within sloughs and other habitats did not differ significantly between periods before and after the marsh drawdown, suggesting that populations “rebounded” rather quickly following this hydrologic disturbance. Finally, eutrophic cattail sites supported ≈4-5 times as many fishes as the interior marsh mosaic. Apparently, cattail stands act as a vast littoral zone for the canal system encircling the Refuge.
Table 4.1. Absolute (#) and relative abundance (%) of fishes collected with throw traps in the Refuge between February 1990 and July 1992.

<table>
<thead>
<tr>
<th>Scientific Name</th>
<th>Common Name</th>
<th>Sloughs</th>
<th>Prairies</th>
<th>Sawgrass</th>
<th>Totals</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Atherinidae</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Labidesthes sicculus</td>
<td>brook silverside</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td><strong>Catostomidae</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Erimyzon sugetta</td>
<td>lake chubsucker</td>
<td>137</td>
<td>1</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td><strong>Centrarchidae</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Chaenobryttus gulosus</td>
<td>warmouth</td>
<td>13</td>
<td>0</td>
<td>7</td>
<td>0</td>
</tr>
<tr>
<td>Enneacanthus gloriosus</td>
<td>bluespotted</td>
<td>132</td>
<td>1</td>
<td>76</td>
<td>1</td>
</tr>
<tr>
<td>Lepomis macrochirus</td>
<td>bluegill</td>
<td>3</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Lepomis marginatus</td>
<td>dollar sunfish</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Lepomis microlophus</td>
<td>redear</td>
<td>13</td>
<td>0</td>
<td>2</td>
<td>0</td>
</tr>
<tr>
<td>Lepomis punctatus</td>
<td>spotted sunfish</td>
<td>333</td>
<td>2</td>
<td>60</td>
<td>1</td>
</tr>
<tr>
<td>Micropterus salmoides</td>
<td>largemouth</td>
<td>3</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td><strong>Cichlidae</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Cichlasoma bifasciatum</td>
<td>black acara</td>
<td>8</td>
<td>0</td>
<td>3</td>
<td>0</td>
</tr>
<tr>
<td><strong>Clariidae</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Clarias batrachus</td>
<td>walking catfish</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>2</td>
</tr>
<tr>
<td><strong>Cyprinidae</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Notemigonus crysoleucas</td>
<td>golden shiner</td>
<td>80</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td><strong>Cyprinodontidae</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Jordanella floridana</td>
<td>flagfish</td>
<td>2,205</td>
<td>12</td>
<td>1,021</td>
<td>11</td>
</tr>
<tr>
<td><strong>Elasmommatidae</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Elasmomma evergladai</td>
<td>Everglades pygmy sunfish</td>
<td>96</td>
<td>1</td>
<td>881</td>
<td>9</td>
</tr>
<tr>
<td><strong>Esoxidae</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Esox americanus</td>
<td>grass pickerel</td>
<td>1</td>
<td>0</td>
<td>2</td>
<td>0</td>
</tr>
<tr>
<td><strong>Fundulidae</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Fundulus chrysotus</td>
<td>golden topminnow</td>
<td>672</td>
<td>4</td>
<td>850</td>
<td>9</td>
</tr>
<tr>
<td>Lucania goodei</td>
<td>bluefin killifish</td>
<td>1,417</td>
<td>8</td>
<td>416</td>
<td>4</td>
</tr>
<tr>
<td><strong>Ictaluridae</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ameiurus natalis</td>
<td>yellow bullhead</td>
<td>5</td>
<td>0</td>
<td>10</td>
<td>0</td>
</tr>
<tr>
<td><strong>Lepisosteidae</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Lepisosteus platyrhincus</td>
<td>Florida gar</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td><strong>Percidae</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Etheostoma fusiforme</td>
<td>swamp darter</td>
<td>4</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td><strong>Poeciliidae</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Gambusia holbrooki</td>
<td>mosquitofish</td>
<td>8,785</td>
<td>49</td>
<td>1,995</td>
<td>21</td>
</tr>
<tr>
<td>Heterandria formosa</td>
<td>least killifish</td>
<td>3,202</td>
<td>18</td>
<td>3,832</td>
<td>41</td>
</tr>
<tr>
<td>Poecilia latipinna</td>
<td>sailfin molly</td>
<td>881</td>
<td>5</td>
<td>216</td>
<td>2</td>
</tr>
<tr>
<td><strong>Totals</strong></td>
<td></td>
<td>17,992</td>
<td>100</td>
<td>9,372</td>
<td>100</td>
</tr>
<tr>
<td><strong>Fishes per m2</strong></td>
<td>42</td>
<td>22</td>
<td>14</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

80
Table 4.2. Effects of habitat, month, habitat x month, and area (nested within month) on the abundance of nine numerically dominant species, total fish abundance, and species richness in the Refuge.

**Log$_{10}$-transformed mosquitofish density**

<table>
<thead>
<tr>
<th>Source</th>
<th>DF</th>
<th>SS</th>
<th>F</th>
<th>P</th>
<th>$R^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Model</td>
<td>191</td>
<td>45.95</td>
<td>2.55</td>
<td>0.0001</td>
<td>67</td>
</tr>
<tr>
<td>Habitat</td>
<td>2</td>
<td>16.38</td>
<td>86.75</td>
<td>0.0001</td>
<td>24</td>
</tr>
<tr>
<td>Month</td>
<td>23</td>
<td>3.99</td>
<td>1.84</td>
<td>0.0132</td>
<td>6</td>
</tr>
<tr>
<td>Habitat x Month</td>
<td>46</td>
<td>9.62</td>
<td>2.22</td>
<td>0.0001</td>
<td>14</td>
</tr>
<tr>
<td>Area (Month)</td>
<td>120</td>
<td>15.95</td>
<td>1.41</td>
<td>0.0134</td>
<td>23</td>
</tr>
<tr>
<td>Error</td>
<td>240</td>
<td>22.66</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

**Log$_{10}$-transformed least killifish density**

<table>
<thead>
<tr>
<th>Source</th>
<th>DF</th>
<th>SS</th>
<th>F</th>
<th>P</th>
<th>$R^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Model</td>
<td>191</td>
<td>53.24</td>
<td>3.31</td>
<td>0.0001</td>
<td>73</td>
</tr>
<tr>
<td>Habitat</td>
<td>2</td>
<td>1.66</td>
<td>9.87</td>
<td>0.0001</td>
<td>2</td>
</tr>
<tr>
<td>Month</td>
<td>23</td>
<td>18.77</td>
<td>9.69</td>
<td>0.0001</td>
<td>26</td>
</tr>
<tr>
<td>Habitat * Month</td>
<td>46</td>
<td>6.40</td>
<td>1.65</td>
<td>0.0088</td>
<td>9</td>
</tr>
<tr>
<td>Area (Month)</td>
<td>120</td>
<td>26.41</td>
<td>2.61</td>
<td>0.0001</td>
<td>36</td>
</tr>
<tr>
<td>Error</td>
<td>240</td>
<td>20.22</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

**Log$_{10}$-transformed sailfin molly density**

<table>
<thead>
<tr>
<th>Source</th>
<th>DF</th>
<th>SS</th>
<th>F</th>
<th>P</th>
<th>$R^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Model</td>
<td>191</td>
<td>20.50</td>
<td>2.28</td>
<td>0.0001</td>
<td>65</td>
</tr>
<tr>
<td>Habitat</td>
<td>2</td>
<td>0.53</td>
<td>5.65</td>
<td>0.0040</td>
<td>2</td>
</tr>
<tr>
<td>Month</td>
<td>23</td>
<td>4.04</td>
<td>3.74</td>
<td>0.0001</td>
<td>13</td>
</tr>
<tr>
<td>Habitat * Month</td>
<td>46</td>
<td>5.11</td>
<td>2.36</td>
<td>0.0001</td>
<td>16</td>
</tr>
<tr>
<td>Area (Month)</td>
<td>120</td>
<td>10.82</td>
<td>1.92</td>
<td>0.0001</td>
<td>34</td>
</tr>
<tr>
<td>Error</td>
<td>240</td>
<td>11.29</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

**Log$_{10}$-transformed flagfish density**

<table>
<thead>
<tr>
<th>Source</th>
<th>DF</th>
<th>SS</th>
<th>F</th>
<th>P</th>
<th>$R^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Model</td>
<td>191</td>
<td>32.38</td>
<td>2.77</td>
<td>0.0001</td>
<td>68</td>
</tr>
<tr>
<td>Habitat</td>
<td>2</td>
<td>2.22</td>
<td>18.16</td>
<td>0.0001</td>
<td>5</td>
</tr>
<tr>
<td>Month</td>
<td>23</td>
<td>12.89</td>
<td>9.17</td>
<td>0.0001</td>
<td>27</td>
</tr>
<tr>
<td>Habitat * Month</td>
<td>46</td>
<td>4.35</td>
<td>1.55</td>
<td>0.0199</td>
<td>9</td>
</tr>
<tr>
<td>Area (Month)</td>
<td>120</td>
<td>12.93</td>
<td>1.76</td>
<td>0.0001</td>
<td>27</td>
</tr>
<tr>
<td>Error</td>
<td>240</td>
<td>14.67</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

**Log$_{10}$-transformed bluefin killifish density**

<table>
<thead>
<tr>
<th>Source</th>
<th>DF</th>
<th>SS</th>
<th>F</th>
<th>P</th>
<th>$R^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Model</td>
<td>191</td>
<td>35.31</td>
<td>4.08</td>
<td>0.0001</td>
<td>77</td>
</tr>
<tr>
<td>Habitat</td>
<td>2</td>
<td>14.11</td>
<td>155.83</td>
<td>0.0001</td>
<td>31</td>
</tr>
<tr>
<td>Month</td>
<td>23</td>
<td>4.81</td>
<td>4.62</td>
<td>0.0001</td>
<td>10</td>
</tr>
<tr>
<td>Habitat * Month</td>
<td>46</td>
<td>4.13</td>
<td>1.98</td>
<td>0.0005</td>
<td>9</td>
</tr>
<tr>
<td>Area (Month)</td>
<td>120</td>
<td>12.26</td>
<td>2.26</td>
<td>0.0001</td>
<td>27</td>
</tr>
<tr>
<td>Error</td>
<td>240</td>
<td>10.87</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Table 4.2. Continued.

Log$_{10}$-transformed golden topminnow density

<table>
<thead>
<tr>
<th>Source</th>
<th>DF</th>
<th>SS</th>
<th>F</th>
<th>P</th>
<th>R$^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Model</td>
<td>191</td>
<td>17.16</td>
<td>2.11</td>
<td>0.0001</td>
<td>63</td>
</tr>
<tr>
<td>Habitat</td>
<td>2</td>
<td>1.53</td>
<td>18.02</td>
<td>0.0001</td>
<td>6</td>
</tr>
<tr>
<td>Month</td>
<td>23</td>
<td>7.27</td>
<td>7.43</td>
<td>0.0001</td>
<td>27</td>
</tr>
<tr>
<td>Habitat * Month</td>
<td>46</td>
<td>2.81</td>
<td>1.44</td>
<td>0.0445</td>
<td>10</td>
</tr>
<tr>
<td>Area (Month)</td>
<td>120</td>
<td>5.55</td>
<td>1.09</td>
<td>0.2945</td>
<td>20</td>
</tr>
<tr>
<td>Error</td>
<td>240</td>
<td>10.21</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Log$_{10}$-transformed bluespotted sunfish density

<table>
<thead>
<tr>
<th>Source</th>
<th>DF</th>
<th>SS</th>
<th>F</th>
<th>P</th>
<th>R$^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Model</td>
<td>191</td>
<td>3.71</td>
<td>1.74</td>
<td>0.0001</td>
<td>58</td>
</tr>
<tr>
<td>Habitat</td>
<td>2</td>
<td>0.23</td>
<td>10.49</td>
<td>0.0001</td>
<td>4</td>
</tr>
<tr>
<td>Month</td>
<td>23</td>
<td>1.11</td>
<td>4.32</td>
<td>0.0001</td>
<td>17</td>
</tr>
<tr>
<td>Habitat * Month</td>
<td>46</td>
<td>0.84</td>
<td>1.64</td>
<td>0.0097</td>
<td>13</td>
</tr>
<tr>
<td>Area (Month)</td>
<td>120</td>
<td>1.53</td>
<td>1.14</td>
<td>0.1957</td>
<td>24</td>
</tr>
<tr>
<td>Error</td>
<td>240</td>
<td>2.67</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Log$_{10}$-transformed pygmy sunfish density

<table>
<thead>
<tr>
<th>Source</th>
<th>DF</th>
<th>SS</th>
<th>F</th>
<th>P</th>
<th>R$^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Model</td>
<td>191</td>
<td>28.10</td>
<td>3.46</td>
<td>0.0001</td>
<td>73</td>
</tr>
<tr>
<td>Habitat</td>
<td>2</td>
<td>7.69</td>
<td>90.41</td>
<td>0.0001</td>
<td>20</td>
</tr>
<tr>
<td>Month</td>
<td>23</td>
<td>4.02</td>
<td>4.10</td>
<td>0.0001</td>
<td>10</td>
</tr>
<tr>
<td>Habitat * Month</td>
<td>46</td>
<td>2.98</td>
<td>1.52</td>
<td>0.0241</td>
<td>8</td>
</tr>
<tr>
<td>Area (Month)</td>
<td>120</td>
<td>13.42</td>
<td>2.63</td>
<td>0.0001</td>
<td>35</td>
</tr>
<tr>
<td>Error</td>
<td>240</td>
<td>10.21</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Log$_{10}$-transformed sunfish density

<table>
<thead>
<tr>
<th>Source</th>
<th>DF</th>
<th>SS</th>
<th>F</th>
<th>P</th>
<th>R$^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Model</td>
<td>191</td>
<td>6.73</td>
<td>2.54</td>
<td>0.0001</td>
<td>67</td>
</tr>
<tr>
<td>Habitat</td>
<td>2</td>
<td>2.10</td>
<td>35.76</td>
<td>0.0001</td>
<td>21</td>
</tr>
<tr>
<td>Month</td>
<td>23</td>
<td>1.10</td>
<td>1.42</td>
<td>0.1479</td>
<td>11</td>
</tr>
<tr>
<td>Habitat * Month</td>
<td>46</td>
<td>1.35</td>
<td>2.11</td>
<td>0.0002</td>
<td>13</td>
</tr>
<tr>
<td>Area (Month)</td>
<td>120</td>
<td>2.19</td>
<td>1.31</td>
<td>0.0389</td>
<td>22</td>
</tr>
<tr>
<td>Error</td>
<td>240</td>
<td>3.77</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Log$_{10}$-transformed total fish density

<table>
<thead>
<tr>
<th>Source</th>
<th>DF</th>
<th>SS</th>
<th>F</th>
<th>P</th>
<th>R$^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Model</td>
<td>191</td>
<td>47.27</td>
<td>3.14</td>
<td>0.0001</td>
<td>72</td>
</tr>
<tr>
<td>Habitat</td>
<td>2</td>
<td>5.80</td>
<td>36.79</td>
<td>0.0001</td>
<td>9</td>
</tr>
<tr>
<td>Month</td>
<td>23</td>
<td>15.08</td>
<td>8.32</td>
<td>0.0001</td>
<td>23</td>
</tr>
<tr>
<td>Habitat * Month</td>
<td>46</td>
<td>11.90</td>
<td>3.28</td>
<td>0.0001</td>
<td>18</td>
</tr>
<tr>
<td>Area (Month)</td>
<td>120</td>
<td>14.50</td>
<td>1.53</td>
<td>0.0028</td>
<td>22</td>
</tr>
<tr>
<td>Error</td>
<td>240</td>
<td>18.92</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Log$_{10}$-transformed species richness

<table>
<thead>
<tr>
<th>Source</th>
<th>DF</th>
<th>SS</th>
<th>F</th>
<th>P</th>
<th>R$^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Model</td>
<td>191</td>
<td>1175.55</td>
<td>2.97</td>
<td>0.0001</td>
<td>70</td>
</tr>
<tr>
<td>Habitat</td>
<td>2</td>
<td>132.17</td>
<td>11.13</td>
<td>0.0001</td>
<td>8</td>
</tr>
<tr>
<td>Month</td>
<td>23</td>
<td>372.39</td>
<td>2.25</td>
<td>0.0064</td>
<td>22</td>
</tr>
<tr>
<td>Habitat * Month</td>
<td>46</td>
<td>273.16</td>
<td>2.87</td>
<td>0.0001</td>
<td>16</td>
</tr>
<tr>
<td>Area (Month)</td>
<td>120</td>
<td>397.83</td>
<td>1.60</td>
<td>0.0011</td>
<td>24</td>
</tr>
<tr>
<td>Error</td>
<td>240</td>
<td>497.33</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Table 4.3. Number and percentage (in parentheses) of sites classified correctly (diagonal) and incorrectly (off-diagonals) with respect to habitat type.

<table>
<thead>
<tr>
<th></th>
<th>Actual Prairie</th>
<th>Actual Sawgrass</th>
<th>Actual Slough</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Predicted Prairie</strong></td>
<td>74 (56)</td>
<td>33 (23)</td>
<td>24 (17)</td>
</tr>
<tr>
<td><strong>Predicted Sawgrass</strong></td>
<td>39 (25)</td>
<td>109 (76)</td>
<td>10 (7)</td>
</tr>
<tr>
<td><strong>Predicted Slough</strong></td>
<td>31 (22)</td>
<td>2 (1)</td>
<td>110 (76)</td>
</tr>
</tbody>
</table>

Table 4.4. Results of partial correlations between species pairs after removing variation associated with the spatiotemporal sampling hierarchy (see text for details). Significant (p<0.05) coefficients are provided, whereas non-significant coefficients are listed as either positive (+) or negative (-).

<table>
<thead>
<tr>
<th>Variable</th>
<th>G</th>
<th>H</th>
<th>P</th>
<th>J</th>
<th>L</th>
<th>F</th>
<th>L</th>
<th>E</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Gambusia</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Heterandria</em></td>
<td>0.3088</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Poecilia</em></td>
<td>+</td>
<td>+</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Jordanella</em></td>
<td>+</td>
<td>-</td>
<td>+</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Lucania</em></td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Fundulus</em></td>
<td>+</td>
<td>+</td>
<td>-</td>
<td>+</td>
<td>+</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Lepomis</em></td>
<td>-</td>
<td>-</td>
<td>+</td>
<td>+</td>
<td>-</td>
<td>+</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Enneacanthus</em></td>
<td>+</td>
<td>+</td>
<td>-</td>
<td>-</td>
<td>+</td>
<td>+</td>
<td>-</td>
<td></td>
</tr>
<tr>
<td><em>Elassoma</em></td>
<td>-</td>
<td>+</td>
<td>-</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>-</td>
</tr>
</tbody>
</table>
Figure 4.1. Mean (+ 1 SE) number of fishes per square meter of wet prairie, slough, and sawgrass habitats comprising the Refuge. Letters denote means that are significantly different (least-squares means).
Figure 4.2. Seasonal variation in mean (± 1 SE) number of fishes per square meter of wet prairie, slough, and sawgrass habitats comprising the Refuge. Data for May 1992 are shown in Figure 4.3.
Figure 4.3. Mean number of fishes in sloughs before, during, and after the marsh drawdown of May 1992. A “yes” above the May bar indicates that numbers were significantly higher than in January and March. A “yes” above the July bar indicates that numbers were significantly different than in January and March. Comparisons were made using a priori contrasts.
Figure 4.4. Dominance-diversity curves for different Refuge habitats (top), and seasonal variation in mean (± 1 SE) number of species per collection site (bottom).
Figure 4.5. Location (i.e., multivariate least-squares means) of nine dominant fishes in community space as revealed by discriminant function analysis. Centroids for sloughs (SL), wet prairies (WP), and sawgrass stands (SG) are shown with 95% confidence ellipses.
Figure 4.6. Temporal variation in water depth, dry plant biomass, canopy height, dissolved oxygen, conductivity, and total fish abundance within four Everglades habitats. Cattail stands were located near perimeter canals in the southern end of the Refuge, whereas other habitats were sampled in the interior of the Refuge.
CHAPTER 5

PREDATION, HABITAT COMPLEXITY, AND
DISTRIBUTION OF THE CRAYFISH *PROCAMBARUS ALLENI*

Introduction

Natural aquatic systems are spatially heterogeneous and often form mosaics comprised of different habitat types (e.g., littoral vs. pelagic zones, pools vs. riffles, depositional vs. erosional banks). These habitat mosaics provide a spectrum of opportunities and risks for their associated aquatic macrofauna in that each habitat type has a characteristic array of food resources, predators, and potential competitors that may all affect the demographics of resident species (Pulliam 1988, Pulliam and Danielson 1991, Rosenzweig 1991). Ultimately, differences in these factors can account for differential habitat use by species and habitat-specific assemblage composition (Wiens 1976). For example, differences in the relative risk and intensity of predation can result in higher densities of prey fishes and invertebrates in densely vegetated habitats (e.g., seagrass beds, vegetated littoral zones) than in adjacent non-vegetated habitats (Orth et al. 1984, Heck et al. 1989, Heck and Crowder 1991, Jordan et al. 1994, 1996a, 1996b). Overall, predators appear to play prominent roles in structuring aquatic communities by reducing or eliminating prey populations, causing shifts in habitat use, acting as selective agents in the evolution of behavior and morphology, and affecting species interactions throughout food webs (see reviews in Kerfoot and Sih 1987).

Although the regulatory importance of aquatic predators is recognized for well studied systems such as streams and lakes, little effort has been made to quantify their role in regulating the abundance and distribution of prey organisms in seasonally dynamic freshwater wetlands (DeAngelis and White 1994). Throughout southern Florida, freshwater marshes are comprised of mosaics of aquatic sloughs, sawgrass stands,
emergent wet prairies, and other distinct habitat types (Loveless 1959, Chapter 2). Field sampling efforts have shown that aquatic macrofauna tend to use these habitats nonrandomly (e.g., Loftus and Kushlan 1987, Jordan et al. 1994, Streever et al. 1995) and it is likely that predators contribute to observed patterns (Jordan et al. 1996a). Perhaps the most striking example of differential habitat use in these freshwater marshes involves the crayfish *Procambarus alleni*. This trophically important (Robertson and Frederick 1994) species is much more abundant in densely vegetated habitats (Jordan et al. 1996a, Chapter 3), which generally support fewer predatory fishes (Dineen 1984, Loftus and Kushlan 1987, Chapter 4). Jordan et al. (1996a) found that crayfish densities were significantly (=900%) greater in wet prairies than in sloughs within the upper basin of the St. Johns River (Indian River County, Florida). Furthermore, they found that the density of crayfish increased with increasing plant density. Quantitative sampling in the northern Everglades (Palm Beach County, Florida) also indicated that *P. alleni* densities were significantly higher in sawgrass stands and wet prairies than in sloughs (Chapter 3). Jordan et al. (1996a) hypothesized that habitat use by *P. alleni* was most likely due to aquatic predators, either directly through differential predation or indirectly through predator-mediated habitat selection.

Previous research has shown that predators (especially fishes) can regulate the size of crayfish populations (e.g., Rabeni 1992) and strongly mediate habitat use by crayfish (e.g., Stein and Magnuson 1976, Stein 1977, Garvey et al. 1994). It seems likely that predation plays an important role in determining the distribution of *P. alleni*, primarily because this species comprises a significant portion of the diet of trophically important predators such as wading birds, alligators, swamp snakes, pig frogs, and predatory fishes (Robertson and Frederick 1994). These predators rely primarily on visual and/or tactile cues to locate crayfish, which may lead to decreased foraging efficiency in densely vegetated habitats due to reductions in their ability to detect and successfully capture vagile prey such as crayfish (Heck and Crowder 1991). Therefore, persistent differences in the complexity (e.g., plant stem density or biomass) of these marsh habitats may result in differential rates of predation
on crayfish and ultimately lead to the evolution of antipredator behavior (i.e., preference for increased cover). I performed laboratory experiments to determine what role, if any, predation plays in determining observed patterns of habitat use by *P. alleni*. First, I assessed preference for vegetated and non-vegetated habitats and determined if preferences varied between day and night (Habitat Selection Experiment). Second, I assessed size-specific survival of crayfish exposed to predatory largemouth bass (*Micropterus salmoides floridanus*) under different levels of habitat complexity (Predation Experiment).

**Methods**

**Animal Collection and Maintenance**

For both experiments described below, crayfish were collected from marsh habitats in southern Florida. For the predation experiment, largemouth bass ranging in size from 100 to 144 mm standard length (122 ± 3 mm; mean ± 1 SE) were collected from Lake Yale in Lake County, Florida. Crayfish and bass were maintained separately in outdoor holding tanks with recirculating water systems. Bass were fed crayfish and small fishes *ad libitum*, whereas crayfish were fed flake food *ad libitum*. Predators were not fed for 48 h prior to experiments to standardize hunger levels. Individual crayfish were used only once in an experiment and then maintained in a separate holding tank.

**Habitat Selection Experiment**

This experiment tested whether groups of crayfish preferred vegetated or non-vegetated habitats and whether preferences varied between day and night. Four rectangular plastic tanks (62 cm length x 47 cm width x 47 cm height) were placed in a small clearing on the campus of Jacksonville University (Duval County, Florida). The bottom of each tank was covered with 2-3 cm of dark sand and filled with ≈120 L of tap water to a depth of 41 cm (0.29-m² surface area, 0.12-m³ or 119-L volume). Tanks were not aerated during the experiment. Two distinct habitats were created within each tank by placing simulated vegetation on one side of the tank and leaving the other side of the tank bare sand.
Vegetation was simulated by tying 22 bipartite strips of dark green plastic (2 cm width x 30 cm length) to a sheet of mesh, which could be buried beneath the sand substrate. Vegetation was stocked at a density of 154 strands per square meter, which approximates the complexity of emergent wet prairies in southern and central Florida (Chapter 2). Simulated vegetation was used to avoid confounding predator avoidance behavior with differential food availability (i.e., omnivorous crayfish feed on plants; Feminella and Resh 1989).

Sand, water, and vegetation were added to tanks between 8:00 and 8:30 EST and allowed to settle for 3 hours. Nine crayfish were then added to each tank (11:00 and 11:30 EST) and the number of crayfish occupying the non-vegetated side of the tanks was measured once in the afternoon (16:00-17:00 EST) and once in the evening (21:00-22:00 EST). Crayfish were collected on the following morning and the process was repeated again on two additional dates with new crayfish being used on each date. The placement of the vegetated and non-vegetated habitats was reversed in each tank after each trial. Preliminary analysis indicated there were no effects due to either tank or date, therefore each tank x date combination was considered an individual replicate (i.e., n=12). Paired t-tests were used to compare use of vegetated and non-vegetated sides and to test for changes in habitat use between day and night observation periods.

Predation Experiment

This experiment tested whether habitat complexity (i.e., plant biomass) affected survival of crayfish exposed to predatory largemouth bass. Thirty-six cylindrical, plastic tanks (48 cm diameter and 43 cm height) were arranged in the laboratory. Tanks were filled with ≈65 L of tap water to a depth of 36 cm (0.18-m² surface area, 0.06-m³ volume). Stems of the common wetland plant *Ludwigia repens* (hereafter *Ludwigia*) were collected from local ephemeral ponds, rinsed thoroughly, and then added to the plastic tanks. One of three habitat complexity treatments was randomly assigned to each tank: low complexity (0 kg of *Ludwigia* stems), medium complexity (0.45 kg of *Ludwigia* stems), or high complexity
(1.35 kg of *Ludwigia* stems). The plant biomasses used in the medium and high habitat complexity treatments are typical of slough and emergent wet prairie habitats in southern Florida (Jordan et al. 1994, Jordan et al. 1996a, Chapter 4). Tanks were filled and allowed to settle for 24 h before adding predators or prey. Tanks were aerated during the experiment and mean (± 1 SE) dissolved oxygen levels did not differ (F2,29=2.4, p=0.1104) among low (9.1 ± 0.1 mg/l), medium (9.3 ± 0.4 mg/l), and high (9.1 ± 0.4 mg/l) habitat complexity tanks. Lights were maintained on a 12L:12D cycle during the experiment.

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

**Results**

**Habitat Selection Experiment**

Crayfish responded strongly to the available habitats, although the magnitude of
their response varied with time of day (Figure 5.1). During the day, crayfish used vegetated habitats significantly (91%) more than non-vegetated habitats ($t=27.5$, $p=0.0001$, 11 df). Crayfish use of vegetated habitats was still greater in the evening ($t=4.5$, $p=0.0009$, 11 df), but there was a significant (31%) increase in use of non-vegetated habitats relative to daytime use ($t=8.2$, $p=0.0001$, 11 df).

**Predation Experiment**

Overall, bass reduced survival of crayfish by 22% relative to controls, and predation accounted for 30% of the variation observed in survival rates (Table 5.1). Survival varied with crayfish size; no large or medium-sized crayfish were eaten during the five day experiment, whereas bass reduced survival of small-sized crayfish by 48% relative to controls.

Habitat complexity accounted for a significant (23%) of the variation in crayfish survival (Table 5.1), with survival rates being significantly higher in the high complexity tanks than in the low and medium complexity tanks, which did not differ from one another (Least-squares means). The effects of habitat complexity varied with predator presence (Table 5.1 and Figure 5.2). That is, the total number of crayfish surviving did not vary among habitats in tanks that lacked predators, whereas survival increased with increasing habitat complexity in the presence of predatory bass (Figure 5.2). Since the interaction between predator presence and habitat complexity was significant (Table 5.1 and Figure 5.2), it was necessary to assess (via Least-squares means) the effects of predatory bass at each level of habitat complexity. Relative to controls, the effects of predators ranged from highly significant ($p=0.0001$) in low complexity habitats, to significant ($p=0.0233$) in medium complexity habitats, to non-significant ($p=0.2414$) in high complexity treatments.
Discussion

_Procambarus alleni_ exhibited a strong preference for habitats containing simulated vegetation relative to adjacent habitats containing only bare sand. Since there were no differences in food availability or water chemistry between these habitats, it seems likely that crayfish were selecting the habitat that was likely to provide the greatest amount of cover (i.e., reduced risk of predation). Other crayfish species tend to select habitats that provide the most cover from predators (Stein 1977, Alberstadt et al. 1995). In addition to selecting complex habitats that provide more cover, many crayfish species also increase their activities at night (Hobbs 1991), which is when most predatory freshwater fishes (e.g., bass, sunfishes, gar) are quiescent. I found that _P. alleni_ substantially increased use of non-vegetated habitats at night. Preference for complexly vegetated habitats and increased nocturnal activity support the idea that crayfish are behaviorally minimizing their vulnerability to predatory fishes. Additional experiments were planned to assess how predators affected habitat selection, but these experiments were deemed unnecessary given that crayfish occupied complex habitats about 95% of the time in the absence of predators.

Habitat preferences observed in this study are highly concordant with results of quantitative sampling performed in the freshwater marshes of southern Florida, where _P. alleni_ densities are substantially higher in densely-vegetated wet prairies than in thinly-vegetated sloughs (Jordan et al. 1996a, Chapter 3). Therefore, observed patterns of habitat use in the field may reflect strong selection for increased cover, because predatory fishes are much more abundant in sloughs than in complexly-vegetated habitats such as emergent wet prairies and sawgrass stands (Dineen 1984, Loftus and Kushlan 1987, Chapter 4). Crayfish are very sensitive to the presence of predators and modify their habitat use and activity levels when the risk of predation increases (Stein and Magnuson 1976, Stein 1977, Blake and Hart 1993, Garvey et al. 1994). Because _P. alleni_ strongly preferred the vegetated habitat in the absence of predators, I suggest that this preference is an indirect evolutionary response to the selective pressure of predation (_sensu_ Bell and Westoby...
Habitat-specific differences in food availability, rates of parasitism, and water chemistry may have also affected the evolution of habitat preference in *P. alleni* (Rosenzweig 1991).

Results from my second experiment are consistent with previous research that has shown that crayfish are vulnerable to predatory fishes. Susceptibility decreases significantly as crayfish reach sizes too large to be handled by the majority of predatory fishes in the freshwater marshes of southern Florida (e.g., gar, bowfin, sunfishes, and largemouth bass). Size selectivity on crayfish appears to be more a function of the defensive abilities of large-sized crayfish rather than gape limitation per se (e.g., Stein and Magnuson 1976, Garvey et al. 1994). Other types of predators (e.g., wading birds, alligators) are likely to prefer and take larger crayfish because of increased handling efficiency relative to predatory fishes (e.g., Frederick and Spalding 1994).

In many aquatic systems, crayfish constitute a significant portion of the diets of predatory fishes (e.g., Pflieger 1975, Etnier and Starnes 1993). For example, Rabeni (1992) found that smallmouth bass (*Micropterus dolomieu*) and rock bass (*Ambloplites rupestris*) relied heavily on crayfish (*Orconectes luteus* and *O. punctmanus*) in an Ozark stream system. Further, he estimated that about half of the crayfish biomass in this system was consumed by smallmouth bass and rock bass, which appeared to be the primary agents of crayfish mortality. Largemouth bass and warmouth sunfish (*Chaenobryttus gulosus*) consume significant numbers of *P. alleni* in southern Florida (unpublished data, Florida Game and Freshwater Fish Commission). Juveniles and small adults (0.1-1.0 g dry weight) are most vulnerable to predatory fishes (Stein and Magnuson 1976, Stein 1977, Rabeni 1992, Garvey et al. 1994; this study), which frequently results in predator-induced demographic bottlenecks occurring around these size-age classes. Jordan et al. (1996a) found that relatively few *P. alleni* recruited into larger size classes (i.e., 1.0 g wet weight) during their 18 month study, indicating a possible demographic bottleneck.
Spatial heterogeneity and habitat complexity play an important role in structuring assemblages of predators and prey (Huffaker 1958, Holt 1987). That is, complex habitats provide more refuges from predators and facilitate the coexistence of predators and vulnerable species and sizes of prey (Hixon and Beets 1993, Beck 1995). I found that the survival of *P. alleni* increased as a function of increasing habitat complexity, which also appears to hold for other crayfish species. For example, survival of *Orconectes* spp. exposed to predatory bass (*Micropterus* spp.) increased with increasing habitat complexity (Stein and Magnuson 1976, Garvey et al. 1994).

Enhanced survival was found in this and previous studies most likely because piscine predators suffer decreased foraging efficiency in more complex habitats due to reductions in the ability of visually-oriented predators to detect and successfully capture prey (Heck and Crowder 1991). Both the lowered foraging efficiency (this study) and abundance (Dineen 1984, Loftus and Kushlan 1987, Chapter 4) of large predatory fishes likely contribute to the relatively high abundance of *P. alleni* in emergent wet prairies and sawgrass stands in the wetland habitat mosaics of southern Florida (Jordan et al. 1996a, Chapter 4).

In the absence of predatory bass, I found that survival of small-sized crayfish (summed across habitats) was reduced significantly (10%) relative to stocking density (t=3.1, p=0.0070, 17 df). Specifically, there were marginal reductions in the numbers of small-sized crayfish surviving in low (t=2.2, p=0.0756, 5 df) and medium (t=2.0, p=0.0756, 5 df) complexity tanks relative to stocking densities, but no decrease in the high complexity tanks (t=1.0, p=0.3632, 5 df). A variety of factors (e.g., escape, dissolved oxygen levels, intraspecific predation) may have affected estimates of crayfish survival in tanks lacking predators. However, crayfish were unable to escape from experimental tanks and dissolved oxygen levels (9 mg/l) were high across all predator treatments (F1,29=0.2, p=0.6812). Although no intact crayfish bodies were recovered, I did find remains in some tanks suggesting that the small-sized crayfish had been eaten by larger conspecifics. Size-based
dominance hierarchies are common in crayfish (Bovbjerg 1953, Caine 1978, Rabeni 1985, Hobbs 1991), and frequently lead to strong negative intraspecific and interspecific effects (Capelli and Munjal 1982, Butler and Stein 1985, Söderbäck 1991, Garvey et al. 1994). Typically, different sized crayfish fight for limited shelter space, resulting in the loser having increased vulnerability to predators (Caine 1978, Garvey et al. 1994).

Variation in the frequency and duration of inundation is generally viewed as the most important factor regulating the abundance of aquatic organisms and determining community composition in seasonally dynamic freshwater wetlands (e.g., Murkin and Kadlec 1986, Kushlan 1987, Neckles et al. 1990, Batzer and Resh 1992, Batzer et al. 1993). However, little effort has been made to determine how other factors (e.g., predation, habitat heterogeneity) affect community composition in wetland systems (Prejs and Prejs 1992, DeAngelis and White 1994). My results indicate that predation and habitat complexity both affect survival of the crayfish *P. alleni* and at least partially account for patterns of habitat use by this crayfish observed in the field. Different hydrological conditions (e.g., duration of inundation) are going to favor different predator assemblages (e.g., predatory arthropods vs. large fishes), which in turn will affect in habitat-specific prey assemblage structure. Therefore, a general model of assemblage regulation in wetland systems should not be based solely on hydrology, but should also incorporate the direct and indirect effects of predators and habitat complexity (see Chapter 8).
Table 5.1. Analysis of variance testing for the effects of predator presence, habitat complexity, and their interaction on the number of crayfish surviving after five days.

<table>
<thead>
<tr>
<th>Source</th>
<th>DF</th>
<th>MS</th>
<th>F</th>
<th>P</th>
<th>R²</th>
</tr>
</thead>
<tbody>
<tr>
<td>Model</td>
<td>5</td>
<td>2.2</td>
<td>9.6</td>
<td>0.0001</td>
<td>62</td>
</tr>
<tr>
<td>Predator</td>
<td>1</td>
<td>5.4</td>
<td>23.3</td>
<td>0.0001</td>
<td>30</td>
</tr>
<tr>
<td>Complexity</td>
<td>2</td>
<td>2.1</td>
<td>9.0</td>
<td>0.0008</td>
<td>23</td>
</tr>
<tr>
<td>Predator x Complexity</td>
<td>2</td>
<td>0.8</td>
<td>3.3</td>
<td>0.0493</td>
<td>9</td>
</tr>
<tr>
<td>Error</td>
<td>30</td>
<td>0.3</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Figure 5.1. Proportion of crayfish (means + 1 SE) occupying vegetated and open sand portions of behavioral tanks during the day and night. For each time period, letters designate means that differ significantly (paired t-tests).
Figure 5.2. Numbers of crayfish (means + 1 SE) surviving after five days as a function of predator presence (open bars) or absence (closed bars) and habitat complexity. For each level of habitat complexity, means with different letters are significantly different (least-squares means).
CHAPTER 6

EFFECTS OF AN ODONATE PREDATOR AND HABITAT COMPLEXITY ON SURVIVAL OF FLAGFISH, JORDANELLA FLORIDAE

Introduction

Traditional analyses of food web structure in freshwater ecosystems tend to segregate predatory arthropods and vertebrates into lower and higher trophic levels, respectively (McCormick and Polis 1982, Schoenly et al. 1991). However, empirical studies have clearly demonstrated that predatory arthropods (e.g., insects, decapod crustaceans) can control the size and structure of aquatic vertebrate populations. The majority of these studies have focused on how predatory insects affect behavior, growth rates, survival, and community dynamics of aquatic stages of amphibians (e.g., Heyer et al. 1975, Caldwell et al. 1980, Holomuzki 1986, Morin et al. 1990, Skelly and Werner 1990, Werner 1991). Surprisingly little research has quantified the effects of predatory insects on fishes. Most information available concerning predation on fishes by insects has come from fish culturists, who have noted that survival of larval and juvenile fishes is inversely related to the abundance of large aquatic insects. Laboratory studies have demonstrated that certain aquatic insects can be voracious predators of larval and post-larval cultured fishes (reviewed in McCormick and Polis 1982). Kipling and Frost (1970) found that aquatic beetle larvae of the family Dytiscidae were dominant predators on juveniles of the pike Esox lucius in small ponds. Few other studies have assessed the effects of predatory insects on fishes in natural systems.

Predation on fishes by aquatic insects is likely to vary with hydrologic conditions, with insect predators being more important in habitats with shorter hydroperiods and/or greater structural complexity. In permanently inundated habitats, fishes gain a size advantage and can effectively eliminate many insect taxa (e.g., Morin 1984), thereby
greatly limiting the influence of predatory insects on fishes. However, insects may be important predators of fishes in seasonally inundated marshes. The seasonal expansion and contraction of these habitats limits the ability of large predatory fishes to achieve significant production (Kushlan 1976, 1980), although small fishes are likely to persist through such disturbance cycles (Loftus and Eklund 1994). Furthermore, early colonization and recruitment into seasonally inundated habitats can afford predatory insects a relative size advantage, which both increases their ability to handle small-sized fishes and reduces their susceptibility to gape-limited predators. The importance of predatory insects may decrease during a wet season (Morin et al. 1990), first as fish prey become too large to handle (e.g., Cronin and Travis 1986, Formanowicz 1986) and then as they become large enough to reverse the predator-prey roles (McCormick and Polis 1982). Habitat complexity may further mediate the effects of predation on fishes by insects in seasonally variable habitats. That is, increased habitat complexity typically reduces the ability of predators to detect and capture prey (reviewed in Heck and Crowder 1991), which could facilitate the coexistence of small-sized fishes and predatory insects. However, increased habitat complexity may also help some foraging insects by providing perches from which they can ambush fishes. In general, natural heterogeneity in plant stem densities is likely to create a habitat mosaic that is characterized by variable foraging success for predators and variable risk of predation for prey.

A variety of small fish species belonging to the families Cyprinodontidae, Fundulidae, and Poeciliidae are quite tolerant of the seasonally variable hydrologic conditions found in the freshwater marshes of southern Florida (Chapter 4). For example, the endemic flagfish *Jordanella floridana* (Teleostei: Cyprinodontidae) is locally abundant in these marshes (Gilbert and Burgess 1981). Certain marsh habitats (e.g., dense wet prairies, sawgrass) rarely support large predatory fishes, whereas they do support high densities of potentially predatory insects (i.e., odonates, coleopterans, hemipterans). Little is known about what role, if any, insects play in regulating the sizes of fish populations in ephemeral
marsh systems. In this laboratory study, I exposed flagfish to naiads of the dragonfly *Anax junius* (Odonata: Aeshnidae) in simple and complex habitats to determine how their susceptibility to predatory insects is affected by habitat complexity.

**Methods**

Flagfish and dragonfly naiads were collected from freshwater marshes and returned to the laboratory, where they were held in water from the collection site for 48 h to allow acclimation to laboratory temperature. Groups of 5 flagfish were then transferred into 16 opaque plastic bins (32 x 22 x 17 cm) containing 8 liters of aerated (≈9 mg/l) tap water. Flagfish were used without regard to sex, and body size ranged between 13 and 37 mm standard length (mean = 24.7 mm, n=80). Flagfish were not fed during the experiment, and water temperatures ranged between 16 and 21°C. Lights were maintained on a 12L:12D cycle during the experiment.

Eight experimental bins each were randomly assigned to either a complex or simple habitat treatment. Complex habitat was created by tying 20 bipartite strands (150 x 20 mm) of dark plastic to mesh that rested on the bottom of the bins. The number of strands used (i.e., 284 per square meter) was within the range of plant stem densities found in similar freshwater marshes in Florida (Chapter 2). No cover was provided in the simple habitat treatment. Two late instar *A. junius* naiads were randomly assigned to each of five bins in both treatments. Larval dragonflies ranged in size between 30 and 45 mm total length (mean = 36.7 mm, n=20). Fewer bins were used as predator controls because preliminary observations indicated minimal mortality of flagfish over a 14-day period in the absence of predators.

The experiment was run for 10 days, and then all surviving flagfish were counted. The percentage of survivors (survivorship) was calculated and used as the response variable in a factorial analysis of variance (ANOVA) to test for the effects of habitat complexity (simple vs. complex), predator (absent vs. present), and the habitat complexity x predator
interaction. Inspection of residual plots and Levene's test (Milliken and Johnson 1992) indicated that variances were unequal; therefore, survivorship values were arcsin-transformed to meet the assumptions for the ANOVA test (Winer et al. 1991). However, means are presented for the untransformed data because they produced very similar ANOVA results.

**Results**

All but one (97%) of the flagfish survived in the bins lacking dragonfly naiads, whereas only 60% of the flagfish survived in the bins containing predators (Figure 6.1). There was a strong predator effect (F\(_{1,12}=14.4\), p=0.0026), which accounted for 55% of the variation in survivorship rates of flagfish. Predation rates ranged from 20 to 80% during the ten-day experiment, suggesting that there was considerable inter-individual variation in the behavior of predators and/or prey. No predators died during the experiment. Habitat complexity did not affect survivorship of flagfish (F\(_{1,12}=0.3\), p=0.6024), and there was no interaction between predator presence and habitat complexity (F\(_{1,12}=0.3\), p=0.5965).

**Discussion**

The distribution patterns of many insect taxa seem to be strongly correlated with the presence or absence of large predatory fishes (e.g., Morin 1984, McPeek 1989), and hence, the importance of aquatic insects as top predators in aquatic systems is largely determined by the presence of large predatory fishes (Schoenly et al. 1991). The relative importance of these two groups of predators tends to vary along a hydrologic gradient, with large predatory fishes prevailing in habitats with long hydropoeriods and predatory insects becoming progressively more important in habitats with shorter hydropoeriods. For example, large insects tend to be more abundant in shallower (and structurally more complex) wet prairies and sawgrass stands. Large predatory fishes are likely to play a role in regulating populations of small-sized fishes (Kushlan 1976, 1980), whereas the
importance of predatory insects is largely unknown. This study demonstrates that larval *A. junius* prey upon small-sized fishes (i.e., < 40 mm standard length) and that predation rates can approach 40% under ideal laboratory conditions.

Quantitative sampling with 1-m$^2$ throw traps has indicated substantial variation in the abundance of flagfish (Chapter 4). Based on this study, predation by *A. junius* and other local predators (e.g., wading birds) could easily account for these large fluctuations in flagfish abundance, although other factors (esp., variation in hydroperiod) are also likely to be important. *Anax junius* is found throughout North America, and the naiads of this species can be locally abundant (e.g., Caldwell et al. 1980) in habitats that typically lack large predatory fishes (Werner 1991). Although there are few quantitative data available for fishes, predation by *A. junius* has been shown to strongly impact larval populations of amphibians (Caldwell et al. 1980, Werner 1991, Babbitt and Jordan 1996). It seems likely that predation by this and other large predatory insects (e.g., *Tramea*, *Lethocercus*, *Dytiscus*) also plays an important role in structuring populations of small-sized fishes in habitats that support few or no large predatory fishes.

Habitat complexity can affect the foraging efficiency of aquatic predators (e.g., Crowder and Cooper 1982, Gotceitas 1990, Babbitt and Jordan 1996). Detection rates, capture success, and predator maneuverability all tend to decrease with increasing habitat complexity (see review in Heck and Crowder 1991). Much of this research has been performed using visually oriented fishes as predators. It is unclear how habitat complexity affects predatory aquatic insects such as dragonfly naiads, which use visual and to a lesser extent tactile stimuli to detect their prey (Pritchard 1965, Folsom and Collins 1984). Foraging efficiency of *A. junius* did not differ between the simple and complex habitats. Although often found clinging to a perch (e.g., the plastic plants and walls of the bins), this species can be a very active forager (cf., ambush predators). Their almost cylindrical bodies were probably unaffected by the density of plant stems used in this study, although maneuverability would probably have been reduced in a deep-bodied predatory fish.
Foraging efficiency does not seem to decrease until some threshold stem density is surpassed (Gotceitas and Colgan 1989). Foraging efficiency of *A. junius* might be lowered at a threshold greater than that used in this study. Babbitt and Jordan (1996) found that the number of *Bufo terrestris* tadpoles eaten by *A. junius* nymphs did not decrease until plant density reached 90 grams of *Ludwigia repens* per m$^2$. The density of plant stems used in this study was about as complex as the medium complexity treatment (10 grams of *L. repens* per m$^2$) used in Babbit and Jordan (1996), which did not affect foraging efficiency of *A. junius*. More research (see Chapter 7) is needed to determine if predation on fishes by aquatic invertebrates is lowered in increasingly complex habitats.
Figure 6.1. Mean (+ 1 SE) survivorship of the flagfish *Jordanella floridae* in the presence and absence of naiads of the predatory insect *Anax junius*. 
CHAPTER 7
BETWEEN A ROCK AND A HARD PLACE:
HABITAT-MEDIATED EFFECTS OF PREDATORY CRAYFISH,
DRAGONFLY NAIADS, AND BASS ON MARSH PREY FISHES

Introduction

Predation plays a central role in natural systems by molding the evolution of morphology and behavior, by restricting the size and distribution of prey populations, and by altering community composition through selective removal of competitively dominant prey species (see reviews in Sih et al. 1985, Kerfoot and Sih 1987, Hairston 1989). The importance of predation as an organizing force is particularly strong in aquatic systems (Strong 1992), where the effects of one or a few keystone predators can cascade down through relatively simple food webs (Kitchell and Carpenter 1993). For example, addition of predatory largemouth bass (*Micropterus salmoides floridanus*, Centrarchidae) to a small Michigan lake resulted in decreased abundance of planktivorous fish, increased abundance of large-bodied zooplankton, decreased phytoplankton abundance, and increased water clarity (Mittlebach et al. 1995). Large fishes such as bass often fill the role of keystone predators (*sensu* Paine 1969) in aquatic systems because they are voracious, gape-limited foragers that consume a diversity of suitably-sized prey and strongly affect prey community structure (Mittlebach et al. 1995).

Predatory fishes are so voracious that they affect local and regional patterns of habitat use by vulnerable prey such as crustaceans, insects, small fishes, and amphibians (e.g., Stein and Magnuson 1976, Woodward 1983, Morin 1984, Bennett and Streams 1986, McPeek 1989, Werner and McPeek 1994, Fraser et al. 1995, Jordan et al. 1996a, Turner 1996). Prey detection, capture success, and maneuverability of predatory fishes all tend to decrease with increasing habitat complexity (e.g., Crowder and Cooper 1982,
Therefore, habitat complexity plays an important role in mediating the coexistence of large predatory fishes and vulnerable prey taxa in aquatic systems (Werner et al. 1983a, 1983b, Cook and Streams 1984, Bennett and Streams 1986). In fact, the abundance and diversity of prey taxa tends to be orders of magnitude higher in complexly vegetated (refuge) habitats than in adjacent non-vegetated (non-refuge) habitats (see reviews by Orth et al. 1984, Heck et al. 1989, Heck and Crowder 1991).

Although direct removal of prey likely contributes to observed differences in prey abundance between refuge and non-refuge habitats, much of this difference appears to be due to predator-mediated habitat selection (e.g., Werner et al. 1983a, 1983b, Turner 1996, Jordan et al. 1996a). Through this behavioral response, predators indirectly affect food web dynamics within refuge habitats by intensifying intra- and interspecific competition (Werner et al. 1983a, 1983b, Mittlebach 1988, Werner and Hall 1988, Diehl and Eklöv 1995, Olson et al. 1995), increasing rates of intraguild predation and cannibalism (Spence and Cárcamo 1991), and altering food web structure (Power et al. 1985, Mittlebach 1988, Diehl and Eklöv 1995, Fraser et al. 1995). In contrast, predators can indirectly affect food web dynamics outside of refuge habitats by reducing competition (Werner et al. 1983a, 1983b), reducing cannibalism, and increasing the abundance of non-adjacent trophic resources (e.g., Werner et al. 1983a, 1983b, Turner and Mittlebach 1990, Diehl and Eklöv 1995, Turner 1996).

Another indirect effect of predator-mediated habitat selection can occur when predators in non-refuge habitats indirectly benefit (facilitate) predators in refuge habitats by causing prey aggregation therein (Soluk and Collins 1988, Werner 1994, Wootton 1994). As mentioned above, predatory fishes affect habitat selection by a wide diversity (and size range) of prey taxa. One result of this exodus of vulnerable taxa is the creation of new predator-prey combinations in refuge habitats, often consisting of pairs of species that formerly shared large fish predators (Werner and Gilliam 1984, Ebenman and Person 1989, Polis et al. 1989). For example, small fishes may be vulnerable to an alternate suite of
predators when they aggregate with large crustaceans and insects in refuge habitats (Kipling and Frost 1970, McCormick and Polis 1982, Turner and Mittlebach 1990, Rodd and Reznick 1991, Savino and Miller 1991). Very little is known about the numerical or behavioral responses that large arthropod predators and small prey fishes exhibit towards one another, or about the general importance of large arthropods as a source of mortality for small prey fishes (Chapter 6). Based upon research with vertebrate taxa such as anuran larvae (e.g., Heyer et al. 1975, Travis et al. 1985, Gascon 1992), it is plausible that populations of small fishes could be strongly affected by large arthropod predators in some aquatic habitats.

The freshwater marshes of the Everglades are comprised of mosaics of sloughs, wet prairies, and sawgrass stands that form gradients of increasing habitat complexity and decreasing water depth (Loveless 1959, Jordan et al. 1994, Chapter 2). Small prey fishes (i.e., members of the families Poeciliidae, Fundulidae, Cyprinodontidae, Elassomatidae, and Centrarchidae) use all of these habitats extensively (Loftus and Kushlan 1987, Chapter 4; Table 7.1). The suite of potential predators encountered by small marsh fishes may vary predictably across these habitats (sensu Werner 1994, Werner and McPeek 1994). Predatory largemouth bass, warmouth (Chaenobryttus gulosus, Centrarchidae), Florida gar (Lepisosteus platyrhincus, Lepisosteidae), and bowfin (Amia calva, Amiidae) are most abundant in structurally simple and relatively deep sloughs and alligator holes (Loftus and Kushlan 1987, Chapter 4; Table 7.1). In contrast, it appears that potential arthropod predators (i.e., spiders, crayfish, and insects of the families Aeshnidae, Belostomatidae, Dytiscidae, Libellulidae, and Naucoridae) are most abundant in wet prairies and sawgrass stands, and that use of these densely vegetated habitats may in part reflect avoidance of predatory fishes (Gunderson and Loftus 1993, Jordan et al. 1994, 1996a, Chapters 3 and 5). Alternatively, Heck and Crowder (1991) hypothesized that predatory arthropods may have increased foraging efficiency in complex habitats because of enhanced concealment,
provision of foraging perches, increased encounter rates with actively swimming prey, and reduced vigilance of prey.

Surprisingly little research has examined the distribution, abundance, and trophic role of large arthropods within the mosaic of sloughs, wet prairies, and sawgrass stands comprising the Everglades landscape (Gunderson and Loftus 1993, Davis and Ogden 1994, Rader 1994). To address this gap, I quantified the abundance of potential arthropod predators relative to the abundance of predatory fishes within a marsh habitat mosaic in the northern Everglades. I then performed laboratory feeding experiments to compare the voracity and selectivity of arthropod (crayfish, dragonfly naiads) and fish (largemouth bass) predators feeding on two common marsh fishes. This research was performed to address the following questions: 1) Does the absolute and relative abundance (importance) of predators vary predictably across sloughs, wet prairies, and sawgrass stands? 2) Are arthropod and fish predators equally voracious when preying upon small marsh fishes? 3) Does increasing habitat complexity affect the foraging efficiency of these predators similarly? 4) Do these predators exhibit preferences for small marsh fishes? 5) Are prey preferences consistent across different levels of habitat complexity?

Methods

Field Survey of Predatory Arthropods

Aquatic insects were collected from the 57,234 hectare Arthur R. Marshall Loxahatchee National Wildlife Refuge (hereafter the Refuge), which forms the northern remnant of the historic Everglades ecosystem (Palm Beach County, Florida, USA). The Refuge is comprised of a mosaic of sloughs (including alligator holes), wet prairies, and sawgrass stands that differ with respect to plant species composition, water depth, canopy height, and plant biomass (Chapter 2). Aquatic macrofauna were collected from these habitats with an aluminum throw trap (100 x 100 x 75 cm), which was thrown into the desired habitat and then pressed firmly into the substrate. The throw trap provides
quantitative estimates of large invertebrates and fishes and is one of the few techniques suitable for sampling aquatic macrofauna in densely vegetated habitats (Kushlan 1981, Freeman et al. 1984, Chick et al. 1992, Rozas and Minello in press). Plants were removed from within the throw trap and then a bar seine with 3-mm mesh was passed through the throw trap until three consecutive empty sweeps were obtained. Aquatic macrofauna were carefully picked from detritus in each sweep of the bar seine, preserved in 10% buffered formalin, and later identified in the laboratory. Large aquatic insects were identified to the order level (i.e., Hemiptera, Odonata, or Coleoptera). Small aquatic insects (i.e., Diptera, Ephemeroptera) were not included in this study because 1) they were not likely to prey upon small fishes, and 2) the throw trap was an inefficient method of collecting these organisms (Turner and Trexler, unpublished manuscript). Finally, large insects were collected concurrently with other potential aquatic predators, including fishes (Chapter 4), crayfish (Chapter 3), and fishing spiders (Jordan et al. 1994).

Collections were made approximately monthly between February 1990 and July 1992 (24 sampling events). During each event, six areas within accessible portions of the Refuge were randomly selected for sampling. Adjacent slough, wet prairie, and sawgrass sites were located within each area and three throw trap samples were collected from each site. This design resulted in 1,296 traps being obtained (24 months x 6 areas x 3 habitats x 3 samples), maximized areal coverage of the Refuge, and minimized vegetation damage due to repeated sampling and airboat travel. Macrofauna abundance data were log10(X + 1)-transformed and then used as response variables in analyses of variance testing for differences among habitat types. Significant F-tests were followed up with Bonferroni-Dunn post hoc multiple comparison tests (Day and Quinn 1989). Partial-correlations were used to test for patterns of association between the log-10 transformed mean abundance of small-size prey fishes, predatory arthropods (i.e., aquatic insects, fishing spiders, crayfish), and large predatory fishes at the scale of the entire landscape (i.e., habitat, area, and month were not included in these analyses).
Predation Experiment

Predation experiments were carried out using 48 plastic tanks (48 cm diameter, 43 cm height) that were arranged into four adjacent blocks of 12 tanks each. Each treatment combination was replicated once within each block and treatments were randomly assigned to tanks within blocks. Tanks were filled with tap water to a depth of 36 cm (0.18-m² surface area, 0.06-m³ volume) and were not aerated because of logistical constraints. Stems of the common wetland plant *Ludwigia repens* (hereafter *Ludwigia*) were collected from local ephemeral ponds, rinsed thoroughly, and then added to the tanks. One of three habitat complexity treatments was randomly assigned to each tank: low complexity (no *Ludwigia* stems), medium complexity (0.45 kg of *Ludwigia* stems), or high complexity (1.35 kg of *Ludwigia* stems). The plant densities used in this experiment represented a gradient in habitat complexity similar to that formed by adjacent sloughs, wet prairies, and sawgrass stands within wetlands of southern Florida (Jordan et al. 1994, 1996a, Chapter 2). Tanks were allowed to sit for 24 h before introducing any predators or prey.

Flagfish (*Jordanella floridae*, Cyprinodontidae), mosquitofish (*Gambusia holbrooki*, Poeciliidae), largemouth bass, odonate naiads (*Anax junius*, Aeshnidae), and crayfish (*Procambarus alleni*, Cambaridae) were collected from a variety of freshwater habitats and returned to the laboratory, where they were held in water from their respective collection sites for at least 24 h prior to placing them in experimental tanks. Mosquitofish and flagfish averaged 22.5 ± 0.5 mm and 24.7 ± 0.5 standard length, respectively. Late instar odonate naiads averaged 35.7 ± 1.6 mm (mean ± 1 SE) total length, adult crayfish averaged 63.9 ± 0.8 mm total length, and juvenile largemouth bass averaged 105.9 ± 4.7 mm standard length. Eight flagfish and five mosquitofish were added to each tank, based on relative densities at their collection site. Twenty four hours later, predators were randomly assigned to tanks within blocks according to the following treatments: no predators (control), 2 odonate naiads, 2 crayfish, or 2 bass. The bass predator treatments
were only run for 48 h due to low oxygen levels, whereas the remaining predator treatments were run for 7 days.

Surviving flagfish and mosquitofish were counted on Day 2 and Day 7 of the experiment and the percentages of surviving flagfish and mosquitofish (survivorship) were calculated for each date. Inspection of residual plots and Levene's test (Milliken and Johnson 1992) indicated that variances were unequal; therefore, survivorship values were arcsin-transformed to reduce observed heterogeneity of variances (Winer et al. 1991). Multivariate analyses of variance (MANOVA) were then used to simultaneously test for the effects of block, habitat complexity (low, medium, or high), predator type (control, crayfish, odonate naiad, or bass), and their interaction on flagfish and mosquitofish survivorship values for Day 2 and Day 7. MANOVAs were used to control for correlations between response variables and to reduce the likelihood of Type I statistical errors (Morin 1983, 1987). MANOVAs were followed up by factorial analyses of variance (ANOVA) to examine how individual species were affected by the experimental treatments. Least-squares means were compared to determine which means differed when main or interaction effects were significant. Means are presented for the untransformed data to simplify interpretation and because they produced very similar results in both the MANOVAs and ANOVAs.

Since both prey were offered simultaneously, I determined whether predators showed a preference for either flagfish or mosquitofish using Chesson's selectivity index (Gascon 1992). This index ranges from 0 to 1, with lower values indicating avoidance, higher values indicating preference, and intermediate values (≈ 0.5) indicating random prey selection. Preferences for flagfish on Day 2 and Day 7 were used as response variables in separate ANOVAs testing for the effects of block, predator type, habitat complexity, and the predator type x habitat complexity interaction. Preferences for mosquitofish were not used in ANOVAs because these are simply the complement of flagfish selectivity values (i.e., 1-flagfish selectivity index). If ANOVAs revealed no differences with respect to experimental
treatments, I combined values across predators and/or habitat complexities and then compared selectivities for flagfish and mosquitofish using paired t-tests (Gascon 1992). Visual inspection of residual plots and Levene's test indicated that data transformation was unnecessary.

**Results**

**Field Survey**

Potentially predatory arthropods were ubiquitous in the Refuge, with at least one individual being present in 78, 95, and 89% of the samples collected from sloughs, wet prairies, and sawgrass stands, respectively. Arthropod taxa differed in their use of sloughs, wet prairies, and sawgrass stands (Table 7.1). Sawgrass stands supported the highest numbers of fishing spiders, crayfish, and coleopterans. Wet prairies supported the highest numbers of hemipterans and dragonfly naiads, although sloughs also supported numerous dragonfly naiads. Overall, wet prairies and sawgrass stands supported about twice as many potentially predatory arthropods as sloughs, whereas sloughs supported about 2-3 times as many predatory fishes as wet prairies and sawgrass stands (Table 7.1). In terms of mean abundance (i.e., averaged across habitat types), the likelihood of a small fish encountering a predatory arthropod was about 27 times as great as the likelihood of its encountering a predatory fish. There was no correlation between the abundance of prey fishes and the abundance of predatory fishes (p > 0.05), whereas the abundance of prey fishes and predatory arthropods was positively correlated (r=0.338, p<0.0001).

**Predation Experiment**

A die-off of predatory bass occurred on the second morning (48 h) of the experiment, with bass mortality varying among the high (100%), medium (37%), and low (0%) habitat complexity treatments. Bass mortality appeared to be due to low oxygen levels associated with nocturnal plant respiration. Dissolved oxygen levels (measured at 10 a.m.
EST on Day 7) were significantly different among low (8.8 mg per L), medium (6.2 mg per L), and high (1.2 mg per L) habitat complexity treatments ($F_{2,24} = 289.2$, $p=0.0001$). No arthropod predators were lost during the experiment, which indicates that they can tolerate lower levels of dissolved oxygen than piscine predators. Due to this unexpected mortality, I performed separate analyses corresponding to Day 2 (bass predators included) and Day 7 (bass predators excluded) of the experiment.

MANOVA indicated that predator type (Wilk's Lambda=0.174, $F_{6,64} = 14.9$, $p=0.0001$) and the predator type x habitat complexity interaction (Wilk's Lambda=0.479, $F_{12,64} = 2.4$, $p=0.0135$) affected survival of prey fishes on Day 2, whereas experimental block (Wilk's Lambda=0.854, $F_{6,64} = 0.9$, $p=0.5190$) and habitat complexity (Wilk's Lambda=0.858, $F_{4,64} = 1.3$, $p=0.2887$) did not affect survival of prey fishes. Univariate ANOVAs (Table 7.2) indicated that both prey species were strongly affected by the different experimental factors.

Predation accounted for about half of the observed variation in flagfish and mosquitofish survivorship on Day 2 of the experiment (Table 7.2). Comparisons of least-squares means indicated that reductions in survivorship of flagfish were accounted for by bass (Figure 7.1), whereas both bass and dragonfly naiads reduced survival of mosquitofish relative to control and crayfish treatments (Figure 7.1). Habitat complexity did not directly affect survivorship of either prey species on Day 2 of the experiment (Table 7.1). However, habitat complexity and predator type interacted to affect survivorship of mosquitofish (Figure 7.1), which required separate comparisons (least-squares means) to assess the effects of predators (vs. controls) at each level of habitat complexity. Bass reduced survival of mosquitofish in low complexity tanks. Bass and dragonfly naiads reduced survival of mosquitofish in medium complexity tanks. Finally, all three predators reduced survival of mosquitofish in high complexity tanks. Survival of mosquitofish did not vary among habitat complexity treatments for tanks that contained either no predators (controls) or
crayfish. For tanks containing dragonfly naiads, survival of mosquitofish was lower in the high complexity tanks than in low complexity tanks. For tanks that contained bass, survival of mosquitofish was lower in low habitat complexity tanks than in either medium or high complexity tanks. Flagfish exposed to bass predators also had lower survivorship in low habitat complexity tanks than in either the medium or high complexity tanks.

Survival on Day 7 was analyzed excluding data from bass predator treatments. MANOVA indicated that predator type (Wilk's Lambda=0.473, $F_{4,46} = 5.2$, $p=0.0015$) and habitat complexity (Wilk's Lambda=0.635, $F_{4,46} = 2.9$, $p=0.0304$) affected survival of prey fishes on Day 7, whereas experimental block (Wilk's Lambda=0.784, $F_{6,46} = 1.0$, $p=0.4423$) and the predator type x habitat complexity interaction (Wilk's Lambda=0.681, $F_{8,46} = 1.2$, $p=0.3096$) did not affect survival of prey fishes. Univariate ANOVAs (Table 7.3) indicated that mosquitofish were strongly affected by the different experimental factors, whereas survival of flagfish was largely unaffected.

Predation accounted for about a third of the variation observed in mosquitofish survivorship on Day 7 (Table 7.3). Comparisons of least-squares means indicated that reductions in survivorship of mosquitofish were accounted for by dragonfly naiads (Figure 7.2), although crayfish were effective predators at high levels of habitat complexity (see below).

Survival of mosquitofish on Day 7 was inversely related to habitat complexity, with survival rates being lowest in high complexity tanks and highest in low complexity tanks. Survivorship was intermediate in medium complexity tanks, although not significantly different from either the high or low complexity tanks. Since survival of mosquitofish did not differ among habitat complexity treatments in control tanks, I assume that mortality was due to the effect of predators and not to differences in dissolved oxygen levels. Habitat complexity and predator type interacted to affect survival of mosquitofish (Figure 7.2), which required separate comparisons (least-squares means) to assess the effects of predators at each level of habitat complexity. Survival did not vary among predator
treatments in low complexity tanks. Dragonfly naiads reduced survival of mosquitofish in medium complexity tanks. Finally, crayfish and dragonfly naiads had similar effects on mosquitofish in high complexity tanks. Survival of mosquitofish did not vary among habitat complexity treatments for tanks that contained no predators. For tanks containing dragonfly naiads, survival of mosquitofish was lower in medium and high complexity tanks than in low complexity tanks. For tanks that contained crayfish, survival of mosquitofish was lower in high habitat complexity tanks than in either low or medium complexity tanks.

There were no significant differences among predators in their selectivity for flagfish or mosquitofish (Figure 7.3) by either Day 2 ($F_{2,23}=0.3$, $p=0.7721$) or Day 7 ($F_{1,15}=4.2$, $p=0.0578$) of the experiment. Further, habitat complexity did not affect patterns of prey selection on either Day 2 ($F_{2,23}=0.5$, $p=0.6110$) or Day 7 ($F_{2,15}=2.7$, $p=0.0960$) of the experiment. Comparison of combined predator selectivity for flagfish or mosquitofish did not differ on Day 2 ($t=0.5$, 46 df, $p=0.6159$). However, odonate naiads and crayfish combined showed a significant preference for mosquitofish by Day 7 of the experiment ($t=2.573$, 35 df, $p=0.0145$; also a marginally significant predator effect in Day 2 ANOVA).

**Discussion**

Predator composition often varies predictably along environmental gradients (Werner 1994, Werner and McPeek 1994). The present study indicates that the relative abundance and presumably importance of arthropod and fish predators varies predictably within the marsh habitat mosaic comprising the Refuge. Structurally-simple sloughs are dominated by bass and other predatory fishes (Dineen 1974, 1984, Loftus and Kushlan 1987, Chapter 4; Table 7.1), whereas structurally-complex wet prairies and sawgrass stands are dominated by fishing spiders, crayfish, and large insects such as *Pelecoris* (Naucoridae), *Erythemis* (Libellulidae), *Anax* and *Coryphaeschna* (Aeshnidae), *Enallagma* (Coenagrionidae), *Belostoma* and *Lethocercus* (Belostomatidae), *Cybister* (Dytiscidae), etc. (Gunderson and Loftus 1993, Jordan et al. 1994, 1996a; Table 7.1).
Habitat Use by Predators

Habitat-use decisions by large arthropods are motivated by a variety of interrelated factors (Lima and Dill 1990, Rosenzweig 1991), but risk of intraguild predation (i.e., predatory fishes eating predatory arthropods) is likely one of the most important determinants of habitat use in large arthropods (Werner 1994, Werner and McPeek 1994). For example, voracious predatory fishes tend to restrict large arthropods to densely vegetated habitats such as littoral zones (Cook and Streams 1984, Bennett and Streams 1986). Since all of the arthropods listed above are vulnerable to the opportunistic predatory fishes of the Everglades (e.g., Hunt 1952), it appears likely that the increased abundance of large arthropods observed in densely vegetated wet prairies and sawgrass stands is due in part to predator-mediated habitat selection. For example, behavioral observations indicate that the crayfish *Procambarus* prefers structurally-complex habitats (Chapter 5), as do other crayfishes and aquatic insects when threatened by predatory fishes (e.g., Stein and Magnuson 1976, Garvey et al. 1994). Shifting habitat use appears to be a prudent decision, because the survival of *Procambarus* exposed to predatory largemouth bass increases considerably with increasing habitat complexity (Chapter 5).

Enhanced survival is not the only benefit of using complex habitats. This study shows that the foraging efficiency of crayfish and dragonfly naiads increases with increasing habitat complexity, indicating that large arthropods may successfully prey upon the small fishes abundant in wet prairies and sawgrass stands of the Refuge (Chapter 4; Table 7.1). Interestingly, the risk of predation associated with predatory fishes can cause vulnerable fishes and arthropods to aggregate together. Although large arthropods overlap in size with small prey fishes (≈10-40 mm total length), they are not gape-limited and can easily prey upon vertebrates equal to or larger than themselves (McCormick and Polis 1982, Polis et al. 1989). Therefore, size-structured behavioral interactions in one habitat (i.e., small fishes and large arthropods avoiding large fishes in sloughs) lead to increased
opportunities for intraguild predation in another habitat (i.e., large arthropods feeding on small fishes in wet prairies and sawgrass stands). It is becoming evident that the effects of this type of indirect behavioral interaction (i.e., predators in one habitat facilitating predators in a second habitat) can cascade through food webs just as the numerical effects of keystone predators cascade through food webs.

Habitat-use decisions by predatory fishes are also motivated by a variety of interrelated factors, albeit on different temporal and spatial scales than predatory arthropods (Wiens 1976, Holling 1992). Large fishes can maneuver and capture prey more efficiently in sloughs and alligator holes because of lower habitat complexity and greater water depth in these habitats. Increased water depth also greatly reduces the vulnerability of large fishes to abundant wading bird predators (Power 1984, Harvey and Stewart 1991), which cannot forage efficiently in deep water (Kushlan 1976). Large fishes likely orient towards sloughs and alligator holes because these habitats are critical to their continued existence in the hydrologically-variable Everglades marshes (Dineen 1974, 1984, Kushlan 1974a, 1974b, Loftus and Kushlan 1987, Loftus and Eklund 1994, Chapter 4). Finally, it should be noted that production of large predatory fishes is generally low in the Everglades (Dineen 1974, 1984, Loftus and Kushlan 1987, Wiechman 1987), and the number of predatory fishes living in a given habitat is contingent upon antecedent hydrologic conditions, distance from permanently flooded habitats (i.e., sources of colonists), and other factors.

The unexpected die-off of largemouth bass on Day 2 of the predation experiment suggests that habitat use by some predatory fishes may be affected by nocturnal declines in dissolved oxygen levels, which are associated with plant respiration. Oxygen levels decreased with increasing habitat complexity (i.e., plant biomass) in this experiment, whereas bass mortality increased with increasing habitat complexity (also see Kushlan 1974a). Bass growth and survival decreases with decreasing dissolved oxygen levels (Stewart et al. 1967). Field measurements indicate that sloughs, wet prairie, and sawgrass stands in the study area regularly exhibit severe nocturnal declines in oxygen levels (Figure
Kushlan (1974) found that the diel dissolved oxygen regime in an alligator hole was less harmful to sensitive fishes (e.g., bass, warmouth) than was the regime in an adjacent wet prairie. Ambient dissolved oxygen levels are probably less influential on habitat selection by the numerically dominant Florida gar and bowfin, which are facultative air breathers (Loftus and Kushlan 1987). Field observations and results from the predation experiment also indicate that dissolved oxygen levels do not affect the distribution of arthropods within the mosaic of sloughs, wet prairies, and sawgrass stands comprising the Refuge. Finally, since prey fish survival did not vary among habitat complexity levels in the control tanks, it seems unlikely that dissolved oxygen levels affect habitat selection by prey fishes. Indeed, the ability of cyprinodontiform fishes (e.g., Cyprinodontidae, Fundulidae, Poeciliidae) to tolerate low oxygen levels by exploiting the oxygenated film of water at the air-water interface explains their ecological success in harsh environments such as the freshwater marshes of southern Florida (Lewis 1970, Kushlan 1974a, Loftus and Kushlan 1987). I intend to repeat this experiment in the future using aerated tanks.

**Habitat Use by Prey**

Small fishes and other vulnerable prey taxa tend to be risk-sensitive foragers that adjust their habitat use in response to the presence of potential predators (Lima and Dill 1990). This response results in vulnerable prey taxa generally being much more abundant in structurally-complex habitats than in adjacent structurally-simple habitats (Stoner 1983, Orth et al. 1984, Heck et al. 1989, Heck and Crowder 1991, Jordan et al. 1996a). In contrast, it appears that structurally-simple sloughs support about 17 and 74% more small prey fishes per m$^2$ than do structurally-complex wet prairies and sawgrass stands, respectively (Chapter 4; Table 7.1). This disparity may reflect the fact that small prey fishes of the Refuge find themselves “between a rock and a hard place”: they must minimize their exposure to predatory fishes in sloughs and predatory arthropods in wet prairies and sawgrass stands. Is the risk of predation greater in wet prairies and sawgrass stands than in
sloughs and alligator holes? Habitat-specific measures of predator abundance from the field survey (Table 7.1) can be combined with habitat-specific measures of voracity from the predation experiment (Figures 7.1 and 7.2) to estimate the relative intensity of predation ($\text{fishes} \cdot \text{m}^{-2} \cdot \text{day}^{-1}$) in different habitats. In sloughs, predatory fishes consume about 0.10 $\text{fishes} \cdot \text{m}^{-2} \cdot \text{day}^{-1}$, whereas predatory arthropods consume about 0.03 $\text{fishes} \cdot \text{m}^{-2} \cdot \text{day}^{-1}$. In wet prairies and sawgrass stands, predatory fishes consume about 0.01 $\text{fishes} \cdot \text{m}^{-2} \cdot \text{day}^{-1}$, whereas predatory arthropods consume about 0.72 $\text{fishes} \cdot \text{m}^{-2} \cdot \text{day}^{-1}$. Surprisingly, it appears that sloughs have a lower overall risk of predation (0.13 $\text{fishes} \cdot \text{m}^{-2} \cdot \text{day}^{-1}$) than do wet prairies and sawgrass stands (0.73 $\text{fishes} \cdot \text{m}^{-2} \cdot \text{day}^{-1}$), and that arthropod predators may have a greater effect on the abundance and distribution of prey fishes than do predatory fishes. These results are even more striking when considering the relative areal coverage of sloughs (1%), wet prairies (40%), and sawgrass stands (36%) in the Refuge (Richardson et al. 1990). Field studies using replicated enclosures should be performed to determine whether data from laboratory experiments provide realistic estimates of voracity for arthropod and fish predators.

Prey selectivity may further illuminate the importance of predatory arthropods in mediating habitat use by small Everglades fishes. Given that mosquitofish were the most abundant prey species in sloughs and alligator holes, it is significant that arthropod predators showed an increasing preference for mosquitofish by Day 7 of the predation experiment. Mosquitofish may be more vulnerable to predatory arthropods than other small fishes, and would therefore need to adjust their behavior accordingly. Mosquitofish were much more active than flagfish during the experiment, and increased activity level is an important determinant of prey selection (e.g., Folsom and Collins 1984, Lawler 1989, Savino and Stein 1989). Mosquitofish were less robust in size (i.e., shallower body depth and narrower girth) compared to flagfish, which may have also contributed to observed prey preferences. Bass were clearly more voracious than either odonate naiads or crayfish, likely reflecting greater metabolic demands arising from increased mobility. Cooper et al. (1985)
found that relatively immobile predators (e.g., crayfish and dragonfly naiads) were likely to show a greater preference for active prey than were more mobile bass (e.g., bass). Unlike crayfish and dragonfly naiads, bass showed no preferences for mosquitofish or flagfish.

**Effects of Habitat Complexity on Foraging Rates**

This study demonstrates conclusively that the effects of increasing habitat complexity varies with predator type. Foraging efficiency of active largemouth bass decreased with increasing habitat complexity, whereas foraging efficiency of odonate naiads and crayfish increased with increasing habitat complexity. Previous researchers have demonstrated that increasing habitat complexity adversely affects foraging efficiency of largemouth bass (e.g., Savino and Stein 1982, 1989, Werner et al. 1983a, 1983b, Schramm and Zale 1985, Gotceitas and Colgan 1987), especially beyond some threshold of habitat complexity (Gotceitas and Colgan 1989). The inhibitory effect of increasing habitat complexity on foraging efficiency appears to be a generality for fishes (Heck and Crowder 1991), although the decline may be greater for more active (searching) fishes than for more sedentary (ambush) fishes (Eklöv and Diehl 1994).

In contrast to fishes, relatively few studies have examined how habitat complexity affects arthropod predators in aquatic systems (Heck and Crowder 1991). Arthropod predators that rely upon structurally complex vegetation for cover and foraging perches may realize increased foraging efficiency with increasing habitat complexity (Heck and Crowder 1991). Furthermore, risk-sensitive predators are likely to have increased activity levels in the presence of suitable cover (Lima and Dill 1990). Previous research indicates that the effects of habitat complexity on *Anax* foraging varies with prey type. For example, Babbitt and Jordan (1996) found that predation rates on toad (*Bufo*) larvae decreased at very high plant densities. Similarly, Folsom and Collins (1984) found that foraging efficiency of *Anax* feeding on amphipods decreased with increasing plant complexity. Finally, predation rates on flagfish did not vary as a function of habitat complexity in an earlier study using
relatively low plant densities (Chapter 6), whereas predation rates on flagfish (and mosquitofish) increased with increasing habitat complexity in this study.

The seemingly disparate results above can be reconciled by taking into account differences in prey behavior (Folsom and Collins 1984, Lawler 1989, Mattila 1992) and the facultative foraging tactics of larval dragonflies (Pritchard 1965, Folsum and Collins 1984). Toad larvae and amphipods both utilize benthic habitats, whereas flagfish and mosquitofish are pelagic. Increasing habitat complexity in the water column facilitates *Anax*; i.e., detection and avoidance of *Anax* by relatively active pelagic prey decreases because the number of possible ambush sites available to predators increases. In contrast, increasing habitat complexity in the benthos inhibits *Anax*; i.e., detection and successful capture of relatively inactive benthic prey by *Anax* decreases because the number of possible refuge sites available to prey increases. *Procambarus* generally occupy complex habitats (Jordan et al. 1996a, Chapters 3 and 5), and results from this study indicate that crayfish foraging efficiency is enhanced in complex habitats. In contrast to dragonfly naiads, crayfish are active predators that search out suitable prey. Therefore, the facilitative effect of increased habitat complexity on crayfish foraging efficiency probably reflects increased foraging activity under less “risky” situations (Chapter 5). Finally, prey selection did not vary in response to habitat complexity.

As mentioned above, dissolved oxygen levels decreased with increasing habitat complexity in the predation experiment, and bass mortality appeared to be due to decreasing oxygen levels. Therefore, differences in the number of prey eaten by bass may reflect dissolved oxygen levels, rather than decreased foraging efficiency. Several lines of evidence argue against this alternative. First, bass were observed about 36 hours after they were introduced and there was no apparent difference in the behavior of bass in the different habitat complexity treatments. Second, another experiment (Chapter 5) was performed using aerated water, identical densities of *Ludwigia*, bass as predators, and crayfish as prey. Dissolved oxygen levels and bass survival (100%) were not affected by habitat complexity,
whereas survival of *Procambarus* prey increased with increasing habitat complexity. Finally, results of the present study are consistent with the findings of previous studies assessing the effects of increasing habitat complexity on bass foraging efficiency (e.g., Savino and Stein 1982, 1989, Werner et al. 1983a, 1983b, Schramm and Zale 1985, Gotceitas and Colgan 1987).
Table 7.1. Mean density (individuals/m²) of potential predators and prey fishes collected from sloughs (including alligator holes), wet prairies, and sawgrass stands during non-drought periods (i.e., May 1992 excluded). Nonrandom habitat use is indicated horizontally by letter superscripts for each predator (ANOVA, Bonferonni-Dunn post hoc test, p < 0.05; ns denotes non-significant F-test). Data for predatory fishes, crayfish, fishing spiders, and prey fishes are taken from Jordan et al. (1994) and Chapters 2 and 3.

<table>
<thead>
<tr>
<th>Taxa</th>
<th>Slough</th>
<th>Prairie</th>
<th>Sawgrass</th>
</tr>
</thead>
<tbody>
<tr>
<td>Araneae (fishing spider, <em>Dolomedes triton</em>)</td>
<td>0.013&lt;sup&gt;a&lt;/sup&gt;</td>
<td>0.046&lt;sup&gt;a&lt;/sup&gt;</td>
<td>0.219&lt;sup&gt;b&lt;/sup&gt;</td>
</tr>
<tr>
<td>Decapoda (crayfish, <em>Procambarus alleni</em>)</td>
<td>1.645&lt;sup&gt;a&lt;/sup&gt;</td>
<td>4.043&lt;sup&gt;b&lt;/sup&gt;</td>
<td>4.816&lt;sup&gt;c&lt;/sup&gt;</td>
</tr>
<tr>
<td>Odonata</td>
<td>1.742&lt;sup&gt;a&lt;/sup&gt;</td>
<td>2.007&lt;sup&gt;a&lt;/sup&gt;</td>
<td>1.080&lt;sup&gt;b&lt;/sup&gt;</td>
</tr>
<tr>
<td>Hemiptera</td>
<td>0.188&lt;sup&gt;a&lt;/sup&gt;</td>
<td>1.814&lt;sup&gt;b&lt;/sup&gt;</td>
<td>1.176&lt;sup&gt;c&lt;/sup&gt;</td>
</tr>
<tr>
<td>Coleoptera</td>
<td>0.039&lt;sup&gt;a&lt;/sup&gt;</td>
<td>0.121&lt;sup&gt;a&lt;/sup&gt;</td>
<td>0.285&lt;sup&gt;b&lt;/sup&gt;</td>
</tr>
<tr>
<td><strong>Total Arthropods</strong></td>
<td>3.627&lt;sup&gt;a&lt;/sup&gt;</td>
<td>8.031&lt;sup&gt;b&lt;/sup&gt;</td>
<td>7.576&lt;sup&gt;b&lt;/sup&gt;</td>
</tr>
</tbody>
</table>

| Predatory fishes<sup>ns</sup> | 0.039 | 0.019 | 0.012 |

| Prey fishes                 | 26.157<sup>a</sup> | 22.362<sup>b</sup> | 15.007<sup>c</sup> |
Table 7.2. Analysis of variance results testing for effects of block, habitat complexity, predator type, and their interactions on arcsin-transformed survivorship of flagfish (top) and mosquitofish (bottom) at Day 2 of the experiment.

**Arcsin-transformed flagfish survivorship**

<table>
<thead>
<tr>
<th>Source</th>
<th>DF</th>
<th>MS</th>
<th>F</th>
<th>P</th>
<th>R²</th>
</tr>
</thead>
<tbody>
<tr>
<td>Model</td>
<td>14</td>
<td>0.5</td>
<td>4.8</td>
<td>0.0001</td>
<td>67</td>
</tr>
<tr>
<td>Block</td>
<td>3</td>
<td>0.0</td>
<td>0.4</td>
<td>0.7294</td>
<td>1</td>
</tr>
<tr>
<td>Habitat</td>
<td>2</td>
<td>0.1</td>
<td>1.2</td>
<td>0.3156</td>
<td>2</td>
</tr>
<tr>
<td>Predator</td>
<td>3</td>
<td>1.9</td>
<td>17.9</td>
<td>0.0001</td>
<td>54</td>
</tr>
<tr>
<td>Habitat x Predator</td>
<td>6</td>
<td>0.2</td>
<td>1.6</td>
<td>0.1786</td>
<td>10</td>
</tr>
<tr>
<td>Error</td>
<td>33</td>
<td>0.1</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

**Arcsin-transformed mosquitofish survivorship**

<table>
<thead>
<tr>
<th>Source</th>
<th>DF</th>
<th>MS</th>
<th>F</th>
<th>P</th>
<th>R²</th>
</tr>
</thead>
<tbody>
<tr>
<td>Model</td>
<td>14</td>
<td>0.7</td>
<td>6.5</td>
<td>0.0001</td>
<td>73</td>
</tr>
<tr>
<td>Block</td>
<td>3</td>
<td>0.1</td>
<td>1.3</td>
<td>0.2755</td>
<td>3</td>
</tr>
<tr>
<td>Habitat</td>
<td>2</td>
<td>0.1</td>
<td>1.3</td>
<td>0.2896</td>
<td>2</td>
</tr>
<tr>
<td>Predator</td>
<td>3</td>
<td>2.2</td>
<td>21.4</td>
<td>0.0001</td>
<td>52</td>
</tr>
<tr>
<td>Habitat x Predator</td>
<td>6</td>
<td>0.3</td>
<td>3.3</td>
<td>0.0115</td>
<td>16</td>
</tr>
<tr>
<td>Error</td>
<td>33</td>
<td>0.1</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Table 7.3. Analysis of variance results testing for effects of block, habitat complexity, predator type, and their interactions on arcsin-transformed survivorship of flagfish (top) and mosquitofish (bottom) at Day 7 of the experiment.

**Arcsin-transformed flagfish survivorship**

<table>
<thead>
<tr>
<th>Source</th>
<th>DF</th>
<th>MS</th>
<th>F</th>
<th>P</th>
<th>R²</th>
</tr>
</thead>
<tbody>
<tr>
<td>Model</td>
<td>11</td>
<td>0.1</td>
<td>0.7</td>
<td>0.7594</td>
<td>23</td>
</tr>
<tr>
<td>Block</td>
<td>3</td>
<td>0.1</td>
<td>0.9</td>
<td>0.4530</td>
<td>9</td>
</tr>
<tr>
<td>Habitat</td>
<td>2</td>
<td>0.1</td>
<td>1.3</td>
<td>0.2783</td>
<td>9</td>
</tr>
<tr>
<td>Predator</td>
<td>2</td>
<td>0.1</td>
<td>0.8</td>
<td>0.4772</td>
<td>4</td>
</tr>
<tr>
<td>Habitat x Predator</td>
<td>4</td>
<td>0.0</td>
<td>0.1</td>
<td>0.9867</td>
<td>1</td>
</tr>
<tr>
<td>Error</td>
<td>24</td>
<td>0.1</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

**Arcsin-transformed mosquitofish survivorship**

<table>
<thead>
<tr>
<th>Source</th>
<th>DF</th>
<th>MS</th>
<th>F</th>
<th>P</th>
<th>R²</th>
</tr>
</thead>
<tbody>
<tr>
<td>Model</td>
<td>11</td>
<td>0.4</td>
<td>4.3</td>
<td>0.0013</td>
<td>67</td>
</tr>
<tr>
<td>Block</td>
<td>3</td>
<td>0.1</td>
<td>1.2</td>
<td>0.3371</td>
<td>5</td>
</tr>
<tr>
<td>Habitat</td>
<td>2</td>
<td>0.5</td>
<td>5.0</td>
<td>0.0157</td>
<td>14</td>
</tr>
<tr>
<td>Predator</td>
<td>2</td>
<td>1.1</td>
<td>11.8</td>
<td>0.0003</td>
<td>33</td>
</tr>
<tr>
<td>Habitat x Predator</td>
<td>4</td>
<td>0.3</td>
<td>2.7</td>
<td>0.0568</td>
<td>15</td>
</tr>
<tr>
<td>Error</td>
<td>24</td>
<td>0.1</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Figure 7.1. Mean (+ 1 SE) survivorship of flagfish (top) and mosquitofish (bottom) on Day 2 in relation to predator type and habitat complexity. For each predator, means with different letters are significantly different (least-squares means).
Figure 7.2. Mean (+ 1 SE) survivorship of flagfish (top) and mosquitofish (bottom) on Day 7 in relation to predator type and habitat complexity. For each predator, means with different letters are significantly different (least-squares means).
Figure 7.3. Mean (+ 1 SE) selectivity for mosquitofish on Day 2 (top) and Day 7 (bottom) of the experiment. For each predator, means with different letters are significantly different (least-squares means).
Figure 7.4. Diurnal variation in dissolved oxygen levels in sloughs, wet prairies, and sawgrass stands in the Refuge. Solid diagonal line is the common regression for these habitats. Light horizontal lines show the oxygen levels observed in the low (bottom), medium (middle), and high (top) habitat complexity treatments during the predation experiment.
CHAPTER 8
CONCLUSION

General Summary

The central conclusion of this research is that the abundance of decapods and fishes at any given location within the northern Everglades landscape is the product of a hierarchy of processes operating at local, regional, and seasonal scales. This finding of scale-dependent spatial and temporal variability is critical given the present interest in developing spatially and temporally explicit models of Everglades ecosystem function. It is also important to note that adopting a landscape perspective greatly facilitated identifying these cross-scale influences. It is reasonable to assume that management and conservation issues in the Florida Everglades and related wetland ecosystems will be resolved most efficiently by adopting a similar landscape perspective. Chapters 1-4 deal with these issues of scale quite extensively; therefore, the remainder of this summary chapter will be used to briefly review other findings from this research project and to present a simple verbal model of how hydrology, habitat complexity, and predation can interact to affect the structure of aquatic macrofaunal communities in freshwater wetland systems.

This research revealed a wealth of information concerning the basic ecology of freshwater wetlands and aquatic macrofaunal assemblages. First, factors that vary over a large scale (e.g., gradients in hydroperiod and nutrient enrichment) play a very significant role in determining the abundance of decapods and small fishes, and these factors are likely mediated through bottom-up (i.e., resource availability) and top-down (i.e., risk of predation) food web processes. Second, local variation in water depth and accumulation of plant biomass (i.e., habitat complexity) also profoundly affect population demographics, and are driven by more localized versions of top-down and bottom-up food web processes. There are distinct patterns of habitat use by prawns, crayfish, and most fishes, and these
patterns of nonrandom habitat use translate into habitat-specific assemblage structure. Third, seasonal changes in water levels result in shifts in the relative quality of adjacent habitats, which leads to shifts in patterns of habitat use by decapods and fishes. This seasonal shift is most extreme during severe marsh drawdowns, when most fishes and prawns are congregated into deep, dry-season refugia (i.e., sloughs and alligator holes in the northern Everglades). In contrast, crayfish apparently respond to drought conditions by burrowing into the peat substrate. Importantly, the relative abundance of small fishes and large invertebrates is about equal in the northern Everglades. This suggests that a rich diversity of size-structured interactions is possible, including a reversal of the typical vertebrate predator-invertebrate prey relationship (McCormick and Polis 1982, Polis et al. 1989).

**Changing Views of Marsh Community Organization**

Few data have been available to evaluate the relationships between hydrologic conditions, predator abundance, and habitat complexity in wetland systems. Kushlan (1976) proposed that the freshwater fish community of the southern Everglades would be dominated by small-sized forage fishes when water levels fluctuated, whereas larger predatory fishes would predominate when water levels were stable. This model was based on data that indicated a significant increase in the relative abundance and biomass of larger fishes during a 27-month period in which the study system was continuously inundated. Additionally, reductions in the abundance of *Procambarus* were also attributed to increased predation intensity during periods of prolonged inundation (Kushlan and Kushlan 1979). The Kushlan (1976) model has been used as a heuristic device to guide management of both water and wildlife in the greater Everglades ecosystem (e.g., Kushlan 1987, Walters et al. 1992).

Unfortunately, the data upon which the model was constructed appear to be inaccurate due to a profound sampling bias (see Loftus and Eklund 1994, Chapter 1).
Analysis of less-biased data sets (Loftus and Eklund 1994) indicate that both predator and prey populations increase during periods of prolonged inundation. Loftus and Eklund (1994) hypothesized that prey populations persisted (and increased in size) despite increases in predator abundance because of the availability of refuges (i.e., densely vegetated habitats) from predation. That is, vulnerable prey taxa shifted their use of habitats to minimize their risk of predation by predatory fishes. Results from this study (Chapters 5-7) and others (e.g., Chick 1992) support this hypothesis and suggest that hydrology, predation, and habitat complexity can interact strongly to structure aquatic communities in freshwater wetland systems.

Significantly, the abundance of small fishes was greatest in deeper, structurally simple sloughs. This finding was unexpected given that small fishes are usually more abundant in densely vegetated habitats within most freshwater and marine systems (e.g., Heck and Crowder 1991). These results can be reconciled by examining variation in predator assemblage structure along a gradient of increasing water depths and decreasing habitat complexity. Large predatory fishes predominate in deep, structurally-simple sloughs, whereas large predatory insects predominate in shallow, structurally-complex wet prairies and sawgrass stands. This gradient in predator assemblage composition is formed because predatory arthropods shift their habitat use to avoid being preyed upon by large predatory fishes. The end result of this shift is that the indirect behavioral effects of predators cascade down through food webs and alter species interactions at lower trophic levels (e.g., Turner and Mittlebach 1990, Mittlebach et al. 1995).

Long-term data sets available for Everglades fishes include several critical drought (disturbance) events that can be used to estimate standing stocks. These data indicate that populations of numerically dominant small fishes quickly rebound and level off (J. Trexler and W. Loftus, personal communication; Loftus and Eklund 1994, Chapter 4). Bottom-up (i.e., resource driven) regulation of small fish abundance is certainly important in the Everglades, because most of this system is nutrient limited (Davis 1994). Indeed, nutrient
enriched portions of the Everglades are characterized by significantly higher numbers of fishes (Chapter 4). Contrary to the hypothesis of Kushlan (1976), there is little compelling evidence for top-down control of small fish abundance by predatory fishes during drought-free periods (Loftus and Eklund 1994). Rather, predatory fishes indirectly affect the abundance of small fishes and large predatory arthropods by causing these vulnerable taxa to aggregate in densely-vegetated wet prairies and sawgrass stands (Chapter 7). The resultant distribution of predatory fishes and arthropods reflects underlying gradients in habitat complexity and water depth, which are closely related in the Refuge (Chapter 2). Results of the present study indicate that predation and habitat complexity both affect survival of flagfish and mosquitofish and at least partially account for patterns of habitat use by these fishes observed in the field. Moreover, this study revealed that predatory arthropods are ubiquitous and may therefore play a prominent role in regulating the size of fish populations. Different hydrological conditions (e.g., duration of inundation) are going to favor different predator assemblages (e.g., predatory arthropods vs. large fishes), which in turn will effect changes in habitat-specific prey assemblage structure (Werner and McPeek 1994). Therefore, a general model of assemblage regulation in wetland systems should not be based solely on hydrology, but should also incorporate the direct and indirect effects of predators and habitat complexity.

Clearly, more research is needed to address gaps in our understanding of ecosystem function in the northern Everglades. Future descriptive research should compare food web structure across the mosaic of habitats comprising the Everglades landscape. Experimental work is needed to examine per-capita consumption rates of a larger complement of arthropod predators feeding on small prey fishes. Additionally, field experiments using relatively large enclosures and exclosures should be performed to determine if arthropod and/or vertebrate predators play a role in regulating the abundance of small fishes. Finally, factorial experiments are desperately needed to detangle the complex relationships between nutrient enrichment, hydrology, and predator regime.
REFERENCES


Bedford, B. L. 1996. The need to define hydrologic equivalence at the landscape scale for freshwater wetland mitigation. Ecological Applications 6:57-68.


139


DeVries, D. R. 1990. Habitat use by bluegill in laboratory pools: where is the refuge when macrophytes are sparse and alternative prey are present? Environmental Biology of Fishes 29:27-34.


productivity and mosquitofish (Gambusia affinis) production in large microcosms. Limnology and Oceanography 17:445-450.


and shrimps. Milwaukee Public Museum Contributions in Biology and Geology 85.


Jordan, F., K. J. Babbitt, and C. C. McIvor. In review a. Habitat use by freshwater marsh
fishes in the Blue Cypress Marsh Conservation Area, Florida.

Jordan, F., K. J. Babbitt, and C. C. McIvor.  In review b.  Distribution of the prawn *Palaemonetes paludosus* within a Florida wetland mosaic.


interactions among piscivores, planktivores, and plankton. Ecology 71:2241-2254/


BIOGRAPHICAL SKETCH

Frank Jordan was born 19 April 1963 in the cultural backwaters of Jacksonville, Florida. He was attracted to aquatic biology at an early age, often collecting fishes and tadpoles from the less than pristine Willowbranch Creek and transporting them to his nearby home to assist in his constant struggle for coexistence with a battalion of dominating sisters. A high school course in marine biology rekindled Frank's early interest in things wet and squishy. Finally, Frank found out that people actually received money to play with fish and the rest is history!

Frank received an A.S. (Liberal Arts) from Florida Junior College at Jacksonville in 1984, a B.S. (Biological Science) from Florida State University in 1987, and a M.S. (Biological Science) from Florida State University in 1989. While at Florida State University, Frank worked for Skip Livingston as an undergraduate research assistant. It was in this capacity that Frank really became interested in studying fishes for a living. Frank also had the good fortune of interacting with the likes of Joe Travis and Chris Koenig, who contributed significantly to Frank’s radically deviant approach to the field of ecology.

While engaged in the graduate school struggle, Frank was involved with entirely too many extraneous projects. He studied Okaloosa darters, Eustis pupfish, Gulf sturgeon, pinfish, crayfish, tadpoles, insects, and myriad other squishy critters. Finally, Frank was last seen at Jacksonville University corrupting young minds and spreading the piscine gospel of the Primitive Piscatory Church of the Second Coming of the Earlier Day Acanthodians. It is rumored that Frank hopes to finally learn how to play his perpetually untuned guitar and start a band called Pot Belly Jesus and Satan’s Flaming Sphincters.
I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

_____________________________
Carter R. Gilbert, Chairman
Professor of Zoology

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

_____________________________
Lauren J. Chapman
Assistant Professor of Zoology

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

_____________________________
C. S. Holling
Arthur R. Marshall, Jr., Professor of Ecological Sciences

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

_____________________________
Wiley M. Kitchens
Associate Professor of Wildlife Ecology and Conservation

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

_____________________________
Frank G. Nordlie
Professor of Zoology

This dissertation was submitted to the Graduate Faculty of the Department of Zoology in the College of Liberal Arts and Sciences and to the Graduate School and was accepted as partial fulfillment of requirements for the degree of Doctor of Philosophy.

December 1996

_____________________________
Dean, Graduate School