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INTRODUCTION

In her influential 1947 book, Marjory Stoneman Douglas coined the phrase "river of grass" to describe the Florida Everglades. Historically, marshes and sloughs of the Everglades extended uninterrupted in the southerly river-like flow of fresh water from Lake Okeechobee to Florida Bay. However, since the late 1800s that flow has been increasingly disrupted and the Everglades ecosystem is now broken into a number of compartments separated by levees and canals. Has this relatively new spatial structure affected the aquatic fauna of the Everglades? Has it disrupted historical linkages between northern and southern portions of the Everglades drainage basin? We examine patterns of spatial variation in fish communities to ask if their density, relative abundance, or population genetic structure has been marked by the relatively new spatial divisions imposed by human alterations of this wetland. Almost no information exists about historical aquatic communities of the Everglades, yet the planned restoration effort must benefit its aquatic communities if wading birds and other predators are to benefit (Frederick and Spalding, 1994; Ogden, 1994) and ecosystem function is to be restored. Our analysis of present-day communities generates hypotheses about the historical ecological functions sought by restoration and provides benchmarks to evaluate future system alterations.

There remains some disagreement about patterns in the structure of fish communities in the Everglades and ecological factors creating them. Published studies on the ecology of Everglades fishes emphasize the interaction of seasonal hydrological variation, vegetation dynamics, and the dynamics of fish communities in its freshwater marshes (Kushlan 1976a, b, 1981; Loftus and Eklund, 1994; Jordan, 1996). Much of this work has emphasized the role of alligator ponds as dryseason refuges determining fish demography and dynamics each year (Kushlan, 1974, 1976b; Karr and Freemark, 1985). However, alligator ponds vary in frequency across the Everglades and are sparsely distributed in many regions. Recent simulation models call into question the capacity of alligator pond refuges to explain the dynamics of Everglades fish communities (DeAngelis et al., 1997). It has been suggested that the density of small fishes has declined in the Everglades because water management extended the period between system-wide drydown, permitting an increase in

the abundance of large piscivorous fishes (Kushlan, 1987). However, the pattern of fishes at sites experiencing different hydroperiods is not consistent with this hypothesis (Loftus and Eklund, 1994). With the increasing emphasis on a scientific basis for Everglades management and restoration, recent studies have provided new information that can be brought to bear on these issues.

The spatial scale of community dynamics, local topographic relief, and spatial variation in nutrient biogeochemistry may play a larger role in determining the structure and function of Everglades fish communities than previously appreciated (Frederick and Spalding, 1994; Chick and McIvor, 1994; DeAngelis, 1994; Jordan, 1996; Jordan et al., 1998). Here, we review the results of several ongoing studies of the spatial scale of fish community structure in the Everglades. Our analysis groups the community into two classes based on body size - large (>8 cm standard length) and small (<8 cm). This break is necessary because of size-based bias in sampling techniques but is also biologically defensible because body size influences the way fish respond to their environment. Compared to small fishes, larger fishes require larger and deeper dry-season refuges and can move longer distances in searching for appropriate habitat, and many are potential predators of smaller fish. Thus, the expedient size-based division of our analyses likely corresponds to sizerelated behavioral responses of fishes to their environment. The break roughly separates the cyprinodontiform segment of the fish community, and juveniles of all species, from adult piscivorous species, including centrarchids, bullhead catfish, gar, and bowfin (Loftus and Kushlan, 1987). Adult lake chubsuckers, with a diverse diet that ranges from detritus to larval fish, are also included in the large-fish group. The adults of most introduced fishes fall into the large-fish category, though these species are not, at present, particularly common in marshes distant from either canals or the mangrove zone (Trexler et al., 2000).

We address three questions related to ecological scaling: What is the spatial scale of variation in fish abundance? Are spatial patterns consistent over time? What is the spatial scale of genetic variation in selected fishes from the Everglades? Our analyses are at three spatial scales arranged in a nested design: among water-management units, within units among sites separated by 10 to 15 km, and among plots separated by approximately 1 km within those sites. The majority of data reported here were gathered between 1996 and 1997, but we also report aspects of a long-term sampling effort conducted at a subset of the study sites in the Everglades National Park. We examine the spatial scale of variability in fish density and relative abundance at these three levels. Then, with a slightly different sampling design, we will examine the pattern of genetic diversity in two species of fish from the same study regions. From these data, we develop hypotheses about the role of environmental fluctuation in setting the scale of fish-community structure in the Everglades.

MATERIALS AND METHODS

NATURAL HISTORY: THE EVERGLADES FISH FAUNA

The native fish community of the Everglades is relatively species poor and lacks endemic species. There are about 30 freshwater-fish species inhabiting the ecosystem (Loftus and Kushlan, 1987), a relatively small number for the spatial area of the drainage basin (Swift et al., 1986; Trexler, 1995). A historical explanation for the paucity of freshwater fish species is compelling. The freshwater Everglades ecosystem is relatively young, 5000 years (Gleason and Stone, 1994), and is found at the tip of a peninsula. However, the low topography and karstic limestone geology limit aquatic habitat diversity and exclude members of the ichthyofauna found in northern Florida (Swift et al., 1986; Gilbert, 1987). In most of North America, cyprinids play a prominent role in fish community composition. However, species composition of the Everglades fauna is dominated by cyprinodontiforms, especially poeciliids and fundulids derived from the U.S. southeastern coastal plain (Loftus and Kushlan, 1987). Cyprinodontiforms are also numerically dominant (Loftus and Kushlan, 1987), Jordan et al., 1998). The Everglades also has low standing stocks (g/m^2) of fishes when compared to other wetland, floodplain, or littoral zone ecosystems (Turner

et al., 1999). Several species of introduced fishes are naturalized members of the fauna, including at least five cichlids, and a poeciliid (Fuller et al., 1999; Loftus, 2000). At present, these species comprise less than 10% of the fishes (numerically or by biomass) in most habitats, with the exception of canals, very short-hydroperiod wetlands peripheral to the sloughs, and the mangrove zone downstream of the sloughs (Trexler et al., 2000). Their ecological impact as predators and competitors of native species in the Everglades is, as yet, unclear, especially in slough habitats.

THE STUDY AREA

Our study is limited to the central and southern Everglades Protection Area encompassing Water Conservation Areas (WCAs) 3A and 3B, and Shark River Slough (SRS) and Taylor Slough (TS) in Everglades National Park (ENP) (Figure 5.1). WCA-3A is subdivided by canals and levees into four separate compartments that we treat individually (Figure 5.1: WCA-3A-nw, -ne, -se, and -sw). Water moves through these compartments roughly from north to south. WCA-3B has been completely isolated from the north-south flow way by barrier levees since 1963 (Light and Dineen, 1994). SRS receives water from rainfall and flow from the WCAs to the north through a series of flood-control gates (S-12 structures). TS, also in ENP, had historical connections with the SRS



FIGURE 5.1 Map of the study area showing sampling sites. Solid lines indicate canal or levee boundaries and dashed lines indicate the boundaries of Shark River and Taylor River sloughs in Everglades National Park. Sites 1 and 2 in TS are each bordered to the east and west by short-hydroperiod plots not visible on the scale of this figure. We treat these short-hydroperiod plots as separate sites to yield a total of five sites in TS.

(Tabb, 1987) but currently functions as a separate drainage basin. The historical headwaters of TS are now drained and developed; since 1968, all water other than rainfall entering TS has come from the South Dade Water Conveyance canal system via pumps (Light and Dineen, 1994).

The phrase "river of grass" is an apt description of the Everglades. The large drainage basin that includes the WCAs and SRS and the smaller drainage basin of TS have shallow but hydrologically significant contours parallel to the roughly north-south direction of flow. Thus, as the water table recedes in the dry season, habitats to the east and west sides of the flow-way dry first while those near the center remain inundated the longest. Marshes of the central flow-way remain inundated year-round in most years, sustaining a peat-forming environment (Gleason and Stone, 1994). We identified study sites as short-hydroperiod marsh if they experience an estimated average inundation of <300 days per year, and a long-hydroperiod marsh if they experience an average inundation of >300 days per year. These designations were based on simulations run by the South Florida Water Management Model (Fennema et al., 1994) and from personal experience at the study sites. There is marked interannual variation in local hydroperiod that results from local and regional rainfall patterns, and water-management decisions.

All sites were located in wet prairie habitats that are dominated by spikerush, mostly *Eleocharis cellulosa* (Gunderson, 1994; Jordan et al., 1997b). Sampling sites were restricted to this habitat for both practical and biological reasons. Wet prairies are typically 10 to 20 cm lower than adjacent dense sawgrass stands (Jordan et al., 1997b). Thus, these habitats retain water and fishes longer in the dry season than adjacent sawgrass habitats. Sampling in sawgrass, the other dominant habitat, is difficult because of its density and abrasive character. Also, stratifying across habitat type was not logistically feasible because of the number of samples required. Throw-trap samples collected in dense sawgrass stands adjacent to some of our spikerush-dominated wet prairie study sites (six sites, eight samples per habitat per site) yielded fewer fish in the sawgrass habitat than in the spikerush (mean number of fish m⁻²: sawgrass = 20.6, spikerush = 39.1; paired t₅ = -3.13, P = 0.03). In a more extensive study, Jordan (1996) also found fewer fishes in sawgrass than in spikerush habitats in the Loxahatchee National Wildlife Refuge in the northern Everglades.

SAMPLING DESIGN

We measured fish density in a nested sampling design to permit analysis at three spatial scales: water-management units, sites, and plots. The water-management units corresponded to areas bounded by canals and levees (e.g., WCAs) or natural drainage features (e.g., TS). We chose sites haphazardly to cover the spatial area of water-management units, and the number of sites per management unit varied roughly with the size of that unit.

Quantitative study of the aquatic-animal fauna of the Everglades is inherently difficult because of the dense aquatic vegetation, extensive unbounded habitats, and logistics of access to the habitats, particularly in the dry season. Sampling fishes in the Everglades is complicated by a problem of scale: The small-bodied cyprinodontiforms are relatively abundant at the 1-m scale, while the larger bodied species (e.g., centrarchids) usually occur at such low densities that few specimens of any age/size class appear in samples collected at the 1-m scale. Thus, we applied two approaches for sampling fishes in the Everglades that targeted different components of the community: throw trapping for small fishes (<8 cm standard length) and boat electrofishing for larger fishes (>8 cm).

Throw Trapping

We obtained density estimates of small fishes with a 1-m² throw trap. Selection of this technique is justified by several comparative studies that examined a variety of alternative techniques and trap sizes (Kushlan, 1981; Chick et al., 1992; Loftus and Eklund, 1994). For sampling over a large spatial area as in this study, we must determine if sampling bias varies across the range of habitat variables encountered at different sites. Jordan et al. (1997a) did that by comparing clearing efficiency and sampling accuracy of throw traps in wet prairies with a range of stem densities. They conducted throw trapping in block nets with a known number of marked fish added and estimated the "true" density by rotenone sampling within the block nets. They concluded that, on average, 63% of the fishes present were collected. More important, they found a high correlation (r = 0.82) between the throw-trap estimated density and block-net estimated density. No effect of water depth, emergent plant stem density, canopy height, or periphyton volume was detected on throw-trap collection accuracy or clearing efficiency.

We selected three plots within each site, where we marked off 100 m \times 100 m grids divided by 10-m increments. Throw-trap samples were taken at randomly selected coordinates in the grids. For logistical reasons, seven samples were taken per visit in the ENP and five samples per visit in the WCAs. Plots were separated by 0.5 to 2.0 km, while nearest-neighbor sites within watermanagement units were separated by 5 to 10 km in SRS and TS, and by 8 to 17.5 km in WCA-3A.

Fish sampling has been conducted for different lengths of time at the study sites indicated on Figure 5.1. Sites 6, 23, and 50 in the ENP have been sampled monthly or approximately bimonthly by throw trap since 1977, a period encompassing a range of hydrological conditions from very dry to very wet years. For this chapter, we report analysis of a 10-year interval from 1985 to 1995, which we will call the "long-term study." The more spatially extensive effort to sample 20 sites was begun in mid-1995 and continues to the present. This study period has included only wet years with relatively long hydroperiods at each site. Data collected from July 1996 to April 1997 were analyzed, and those analyses will be referred to as the "short-term study." Routine electrofishing at a subset of the study sites was begun in 1997. We visited the study sites five times per year during February, April, July, October, and December. These months coincide with important transitional phases of Everglades wet–dry season hydrology (Fennema et al., 1994). Not all sites can be sampled by one or both of these techniques in any particular month because water recession depends on local topography, and water depth may exceed that amenable to sampling by throw trap (>1.1 m). In this paper, analysis of subsets of the data that are most useful for illustrating the issues of spatial scale in fish-community composition and dynamics are reported.

Electrofishing

We used airboat electrofishing to examine patterns in the abundance and composition of large fishes (standard length > 8 cm) across space and time. Electrofishing catch per unit effort (CPUE) is a reliable index of fish density (measured by block nets) in freshwater marshes of the Everglades (Chick et al., 1999). Electrofishing samples were collected quarterly (10/97, 2/98, 4/98, 7/98, 10/98) from wet prairies in the vicinity of a subset of the throw-trap sites. We sampled four sites within WCA-3A (1, 3, 4, 5), four sites within SRS (6, 7, 8, 37), and three sites within the smaller TS (1, 2, 3) (Figure 5.1). At each site, we conducted three 5-min electrofishing transects in the vicinity of each of the three 1-ha plots permanently established at each site. To improve our sampling consistency, we standardized electrofishing power (wattage = voltage × amperage) at 1500 W over different temperature and conductivity conditions using the methods described by Burkhardt and Gutreuter (1995).

For each transect, we identified the major vegetation types present, visually estimated the percentage cover of periphyton, measured water depth (cm), temperature (°C), and specific conductance (μ S/cm). Each transect was separated by a 50-m buffer and covered approximately 150 to 250 m of marsh with the airboat running at idle speed. We also conducted electrofishing within alligator ponds once during the dry (4/98) and wet (10/98) seasons. We located 10 to 12 ponds in each water management unit and electrofished for 5 minutes within each pond.

POPULATION GENETIC ANALYSIS

Spatial patterns of genetic variation are sensitive to migration and gene flow, population size and sex ratio, and mating patterns of individuals (Slatkin, 1985). Thus, analysis of population genetic structure provides a useful surrogate measure for fish migration because direct analysis of movement

is not practical for the abundant small fishes of the Everglades. Analysis of population structure has other benefits: It is reflective of average movement and mating patterns over multiple generations and is less subject to the idiosyncratic behavior of individuals than direct measures of movement. We examined allozymic diversity in eastern mosquitofish, *Gambusia holbrooki*, and spotted sunfish, *Lepomis punctatus*, from population samples taken across the study area (Trexler et al., unpubl. data). In 1996, 50 individuals from each of 52 populations of mosquitofish and 12 to 24 individuals from each of 20 populations of spotted sunfish were genotyped at 10 to 12 loci, respectively. This permitted us to examine patterns of heterozygosity and partition genetic variation at three spatial scales using Wright's *F*-statistics comparable to partitioning variance by analysis of variance (Hartl and Clark, 1997): among water-management units (F_{pl}), among local sites within units (F_{sp}), and within individuals in local sites (F_{is}). Most of the locations where eastern mosquitofish were collected were re-sampled in 1999, a year when much of the ecosystem dried and aquatic animals were forced into local alligator ponds and other aquatic refuges.

A NOTE ON STATISTICAL TECHNIQUES

The analyses reported generally used standard statistical methods not requiring detailed discussion here. However, two decisions regarding analysis of the community-structure data warrant mention. We used nested analysis of variance (ANOVA) and multiple analysis of variance (MANOVA) to partition variance into different spatial and temporal sources. We have opted not to employ repeated-measures designs to test for temporal effects. Use of a repeated-measures design would not alter our partitioning of variance to spatial and general temporal effects, but would affect partitioning of variance among interactions of space and time. These temporal effects are not the focus of discussion in this work. Also, there is no general agreement on consideration of "plot" as a repeated factor because random sampling is applied within plots and the same fish are not sampled each visit. Detailed analysis of temporal autocorrelation in fish communities from the long-term study plots have found that it is limited to adjacent bimonthly samples from longhydroperiod sites (Trexler and Loftus, 2000), probably because of the marked inter-year variance in hydropattern at each study site. Little or no temporal autocorrelation is seen in throw-trap samples collected bimonthly from short-hydroperiod marshes.

We used nonmetric multidimensional scaling (NMDS) to ordinate the Bray-Curtis dissimilarity indices (Kuskal and Wish, 1978) and to identify latent patterns in our species composition data. This technique configures samples along axes based on the proximity of their dissimilarity scores. The location of samples on each axis is independent from that on other axes, and can thus be used as dependent variables in analyses with environmental data. A stress statistic is produced as a measure of goodness-of-fit of the newly created axes and the ordering of the dissimilarity matrix (Kuskal and Wish, 1978). The preferred ordination has the minimum number of axes necessary to describe the data; this is indicated by a Monte Carlo analysis of ordinations starting with one axis and incrementally adding more until the stress no longer differs from the randomized data. NMDS was chosen because it is robust to nonlinearities in the patterns of density among species (Faith et al., 1987; Minchin, 1987; Legendre and Legendre, 1998: 413).

RESULTS

WHAT IS THE SPATIAL SCALE OF SMALL-FISH ABUNDANCE PATTERNS? (SHORT-TERM STUDY)

We addressed this question by analysis of absolute abundance and relative abundance of fishes collected by throw-trap between July 1996 and April 1997 from our 20 study sites scattered across WCA-3A, WCA-3B, SRS, and TS. We examined 37,718 specimens of 33 different species (Table 5.1).

TABLE 5.1 Fishes Collected by Throw-Trap Between July 1996 and April 1997 from Everglades Marsh Study Plots

Species	Common Name	Total Collected	Maximum No. per m ²
Lepisosteus platyrhincus	Florida gar	1	
Esox niger	Chain pickerel	5	3
Notropis maculatus	Taillight shiner	1	4
Notropis petersoni	Coastal shiner	60 ^b	9
Erimyzon sucetta	Lake chubsucker	145 ^b	5
Ameiurus natalis	Yellow bullhead	29	3
Noturus gyrinus	Tadpole madtom	8	-
Clarias batrachus (I)*	Walking catfish	4	3
Cyprinodon variegatus	Sheepshead minnow	41 ^b	11
Fundulus chrysotus	Golden topminnow	1,844 ^b	10
Fundulus confluentus	Marsh killifish	87 ^b	4
Fundulus seminolis	Seminole killifish	1	1
Jordanella floridae	Flagfish	1,783	34
Lucania goodei	Bluefin killifish	8,391	33
Lucania parva	Rainwater killifish	1	1
Belonesox belizanus (I)*	Pike killifish	3	1
Gambusia holbrooki	Eastern mosquitofish	9,825 ^b	98
Heterandria formosa	Least killifish	12,713	65
Poecilia latipinna	Sailfin molly	1,699 ^b	48
Labidesthes sicculus	Brook silverside	5	2
Elassoma evergladei	Everglades pygmy sunfish	487 ^b	9
Enneacanthus gloriosus	Bluespotted sunfish	238 ^b	6
Chaenobryttus gulosus	Warmouth	18	3
Lepomis macrochirus	Bluegill	6	1
Lepomis marginatus	Dollar sunfish	14	1
Lepomis microlophus	Redear sunfish	55 ^b	4
Lepomis punctatus	Spotted sunfish	197°	
Lepomis sp.	Unidentified sunfish	16	2
Micropterus salmoides	Largemouth bass	4	3
Etheostoma fusiforme	Swamp darter	2	1
Cichlasoma bimaculatum (I)ª	Black acara	7	1
Cichlasoma urophthalmus (I)*	Mayan cichlid	21	
Tilapia mariae (I)	Spotted tilapia	4	
Total		37,718	
 (I) = introduced species. ^b species used in NMDS. 			

Small-Fish Density

Most of the variation in fish density was among our study sites within water-management units (Table 5.2). Inter-site variation explained over 23% of the total variation in fish density (all species pooled), and no additional variation could be attributed to sources among water management units. Variation among plots within sites explained less than 3% of the total variation, and temporal variation explained a little over 16% of the total variation. Low variance among plots indicates that they tend to be similar; this pattern is illustrated in the high spatial autocorrelation seen at the 3-and 5-km scale (Figure 5.2). Spatial autocorrelation becomes negative with comparisons at the 18-km to 43-km scale, and then positive at longer scales. Positive correlations at the extreme comparisons may be because the nutrient-enriched study sites were at the extremes of the study area, particularly sites 11 and 37 (see environmental factors discussion, below).

TABLE 5.2
Partitioning Variation in Transformed Fish Density ($\sqrt{\#fish/m^2}$) from Throw-Trap
Samples Collected July 1996 through April 1997

Source	55	df	MS	Den	F	P	CD
Spatial variation							
Units	74.561	3	24.854	2	0.267	0.80	_
Site(units)	1118.263	12	93.189	3	24.408	⊲0.001	23.9
Plot(site)	114.545	30	3.818	8	3.097	⊲0.001	2.5
Temporal variation							
Time	0.608	3	0.203	6	0.030	>0.80	_
Time × unit	163.196	17	9.600	6	1.433	0.10	3.5
Time × site (unit)	281.306	42	6.698	7	2.310	<0.001	6.0
Time × plot (site)	327.746	113	2.900	8	2.352	<0.001	7.0
Error	1787.220	1449	1.233				_

Note: Sources listed in parentheses denote nested factors. "Den" indicates the MS used as the denominator for each F statistic. Data were collected from *Eleocharis*-dominated sloughs and wet prairies. Using type III sums of squares, the coefficients of determination for each separate factor do not sum to the total variance explained for the full model; for the full model, $R^2 = 0.68$; CD = coefficient of determination.



FIGURE 5.2 Spatial autocorrelation measured by Moran's *I* relative to the distance separating pairs of sampling sites. Estimated annual average density of all fish species was the dependent variable. The value of *I* for groups of sites separated by a given distance is plotted. Only values derived from at least 20 pairs of mean density are plotted.

Species Patterns

We identified three independent dimensions that cumulatively explained 95% of the variation in small-fish community composition at our 22 study sites (NMDS: three-axes mean stress = 8.330, P = 0.020; axis 1, $R^2 = 0.27$; axis 2, $R^2 = 0.49$; axis 3, $R^2 = 0.19$). Of the 14 species included in this analysis, only the coastal shiner and redear sunfish were not significantly correlated with at least one axis in this analysis (Figure 5.3). The composition of small-fish communities differed among water-management units (MANOVA: Region Wilk's lambda = 0.199, P < 0.001), primarily because differences in the species correlated to axes 2 and 3 (univariate analyses: axis 1, $F_{2,19} = 1.798$, P = 0.193; axis 2, $F_{2,19} = 15.124$, p < 0.001; axis 3, $F_{2,19} = 1.219$, P = 0.009). In particular, TS had relatively more golden topminnows and bluefin killifish, and fewer mosquitofish, least killifish and

sailfin mollies than SRS or the WCAs; sites from WCA and SRS tended to ordinate in a mixed cluster. The source of regional variation can be seen in more detail in the patterns of individual species (Figure 5.4). Three species were collected in only one or two of the water-management units. Marsh killifish and coastal shiners were only collected in SRS and TS (Figure 5.5), and sheepshead minnows were only collected in SRS. Further, sheepshead minnows were only collected at sites 6, 23, and 50, the northern SRS sites. Marsh killifish and coastal shiners were collected more widely throughout the water-management units, though marsh killifish were restricted to three sites in SRS. Flagfish were routinely collected in SRS and TS and were found at only three of the five sites in WCA-3A-sw; they were not collected in the other northern study water-management units. Because these species were never caught in large numbers, they are likely to occur in the areas where we failed to collect them, but at densities below our detection limits.



FIGURE 5.3 NMDS ordination of fish species composition at study sites. Fish species correlated with each axis (r > 0.2) are shown, and arrows indicate positive or negative correlations. Species names are represented by the first three letters of each genus and first three letters of species names, and the order of listing corresponds to the relative strength of the correlation with each axis. Letters indicating the water-management region where each site is located are plotted: S = SRS, T = TS, and W = WCA-3.



FIGURE 5.4 Mean density (number/m²) of each species and all species summed collected in each watermanagement unit. Annual means are plotted for each site.



FIGURE 5.5 Partitioning of variance in the six most abundant species for 1996–1997 collections. Height of the bars indicates the percentage of total variance attributable to each source.

Variation among sites within water-management units was the major source of spatial heterogeneity for four of the six most common species of fish (Figure 5.5). In general, the sources of spatial variance ranked site, water-management unit, and plot in decreasing order of importance. In no case did seasonal variance explain a marked amount of the total variation (time as a main effect, Figure 5.5). For flagfish, golden topminnows, and sailfin mollies, there was a substantial amount of variance attributable to interactions of temporal and spatial variance at the plot and site scales. The time by plot-within-site variance may be best considered as sampling error because each plot-time combination is based on only five to seven throw-trap samples. These interactions explain the most variance in the rarest species whose densities are near our lower limit of sampling efficiency. If densities of these species fluctuate slightly, they may become too rare to be captured in five to seven samples, yielding many zero estimates and inflating the temporal variance estimates. These results reinforce the impression that much of the heterogeneity in fish communities is at the inter-site scale (tens of kilometers) within water-management units, rather than among units.

Environmental Factors

We tested for correlations among environmental variables (hydroperiod and nutrient status) and measures of fish community structure (fish density and relative abundance). We analyzed fish density averaged across plots and sampling events to test for these correlations. This averaging was appropriate based on the partitioning of variance from the previous section. Hydroperiod and nutrient status are related in Everglades marshes. The percent organic matter in our soil samples was highly correlated with hydroperiod (r = 0.84, P < 0.001, n = 21). This is consistent with the use of soil type (peat vs. marl) to distinguish hydroperiod. Also, there was a tendency, though not statistically significant, for total phosphorus to be positively related to hydroperiod (r = 0.32, P = 0.15, n = 21). Sites 11 and 37 had the highest soil total phosphorus of our study sites, but they had moderate hydroperiods. If those sites are omitted, the correlation of TP and hydroperiod increases (r = 0.41, P = 0.08, n = 19). Those sites were uniquely affected by their location: site 11 received nutrient-enriched runoff from a nearby canal and site 37 is at the estuarine-freshwater interface and abuts natural creeks (Rudnick et al., 1999).

Both hydroperiod and nutrient status influenced the density of fish at our study sites, though the correlation of these factors makes separating their effects difficult. In general, increasing hydroperiod or nutrient status (over the range sampled) led to greater densities of throw-trap collected fishes (Figure 5.6). When all 20 study sites were considered, soil-nutrient status explained more variation than hydroperiod and was the only significant factor in the model (TP, $F_{1,17} = 7.31$, P = 0.015; hydroperiod $F_{1,17} = 2.85$, P = 0.161; TP × hydroperiod $F_{1,17} = 1.24$, P = 0.28; $R^2 = 0.45$). However, site 11 is indicated as an outlier with a Studentized residual = 3.77. Because both sites 11 and 37 are influenced by unique circumstances, we repeated the analysis, dropping those sites. Hydroperiod then became the only significant factor (TP, $F_{1,15} = 0.48$, P = 0.50; hydroperiod $F_{1,15} = 4.58$, P = 0.049; TP × hydroperiod $F_{1,15} = 2.01$, P = 0.18; $R^2 = 0.55$). This suggests that in spikerush marshes across the Everglades, hydrology is the primary factor explaining variation in fish density unless variations in nutrient levels are exaggerated by natural or anthropogenic sources.



FIGURE 5.6 Annual average fish density (square-root transformed) estimated from throw-trap samples relative to hydroperiod index and nutrient status in 1997. (A) The hydroperiod index is based on estimates of the average number of days the marsh surface in an area was inundated between 1970 and 1990. 0 = <120 days, 1 = 120-180 days, 2 = 180-240 days, 3 = 240-300 days, 4 = 300-340 days, and 5 = 340-365 days. (B) Nutrient status is estimated by the average total phosphorus in soil samples taken at each study site. A composite sample from each study plot was analyzed.

WHAT IS THE SPATIAL SCALE OF LARGE-FISH ABUNDANCE PATTERNS? (SHORT-TERM STUDY)

We addressed this question by analysis of airboat-electrofishing CPUE from October 1997 through October 1998, collected from 11 study sites scattered across WCA-3A, WCA-3B, SRS, and TS. We collected 583 specimens from marshes and ponds in our electrofishing study representing 16 species (Table 5.3).

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TABLE 5.3

Fishes Collected by Electrofishing Between October 1997 and October 1998 from Everglades Marsh Study Sites

Species	Common Name	Total Captured	Maximum CPUE (per plot)
Lepisosteus platyrhincus	Florida gar	121	2.00
Amia calva	Bowfin	42	0.67
Esox americanus	Grass pickerel	9	1.00
Esox niger	Chain pickerel	8	0.67
Erimyzon sucetta	Lake chubsucker	187	4.00
Ameiurus natalis	Yellow bullhead	23	0.67
Clarias batrachus (I)*	Walking catfish	7	0.33
Centropomus undecimalis	Snook	2	0.33
Micropterus salmoides	Largemouth bass	45	1.33
Chaenobryttus gulosus	Warmouth	40	1.33
Lepomis punctatus	Spotted sunfish	40	1.00
Lepomis macrochirus	Bluegill	12	0.67
Lepomis microlophus	Redear sunfish	6	0.67
Cichlasoma urophthalmus (1) ^a	Mayan cichlid	25	1.00
Oreochromis aureus (I)*	Blue tilapia	15	1.00
Tilapia mariae (I)*	Spotted tilapia	1	0.33
Total		583	9.33

Note: Maximum CPUE is the average of three 5-minute transects in one plot area.

* (I) = introduced species.

Large-Fish Abundance

Variation among water-management units accounted for the largest amount of variance in electrofishing CPUE (Table 5.4). Large-fish CPUE was consistently greater in WCA-3A and SRS than in TS, although the magnitude of these differences was variable through time (Figure 5.7). This was consistent with our expectations of short-hydroperiod marshes which experience more severe drying. Over long time periods, we expected that the higher frequency of severe drydowns would limit the population size of large fishes because of mortality associated with crowding in deepwater refuges (Loftus and Kushlan 1987, Loftus and Eklund 1994). Although water depths were relatively similar in SRS and TS during our study (Figure 5.7), drydowns tend to be more severe in TS (Fennema et al. 1994). Water depths in WCA-3A were greater than both SRS and TS, and it is interesting to note that CPUE for alligator ponds in the dry season was substantially lower for this water management unit (9.1 vs. 25.4 and 25.6 fish/5 min).

Differences in CPUE among sites within water-management units were also significant, both as a main effect and over time (Table 5.4; Figure 5.8). Large fishes are known to congregate in canals and the marsh areas adjacent to these canals (Loftus and Kushlan, 1987; Turner et al., 1999).



FIGURE 5.7 Variation in electrofishing CPUE among sites by date. Data were collected from three watermanagement units within the southern Everglades: WCA-3A, SRS, and TS. Error bars are ±1 standard error.

For example, in October 1997, we collected a series of 27 electrofishing transects in marshes adjacent to canals and compared these to 73 transects from central marsh localities. CPUE was significantly greater ($F_{1,98} = 25.16$, P = 0.0001, $R^2 = 0.20$) for canal-adjacent marshes than for central marshes (3.44 vs. 1.59 fish per 3 min).

Species Patterns

In addition to these differences in abundance, we also observed conspicuous differences in the composition of large fishes among regions. The lake chubsucker, *Erimyzon sucetta*, was the dominant species in SRS. This species also was abundant in WCA-3A, but was far less abundant in TS (Figure 5.9). As with overall CPUE, the lower abundance in TS marshes may be related to hydroperiod. Two species of pickerel, *Esox americanus* and *Esox niger*, reach the southern limits of their range in or just south of WCA-3A. We never captured these species in either SRS or TS. *Esox niger* has occasionally been observed in ENP (see Loftus and Kushlan 1987), but *Esox americanus* has not. The relative abundance of cichlids was far greater in SRS and TS than in WCA-3A (Figure 5.9). Within SRS and TS, we captured these species most frequently in marshes adjacent to deep-water refuges such as natural streams or man-made canals.



FIGURE 5.8 Electrofishing CPUE from alligator ponds compared with the ratio of pond depth to marsh depth. Data were collected from 10 to 12 ponds located within three water-management units of the southern Everglades: WCA-3A, SRS, and TS. The line depicted in the dry season was fitted through linear regression: $log_{10}(CPUE + 1) = 0.187 + 0.403$ (pond depth/marsh depth).

Environmental Factors

Two variables that appeared to influence the patterns of CPUE variation among sites were soil nutrients and proximity to natural streams or man-made canals. No short-hydroperiod marshes were sampled because of the difficulty of electrofishing in such shallow, rocky conditions. The greatest CPUE levels found in our study occurred in site 37 within SRS, the southernmost site. The marshes at this site are adjacent to natural streams and have the greatest concentration of soil nutrients of any of our sites. By comparison, the southernmost site within TS, site 3, was characterized by low CPUE and the lowest concentration of soil nutrients among our sites.

Temporal variability of our CPUE data appeared to largely reflect seasonal variation in water depth (Table 5.4). For example, within WCA-3A and SRS, CPUE varied substantially among sites for all sampling dates except July 1998 (Figure 5.8). The July sample was taken at the end of a mild, but protracted dry season, apparently before most large fishes had returned to the marshes from deep-water refuges. Even though this dry season was not severe, the abundance of large fish within alligator ponds was still substantially greater than during the following wet season. Comparing our alligator pond data from the end of April 1998 (dry season) and October 1998 (wet season), CPUE of large fishes was almost 10-fold greater in April for ponds within TS (25.6 vs. 2.6 fish/5 min), almost 6-fold greater in April for ponds within SRS (25.4 vs. 5.91 fish/5 min), and 6.5-fold greater in April for ponds in WCA-3A (9.1 vs. 1.4 fish/5 min). During this dry season, CPUE was positively related to the ratio of pond depth to marsh depth ($F_{1,34} = 4.05$, P = 0.0001, $R^2 = 0.48$). This indicated that large fishes were more abundant in ponds that provided greater refuge (Figure 5.10). This relationship was not significant during the wet season.



FIGURE 5.9 Variation in electrofishing CPUE and water depth among water-management units by date. Data are averaged across three or four sites sampled within each of three water-management units of the southern Everglades: WCA-3A, SRS, and TS. Error bars are ± 1 standard error.

TABLE 5.4

Results of an Analysis of Variance Examining Patterns in Electrofishing CPUE (Number of Fish per 5-min Electrofishing) Through Time, Across Water-Management Units (WCA-3A, SRS, TS), and Sites Within Water-Management Units

Source	SS	DF	MS	Den	F	Р	CD
Spatial variation							
Water management unit	6.99	2	3.495	2	10.10	0.006	0.23
Site(unit)	2.77	8	0.346	6	3.76	0.001	0.09
Temporal variation							
Time	5.75	4	1.435	5	7.93	<0.001	0.19
Time × unit	2.22	8	0.278	5	1.54	0.188	
Time × site (unit)	5.07	28	0.181	6	1.97	0.025	0.17
Error	8.55	93	0.0919				

Note: Data were collected from *Eleocharis*-dominated sloughs and wet prairies from October 1997 to October 1998. "Den" indicates the MS used as the denominator for each F statistic. CD = coefficient of determination; Model $R^2 = 0.72$.





FIGURE 5.10 Variation in the relative abundance of fishes captured by electrofishing among water-management units by date. Data were collected from three water-management units within the southern Everglades: WCA-3A, SRS, and TS.

ARE LOCAL PATTERNS IN SMALL-FISH ABUNDANCE AND COMPOSITION CONSISTENT OVER TIME? (LONG-TERM STUDY)

We examined throw-trap data collected at sites 6, 23, and 50 (Figure 5.1) between 1985 and 1995 to determine how community structure varied among these sites during this time period. The three study sites were chosen to represent three levels of hydroperiod from very short (site 50 experienced prolonged dry periods in 7 of 10 years between 1985 and 1995) to long (site 6 dried briefly in 3 years during that period). Hydroperiod was intermediate at site 23. There was a 2-year drought from 1989 to 1990 when all of the Everglades were dry for some period of time. At site 6, the marsh surface was exposed for a short time only in the two drought years of this 10-year interval, while sites 23 and 50 went dry in 6 and 7 of the 10 years, respectively.

Small-Fish Abundance

Results from the short-term study indicated the importance of hydroperiod to spatial variation in fish abundance and species composition over the course of a year. A similar result was noted for a comparison of sites 6, 23, and 50 in SRS between 1985 and 1995. The 10-year average density of fishes at these three sites by month is consistently ranked from short hydroperiod with the fewest fishes to long with the most fishes (Figure 5.11; Loftus and Eklund, 1994).

Small-Fish Species Composition

The nonmetric multidimensional scaling of angular-transformed relative abundance indicated that these sites differed consistently in the composition of their fish communities. Two dimensions were observed that explained over 84% of the total variance in relative abundance (NMDS: two-axes mean stress = 24.653, P = 0.020; axis 1, $R^2 = 0.40$; axis 2, $R^2 = 0.44$). When the scores from the six factors were analyzed in a MANOVA, significant differences were noted among sites and over time within sites (site: Wilks' lambda = 0.944, P < 0.001; year: Wilks' lambda = 0.419, P < 0.001; site \times year: Wilks' lambda = 0.533, P = 0.011). Site 50 was distinguished from site 6 in having relatively more marsh killifish and sheepshead minnows and fewer bluefin killifish, spotted sunfish, and mosquitofish, while site 23 was intermediate (Figure 5.12). Perhaps more interesting was the effect of the drought years 1989 and 1990 on the patterns of relative abundance. Fish species composition was affected by the drought event at site 6 (Figure 5.12: pre-drought 1985-88 vs. drought years 1989-90 vs. post-drought 1991-95: Wilks' lambda = 0.028, P < 0.001) and site.23 (Wilks' lambda = 0.151, P = 0.007), but not site 50 (Wilks' lambda = 0.596, P = 0.424). The preand post-drought years differed in species composition at site 6, but not at site 23. Thus, the severity of effect of the drought on small-fish species composition appeared to be related to the long-term hydroperiod at the site. Much of the shift at site 6 in 1989 was related to a greater relative abundance of marsh killifish and sheepshead minnows and fewer bluefin killifish, least killifish, and mosquitofish. This pattern was also observed after droughts at site 6 in previous years (Loftus and Eklund, 1994). The fish community during the post-drought years at site 6 could be characterized as having relatively greater density of fishes typical of longer hydroperiod sites in the Everglades (bluefin killifish, spotted sunfish, least killifish). This is probably linked to a series of very wet years in the 1990s (Trexler and Loftus, 2001).

Recovery of species composition after a drought is influenced by patterns of recovery for individual species (Table 5.5). The average time for mosquitofish and flagfish to reappear in samples



FIGURE 5.11 Average density of all fishes between 1985 and 1995 plotted by month. Sites 6, 23, and 50 are plotted.

following a drydown was more than one census period (≈ 2.5 months). On the other hand, bluefin killifish took, on average, over 9 months to reappear in samples from the long-hydroperiod site and much longer at the short-hydroperiod site. It appears that the relative abundance patterns are site characteristics that are regained following hydrological perturbation over a time period set by



FIGURE 5.12 NMDS ordination of inter-annual variation in fish species composition plotted by study sites. Fish species correlated with each axis (r > 0.2) are shown, and arrows indicate positive or negative correlations. Species names are represented by the first three letters of each genus and first three letters of species names, and the order of listing corresponds to the relative strength of the correlation with each axis. Numbers indicate the year when each collection of samples was made. Circles enclose years in pre-drought and post-drought periods except for site 50, where there were no differences among the three time periods.

the recolonization abilities of the species living there. Slow times could be the result of slow dispersal rates or low reproductive, and therefore population growth, capacities. It is also possible that mosquitofish, an early colonizer, could resist the re-invasion of some species by predation on immigrating juveniles or by resource competition (Hurlbert et al., 1972; Meffe, 1985).

TABLE 5.5

The Average Time Following a Drydown Before Each Species Reappears in Samples and Their Rank Density at That Site

	Long Hydro	period (Site 6)	Short Hydroperiod (Site 50)		
Species	Rank Density	No. of Surveys	Rank Density	No. of Surveys	
Mosquitofish	1	1.3	1	1.4	
Bluefin killifish	2	3.4	4	17.6	
Least killifish	3	3.0	7	4.5	
Flagfish	4	1.3	2	1.4	
Golden topminnow	5	2	6	7	
Sailfin molly	6	5.7	8	9.5	
Marsh killifish	8	3.4	3	1.3	
Sheepshead minnow	_	_	5	4	

Note: Ranks were based on the average density of each species between 1985 and 1995. Approximately 2.5 months passed between surveys, on average.

WHAT IS THE SPATIAL SCALE OF GENETIC VARIATION?

In both species studied, the level of genetic differentiation was greatest among local sites within regions, although, in general, the total amount of differentiation was low (Table 5.6A). This is an unusual pattern of differentiation; we did not observe the typical isolation by distance (Slatkin, 1985) indicated when allele frequency variation is correlated with geographic distance separating pairs of sampling sites. Our result may indicate that, at the time of our sampling, local fish populations were not at genetic equilibrium following a major drought event in 1989-1990, a period of about 14 mosquitofish generations and three to seven spotted sunfish generations prior to our collections. We hypothesize that major population events, fish concentration, and mortality resulting from the drought, followed by marsh recolonization and rapid population growth, may have taken place at spatial scales shorter than the distance among sampling sites (approximately 2 to 10 km), because that was the spatial scale of greatest genetic variation. In addition, we hypothesize that the overall low levels of genetic differentiation were the result of routine movements of individuals in the post-drought years, which homogenized the local pattern generated by the drought years prior to sampling in 1996. This is supported by low heterozygosity of mosquitofish from WCA-3B relative to the rest of the study area (Table 5.6B); WCA-3B is completely isolated from the rest of the Everglades by levees and lacked significant access to large aquatic refuges such as major canals in droughts such as the one in 1989-1990.

In 1999, the Everglades experienced a drydown event not as severe as in 1989–1990 but one that affected patterns of heterozygosity in mosquitofish consistent with those hypothesized for the drought. In 1999, we observed overall deviation from Hardy–Weinberg expectations and a significant deficiency of heterozygosity as might be expected from a rapid diminution of population size. For example, observed heterozygosity at highly polymorphic loci were consistent with Hardy–Weinberg expectations, but loci with low observed polymorphism displayed significant deviations from Hardy–Weinberg expectations. Deviation from Hardy–Weinberg expectations at loci with low polymorphism resulted primarily from the lack of rare-allele heterozygotes. There was no pattern of deviation related to hydrology of the sites sampled. The level of genetic differentiation was again

TABLE 5.6

Patterns of Genetic Diversity in Mosquitofish and Spotted Sunfish Collected from the Southern Everglades

A. Population Structure Estimates^a

	Mosquitor	Mosquitofish (1996)		Mosquitofish (1999)		Spotted Sunfish (1996)	
	Г _{SP}	Fpt	Fsp	Fpt	Fsp	F _{PT}	
Estimate	0.0106	0.0033	0.0072	0.0004	0.0203	-0.0076	
Upper bound	0.0199	0.0069	0.0167	0.0024	0.0579	0.0006	
Lower bound	0.0034	0.0004	0.0033	-0.0010	-0.0044	-0.0180	
B. Average Hetero	ozygosity ± Star	ndard Error ^b					
	Mosquitor	iish (1996)	Mosquito	fish (1999)	Spotted Su	nfish (1996)	
WCA-3A	0.158 + 0	.004 (25)	0.091 + 0	0.005 (11)	0.102 +	0.001 (3)	
WCA-3B	0.117 + 0	.001 (3)	0.101 + 0).006 (4)	0.140 (1))	
SRS	0.149 + 0	.004 (16)	0.087 + 0	0.004 (15)	0.101 +	0.029 (3)	
TS	0.137 + 0	.004 (8)	0.106 + 0	0.007 (13)	N	//	
Canal	N	/A	N	/A	0.125 +	0.006 (8)	

Note: For mosquitofish, the same locations were sampled in 1996 and 1999 whenever possible.

^a Spatial partitioning of genetic variation for fishes. F_{SP} indicates the genetic variance in samples relative to among samples, and F_{PT} indicates the genetic variance among samples relative to the total study. Upper and lower bound estimates are 95% confidence interval estimates from bootstrap sampling.

^b Heterozygosity of fishes collected from the Everglades. Number of populations sampled for both *F*-statistics and heterozygosity estimates are indicated in parentheses.

greatest among local sites within regions and the total amount of differentiation was low (Table 5.6A). Also, differences in allele frequencies did not generally increase with greater geographic distances separating pairs of sampling sites. Mosquitofish sampled in 1999 displayed less heterozygosity than mosquitofish sampled in 1996 (Table 5.6B). Also, unlike the 1996 samples, the levels of heterozygosity did not significantly differ among regions in the 1999 mosquitofish samples. The observed reduction in genetic variation is consistent with predicted effects of a drought yielding reduction in mosquitofish population sizes.

Long-hydroperiod marshes and canals may serve as source locations for colonists to nearby short-hydroperiod marshes following drydown events. We tested this hypothesis following the method of McCauley et al. (1995) who noted that source populations should be less genetically differentiated than nearby populations experiencing frequent extinction and recolonization. Some support was found for this hypothesis in mosquitofish, and possibly sunfish, though with less statistical power. The genetic variation among samples of mosquitofish collected in 1996 from short-hydroperiod sites was greater than that among nearby long-hydroperiod sites, which in turn was greater than among canal sites (combining results from WCA-3A, SRS, and TS, $z_p = 1.498$, P = 0.067). Also, samples of spotted sunfish from small ponds in the interior Everglades tended to be more heterogeneous than samples from canals and natural stream sites, though the trend was not statistically significant.

Preliminary analyses using a new maximum-likelihood method that estimates population parameters by integrating over all possible genealogies and migration events between subpopulations (Beerli and Felsenstein, 1999) indicated that two uncorrelated factors affect gene flow in TS. These are distance between the sites and the presence of a road or barrier. The estimate of gene flow between pairs of sites located along a road was significantly greater than gene flow between other sites in TS long-hydroperiod marshes, or between the slough and the road. These data suggest that

barriers to fish movement imposed by human alterations do shape fish migration across the landscape and could affect population structure. The new analytical protocol is promising because it does not make ecologically unrealistic assumptions of equal population sizes and symmetric migration inherent in traditional F_{ST} -based estimates of gene flow. However, it is also computer intensive and cannot be used for simultaneous analysis of our entire data set until a parallel computing version is completed (Beerli, pers. comm.). We are proceeding with re-analyses of our data one water management region at a time; however, analysis of the TS data alone required 5 weeks of computer time!

DISCUSSION

We addressed three questions regarding the scale of variation in different aspects of the Everglades fish community: scale of density and species composition, temporal stability of that scale, and scale of genetic variation in selected species. We found that the major scale of variation in both community structure (measured as density and relative abundance) and genetic variation of small fishes is in the approximately 10-km range. Patterns of small-fish community structure appear to be related to local environmental parameters, especially hydroperiod, and they may vary over time as local hydroperiod changes. This raises an important caveat: Our short-term study of spatial variation in small and large fishes was conducted during a period of wetter-than-average years when water levels were high across the ecosystem. Our long-term study, conducted over a smaller spatial area and only on small fishes, underscores that spatial relationships of community structure at our shortterm study sites are likely to change during periods of drier years. Given this limitation, what generalities and hypotheses can we draw from our results?

THE SCALE OF COMMUNITY DYNAMICS IN THE EVERGLADES

The spatial scale of fish density and community composition differs for small and large fishes. We have compared density and species-composition data at three spatial scales for small fishes and at two scales for large fishes: 1-km (among plots, small fishes only), 10-km (among sites within watermanagement units), and among water-management units. Two classes of explanations are possible for this difference: sampling artifacts and meaningful biological effects. We have strived to document and minimize the sampling biases of these two techniques, a measure of sampling accuracy (Jordan et al., 1997a; Chick et al., 1999). It is more difficult to equalize the variance about our estimates (a measure of precision) from such different techniques. Thus, the statistical power to detect patterns probably differs between our two datasets. We have repeated our small-fish analyses on a limited data set that included only those sites at which large fishes were also sampled, and obtained the same results as analysis of the full dataset. Potential differences in precision cannot explain the rank differences are biological in origin.

While regional distinctions could be identified in the small-fish data, most of the variation was among sites within water-management units in fish density and species composition. These results held up when two high-nutrient sites were removed. On the other hand, our large-fish data indicated consistent differences among the water-management units that greatly exceeded the inter-site variation. For both large and small fish, the WCAs and SRS were more similar to each other than either was to TS. The WCAs and SRS were historically part of a single drainage basin while TS was historically a separate drainage. TS has been severely drained in recent years such that recent management may also explain its distinctiveness. However, TS had relatively more golden topminnows and bluefin killifish than SRS and WCAs, a pattern not consistent with it having a shorter hydroperiod; these species tend to increase in abundance in wetter periods in SRS.

The different spatial scales of variability in small and large fish could be explained by the way body size influences the dispersal ecology and generation time of fishes. Our "large fishes" group

includes species with longer generation times and generally slower population growth capacities than most of the species in our "small fishes" group. Also, dispersal distance and swimming performance scale positively to body size in fishes (Ware, 1978), indicating that our large fishes can probably cover a larger area within their lifespan. Thus, small fishes may recover more quickly following a drought by way of *in situ* reproduction, while larger fishes may locate aquatic refuges more effectively than smaller ones. Either or both of these factors could contribute to the difference in major scale of variation we observed.

Much of the variation we noted in fish density and species relative abundance of both small and large fishes is well explained by hydrological variation. For example, TS has lower small- and large-fish density, probably because it lacks the extensive long-hydroperiod marshes present in SRS and WCAs. Overall, we noted marked differences in density and species composition between short- and long-hydroperiod sites in the small-fish data. These distinctions indicate that a better understanding of fish response to hydrological variation is needed. In the following section, we propose two scale-based conceptual models of fish response to drought.

Our genetic studies of mosquitofish and spotted sunfish are consistent with these results. They are consistent with the interpretation that drydown events leave lasting effects on the population structure of these species, probably reflecting a history of population collapse and expansion from local refuges. Also, the spatial scale of this dynamic for mosquitofish appears to be at a similar one to the patterns of small-fish density. Spotted sunfish are not abundant enough in marshes to sample at the same scale as mosquitofish. However, our results support the hypothesis that alligator ponds are local refuges for spotted sunfish and that they move widely when inhabiting canals. Less well supported by the genetic data, but intriguing, are hints that long-hydroperiod marshes by mosquitofish. Also, it appears that barriers to mosquitofish movement across the landscape do affect patterns of gene flow and reshape their dispersal ecology. This result is well supported by a recent sampling study in the same study area (Loftus, unpubl. data).

ALTERNATIVE MODELS FOR MARSH DYNAMICS

AND RECOLONIZATION FOLLOWING DROUGHT

Seasonal displacement of fish across the Everglades by fluctuating water level is thought to have profound effects on the dynamics of its fish communities (Kushlan, 1974, 1976a; Karr and Freemark, 1985; Loftus and Kushlan, 1987). For example, this may provide the concentrations of fish that feed wading birds (Bancroft et al., 1994; Frederick and Spalding, 1994; Ogden, 1994). To what extent do density fluctuations reflect changes in local population size vs. different levels of population concentration? Alternatively, we may ask over what spatial scales do fishes interact and how are those scales affected by seasonal cycles in water level? Are long-hydroperiod marshes stable sites that serve as sources of individuals (*sensu* Pulliam, 1988) for short-hydroperiod marshes, where they die in the next season?

Though the topographic relief of the Everglades is slight, small variations in elevation can have marked effects on the vegetation of an area and its hydroperiod. Marshes in the Everglades are a complex mixture of vegetatively defined habitats that appear to reflect local elevation (Jordan et al., 1997b). Wet prairies are often dominated by spikerush (mostly *Eleocharis cellulosa*), though they may be dominated by maidencane, *Panicum hemitomon*, or beakrush, *Rynchospora tracyi*, in local low sites where water is last to dry (Busch et al., 1998; McPherson, 1973). Wet prairies form braided habitats subdivided by patches of sawgrass-dominated marsh. Sawgrass (*Cladium jamaicense*) often dominates areas with locally high topography and can grow in very dense stands that may hamper or preclude passage of fishes. Sawgrass marshes typically form strands, with a long axis parallel to the direction of water flow (Figure 5.13), that form a maze-like barrier for animals attempting to move perpendicular to water flow.



FIGURE 5.13 Map of the distribution of dense sawgrass strands in the SRS. (Redrawn from Olmsted et al., 1982.)

The matrix of wet prairies and sawgrass marshes has the potential to limit the spatial scale of fish concentration during dry-season water recession, as well as expansion upon reflooding. Two extreme patterns of fish movement are possible. Fish may concentrate at a regional scale with fish from short-hydroperiod marshes on the eastern and western fringes of the ecosystem moving toward the central flow-way and its long-hydroperiod marshes as water recedes (Regional Concentration Model, Figure 5.14). An alternative model is that fish become stranded in local wet prairies as water recedes, precluded from long-distance movement at the boundary by sawgrass marshes (Local Concentration Model, Figure 5.14). These extremes predict two different magnitudes of fish concentration as drydown proceeds, with potentially important implications for food availability for wading birds. Individual species probably differ in the propensity to disperse across the landscape, and so we may not expect a single scale of dynamics to describe the entire community. This is, in fact, what we see when comparing our large- and small-fish datasets.

Unlike some fishes in seasonal tropical wetlands and floodplains (Lowe-McConnell, 1987), we have not detected directed long-distance migrations of fishes as water recedes in the Everglades.



FIGURE 5.14 Conceptual model of alternative hypotheses for fish concentration during Everglades dry seasons.

However, as water rises, the surviving fishes of all size classes are at times seen "streaming" in mass-directed movements into recently reflooded habitats. It is not clear if these fishes are leaving dry-season refuges because water conditions have degraded, or if they are actively invading recently accessible habitats in search of food. We hypothesize that water recession in the Everglades is generally too slow, and topographic gradients are too shallow, for small fishes to respond in mass, long-distance migrations to deep-water refuges. In contrast, the expansion of aquatic habitats and reflooding of marshes in the early wet season are often rapid (one day or less) as a result of dramatic rainfall events; both small and large fishes appear to respond actively to these dramatic changes in habitat availability. This pattern supports the local concentration model for small-fish population dynamics and the hypothesis that long-hydroperiod marshes serve as source habitats in drought years while short-hydroperiod regions are generally sinks in those years. Local concentration of small fish is indicated by the lack of an increase of fish density in long-hydroperiod marshes during the early dry season, as nearby short-hydroperiod marshes are drying. The concentration of fishes in ponds, while at times dramatic, may be explained by local movements from adjacent marshes (Turner et al., 1999). Large fishes, on the other hand, may be successful at moving across the landscape to locate alligator ponds and other deep-water refuges as water recedes. This was demonstrated by the increase of large fishes in alligator ponds even in years when the marsh surface did not dry (see electrofishing study by Nelson and Loftus, 1996). Thus, large fishes may be better described by the regional concentration model.

EVERGLADES RESTORATION AND MANAGEMENT: WHAT DOES A SPATIAL VIEW ADD?

The largest, most costly environmental restoration project in history has been authorized by the United States and the state of Florida, which will dramatically redesign the hydrology of the Everglades ecosystem (U.S. Army Corps of Engineers, 1998). Although uncertainties exist about the extent of restoration possible given the constraints of a smaller ecosystem, competing demands for water, and maintenance of water quality, a major goal of the Everglades restoration project is to restore the ecological integrity of the remaining Everglades. Our fish-community data serve three major roles in the restoration process. These data will be used for ecological backcasting to estimate fish community structure at locations within the "historic" Everglades by use of hydrological and ecological simulation models (DeAngelis et al., 1997) and to set restoration targets and success criteria. Also, the statistical relationships between environmental and fish community parameters we generate lead to hypotheses about the origins of community structure that provide a motivation for both experimental work and improvement of simulation models used in hydrological management. Finally, the network of sampling sites provides baseline data, and their continuation is essential to monitor conditions that result from future hydrological restoration.

Our results at the local and regional scales suggest that hydrological restoration of over-drained areas of the Everglades will lead to changes in the abundance and composition of fish communities (see also Loftus and Eklund, 1994). Patterns of drying have clear implications for management, and choices made have great potential to influence the food base for wading birds and other predators (Kushlan, 1987; Frederick and Spalding, 1994). Our results provide a clear indication that hydrological pattern is a major factor in shaping fish communities and presumably in shaping historical Everglades communities. We also found that increases in nutrient status can lead to marked changes in the local fish community. Ongoing and future research will address these changes in more detail, but a clear lesson is that hydrological management must not ignore nutrient effects from natural and anthropogenic sources (Turner et al., 1999).

CONCLUSIONS

The system of canals and levees that now directs the flow of water through the Everglades has changed the spatial arrangement of long- and short-hydroperiod marshes and their associated aquatic

communities. For example, the main route of water into the Everglades National Park now lies substantially westward of its historical path. Our data indicate that this water-management system has imposed a structure to the fish communities there, but possibly in more subtle ways than we might have guessed. Our studies indicate that communities of small fishes in the Everglades are most variable at the 10- to 15-km scale in density, relative abundance, and genetic variation (though more species need to be examined). Large-fish density and relative abundance appear to vary more across larger spatial scales. There were notable differences among the water-management units in small-fish species composition, mostly in the rare taxa, and density, mostly in TS. The complete isolation of WCA-3B may explain the modest, but significant, decrease in genetic variation of mosquitofish there. Our large-fish data displayed more marked differences among management units. Local environmental factors, especially hydroperiod, are important in determining these patterns in both small and large fishes. The effects of hydrological fluctuation may vary with fish size because larger fish can move greater distances in response to gradual drying than smaller ones. We propose alternative conceptual models of community dynamics based on local and regional scales of fish concentration in the dry season to explain the differences between our small- and large-fish data. Future research will test these models with direct study of fish movement. Ultimately, this information will help in assessing the plans and future activities of restoration of the Florida Everglades.

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