# SPATIAL SCALE AND ABUNDANCE PATTERNS OF LARGE FISH COMMUNITIES IN FRESHWATER MARSHES OF THE FLORIDA EVERGLADES

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Abstract: Anthropogenic habitat alterations and water-management practices have imposed an artificial spatial scale onto the once contiguous freshwater marshes of the Florida Everglades. To gain insight into how these changes may affect biotic communities, we examined whether variation in the abundance and community structure of large fishes (SL > 8 cm) in Everglades marshes varied more at regional or intraregional scales, and whether this variation was related to hydroperiod, water depth, floating mat volume, and vegetation density. From October 1997 to October 2002, we used an airboat electrofisher to sample large fishes at sites within three regions of the Everglades. Each of these regions is subject to unique watermanagement schedules. Dry-down events (water depth < 10 cm) occurred at several sites during spring in 1999, 2000, 2001, and 2002. The 2001 dry-down event was the most severe and widespread. Abundance of several fishes decreased significantly through time, and the number of days post-dry-down covaried significantly with abundance for several species. Processes operating at the regional scale appear to play important roles in regulating large fishes. The most pronounced patterns in abundance and community structure occurred at the regional scale, and the effect size for region was greater than the effect size for sites nested within region for abundance of all species combined, all predators combined, and each of the seven most abundant species. Non-metric multi-dimensional scaling revealed distinct groupings of sites corresponding to the three regions. We also found significant variation in community structure through time that correlated with the number of days post-dry-down. Our results suggest that hydroperiod and water management at the regional scale influence large fish communities of Everglades marshes.

Key Words: Everglades, large fish communities, hydroperiod, abundance patterns, spatial scale

# INTRODUCTION

Understanding the spatial and temporal scale of ecological processes is fundamental to interpreting patterns in the environment (Levin 1992). During the past two decades, ecologists have gained greater appreciation for limitations imposed by scale on the generality of observed patterns, and they are gaining greater insights on how patterns observed at one scale are influenced by mechanisms and constraints operating at larger and smaller scales (Turner 1989, Wiens 1989, Levin 1992). Scaling issues are especially important to the field of applied ecology because humans alter ecosystems at several temporal and spatial scales (Goodwin and Fahrig 1998, Hobbs 1998). Fragmentaton, isolation of habitats, and other anthropogenic disturbances to ecosystems and landscapes can be viewed as new scales imposed onto natural systems. Examining how patterns vary across scales, including human imposed scales, may be a useful tool to detect effects of, and/ or establish hypotheses regarding, anthropogenic changes to ecosystems.

The Florida Everglades is both one of the most

unique and dramatically altered freshwater ecosystems in the world. Once a contiguous wetland ecosystem extending from the southern shores of Lake Okeechobee to Florida Bay, changes in land use have reduced the spatial extent of Everglades marshes by more than 40% (Davis et al. 1994). Furthermore, the system has been subdivided into a series of marsh reservoirs (known as water conservation areas) separated by levees and canals. Whereas water once moved southward in sheet flow across the entire system, water movement through the Everglades today is disjunct and controlled by humans. By subdividing the Everglades, humans have imposed an artificial spatial scale onto the system, with each water-management "region" having its own hydroperiod (the number of days inundated with water per year), nutrient loading rate, and level of connectivity with other regions. These changes are thought to have contributed to declines in the abundance of wildlife (Ogden 1994). Large scale restoration efforts are being planned and initiated with the goal of improving habitat quality of Everglades marshes for fish and wildlife. However, our understanding of how large-scale habitat alterations affect Everglades fish and wildlife communities is insufficient to develop sound restoration projects (Davis and Ogden 1994, Ogden 1994, Gaff et al. 2000).

Fishes of the Everglades can be divided into two groups on the basis of size (Trexler et al. 2002, 2003). Small-bodied fishes (SL < 8.0 cm as adults), mainly composed of poeciliids and cyprinodontids, are the dominant taxa both numerically and in standing crop (Loftus and Kushlan 1987, Loftus and Eklund 1994, Turner et al. 1999, Trexler et al. 2002). More than twenty years of density and compositional data are available for this group of fishes, and these data have provided important insights into how the Everglades ecosystem functions (Loftus and Eklund 1994, Turner et al. 1999, Trexler et al. 2002). The other group of fishes inhabiting Everglades marshes is large-bodied fishes (SL  $\geq$  8.0 cm), including several important predators such as largemouth bass Micropterus salmoides Lacepede and Florida gar Lepisosteus platyrhrincus De Kay. Less is known about large fishes in the Everglades because effective techniques for sampling them in shallow, vegetated habitats have only recently been developed (Chick et al. 1999). The ecological role of large fishes in Everglades marshes is currently a topic of debate. Some studies suggest that large fishes are important top-down regulators of small fish abundance (Kushlan 1976), whereas others suggest that large fishes are too rare to affect small fish abundance (Loftus and Eklund 1994, Jordan 1996).

Trexler et al. (2002) provided evidence that the abundance and community composition of large and small fishes varied at different spatial scales in Everglades marshes. Variation in small fish abundance occurred mostly at local scales (i.e., 10 km), whereas limited data on large fishes suggested that larger scale variation (i.e., among management units) was more important. These differences may reflect differences in migrational ability between these two groups because movement by fishes tends to scale with body size (Ware 1978). These differences may be particularly important in Everglades marshes, where the ability to locate deep-water refugia is critical for survival during seasonal dry downs. Differences in proximity to deepwater refugia and micro-topographic variation may structure populations and communities of small fishes at local scales. If large fishes are more successful at long distance dispersal and locating deep-water refugia, proximity to deep-water refugia at local scales may be less important to their population and community structure.

We conducted the first large-scale study of the distribution and composition of large fishes in the Everglades. Our objectives were to 1) examine patterns in the abundance (all species, all predators, and individual species) and community structure of large fishes across the central and southern portions of the Florida Everglades in relation to spatial scale, time, and habitat factors (hydroperiod, floating mat volume, vegetation density); 2) determine which spatial scale, regional (an anthropogenic scale corresponding to water-management practices) or intra-regional (i.e., variation among sites within a region), is most relevant to variation in large fish abundance and community structure; and 3) examine relationships between the community structure of large fishes and hydroperiod, water depth, floating mat volume, and vegetation density.

# STUDY SITE

From October 1997 to October 2002, we sampled fishes at 11 sites in freshwater marshes from three regions of the Florida Everglades: Water Conservation Area-3A (WCA-3A) and both Shark River Slough and Taylor Slough in Everglades National Park, Florida, USA (Figure 1). We limited our sampling to wet prairies and sloughs dominated by spikerush Eleocharis spp., which are important habitats for fishes and wading birds (Loftus and Eklund 1994, Jordan et al. 1997a). Our sites were typical of many shallow, densely vegetated Everglades marshes that contain abundant mats of floating, benthic, or epiphytic periphyton (Gunderson 1994, Jordan et al. 1997b, Turner et al. 1999, Trexler et al. 2002). Everglades marshes are typically mosaics of spikerush-dominated wet prairies and sloughs, intermixed with dense stands of sawgrass Cladium jamaicense Crantz. Compared to adjacent spikerush habitats, sawgrass stands are typically 10 to



Figure 1. Map of the central and southern portions of the Florida Everglades showing the three regions (WCA-3A, Shark River Slough, Taylor Slough) and eleven sites (black dots) sampled during this study.

20 cm shallower (Jordan et al. 1997b), support lower densities of small fishes (Jordan 1996, Trexler et al. 2002), and are thought to be poor habitat for large fishes due to high stem density.

Our sites were selected from an existing network of permanently established monitoring stations for small fishes. At each site, three 1-ha plots were delineated for throw-trap sampling, and we use data on water depth, stem density of emergent vegetation, and floating mat volume (periphyton, submergent macrophytes, and epiphytic algae) collected through this small-fish monitoring study (J.C. Trexler, F. Jordan, S. Perry, unpublished data; for methodology see Loftus and Eklund 1994, Trexler et al. 2002). Distances among plots within a site ranged from 0.5 to 2 km, distances among sites within a region ranged from 3 to 23 km (intraregional scale), and distances among sites in different regions ranged from 25 to 87 km (regional scale).

Each of the three regions was subject to unique water-management schedules. Taylor Slough has the shortest hydroperiod marshes as a result of water diversion projects in the 1960s combined with drainage and development of the headwaters of this region (Light and Dineen 1994). The longest hydroperiod marshes occur in WCA-3A, where water flow out of this region is restricted by levees, and Shark River Slough contains marshes of intermediate hydroperiod. Because these three regions were formerly connected in terms of flow (Light and Dineen 1994), the regional scale represents a human-imposed spatial scale corresponding to water management. Nevertheless, habitat was not uniform within a region, and several environmental variables varied at the intra-regional scale, including hydroperiod (a result of micro-topographic variation), nutrient concentration, density and species composition of vegetation, and proximity to deep-water refugia.

### METHODS

# Sampling Protocol

We sampled fishes four times each year during the months of February/March, April/May, July/August, and October/November using an airboat electrofisher. Low water levels prevented us from sampling on several occasions during the months of April/May. Catchper-unit-effort (CPUE) from airboat electrofishing provides a meaningful index of the density and biomass per unit area of large fishes in freshwater marshes of the Everglades (Chick et al. 1999). We conducted three 5-min (pedal time) electrofishing transects near each of the three throw-trapping plots at each of our 11 sites (i.e., nine transects per site). Each transect was separated by at least 50 m and covered approximately 150 to 250 m of marsh with the airboat running at idle speed ( $\approx 4-8$  km/h; see Chick et al. 1999 for further details). All electrofishing was conducted between 07: 30 and 17:00 hours.

The electrofishing apparatus had two anodes suspended 2.5 m in front of the boat (2 m apart), with the hull of the airboat serving as the cathode, and produced pulsed DC current regulated with a Smith-Root Inc. model GPP 9.0 control box. We standardized electrofishing power at 1500 W over different temperature and conductivity conditions using the methods described by Burkhardt and Gutreuter (1995). Water temperature (range from 16 to 34 °C) and conductivity (range from 189 to 650  $\mu$ S/cm) was measured prior to the first electrofishing transect at each plot (YSI model 33 conductivity meter), and we selected a voltage and amperage needed to achieve 1500 W (amperage was fine-tuned with the peak voltage rheostat). Variation in temperature and conductivity was minimal among plots within a site, and sampling at all transects within a site was conducted at the same voltage and pulse

settings. Fishes were identified to species, measured to the nearest 1 mm SL, maintained in a holding tank until completely recovered, and then released.

## Analyses

We examined how abundance of large fishes varied through time, among regions, and among sites within regions with nested, repeated measures analysis of variance (ANOVA). Response variables were mean CPUE (number of fish per 5-min electrofishing) of all species combined, all predators combined, and the seven most abundant species (each comprising > 5 % of total catch): lake chubsucker Erimyzon sucetta Lacepede, Florida Gar, bowfin Amia calva Linneaus, spotted sunfish Lepomis punctatus Valenciennes, largemouth bass, warmouth Lepomis gulosus Cuvier, and Mayan cichlid Cichlasoma urophthalmus Gunther. Predator species included Florida gar, bowfin, redfin pickerel Esox americanus Gmelin, chain pickerel Esox niger Lesueur, yellow bullhead Ameiurus natalis Lesueur, largemouth bass, and warmouth. Mean CPUE from airboat electrofishing was calculated for the three plots within each site, and we used an ANOVA model including the main effects of time, region, and site nested within region. The subject for the repeated measures was plot nested within site and region (a random effect) using the mixed model procedure (Proc Mixed) in SAS for Windows (version 8) (Littell et al. 1996, SAS 1999).

Seasonal fluctuations in water level caused significant autocorrelation in our fish abundance time series. Therefore, our analyses were adjusted by assuming a first-order autocorrelation structure in the error terms (Littell et al. 1996). To allow for a direct comparison of variation at the regional and intra-regional scale, we calculated effect size for region and site nested within region as the mean of the range of differences in CPUE among regions (or among sites within regions) divided by the overall standard deviation among observations. This calculation is similar to the formula used to calculate effect size in meta-analysis of ecological experiments (Osenberg et al. 1997). Effect size was calculated for CPUE of all fishes, all predators, and for the seven most abundant species. To conform to the assumptions of normality and homoscedasticity, we log-transformed all CPUE data. We used Tukey's multiple comparison test for post-hoc comparisons of the levels of significant main effects.

To examine patterns in the abundance of fishes in relation to hydroperiod, we estimated the days between a sampling event and the last major dry-down event at each plot. We used linear regression to estimate the relationship between mean water depth measured at each plot during throw-trap sampling (n = 5-7 for

each sampling event) and the water level recorded on the same day at nearby hydrologic recording stations over 6-9 years (J. Trexler and F. Jordan, unpublished data). Much of the variation in mean water depth was explained by the regression models ( $R^2 = 0.839$ -0.993), and we used the corresponding regression equations to predict daily water depth at each plot. We defined a major dry-down event as when the predicted, daily water depth was  $\leq 10$  cm. At this depth, little standing water remains, and fish are submerged in a flocculent slurry that may clog their gills and increase mortality. Number of days post-dry-down was logtransformed and used as a covariate in our nested, repeated measures ANOVA. We removed non-significant interactions between this covariate and main effects from the model. When dry-down event was significant as a covariate, we tested for significant slopes for each region and generated predicted trends for all significant slopes.

Density of emergent vegetation affects the efficiency of airboat electrofishing (Chick et al. 1999); therefore, we added stem density (emergent stems/m<sup>2</sup>) to our ANOVA model as a covariate to examine its effect on CPUE for all species combined. We conducted a similar analysis of covariance using floating mat volume (ml / m<sup>2</sup>) as a covariate. To normalize these covariates, both stem density and floating mat volume were log-transformed. For both ANCOVAs, we determined that all interactions between the covariates and main effects were non-significant and subsequently eliminated these interaction terms from the final analyses.

To examine how fish community structure varied at the regional and inter-regional scale, we used a twoway nested analysis of similarity model (Clarke and Warwick 1994). For this analysis, we limited our data to the thirteen most abundant species (i.e., where total catch was at least 30 individuals) and used a Bray-Curtis similarity matrix calculated from square-root transformed (for normality and homoscedasticity) CPUE averages for each site on each date sampled. We conducted a similarity breakdown to determine which species were contributing to the observed groupings (Clarke and Warwick 1994). The average Bray-Curtis dissimilarity between all inter-group samples was calculated, and the percent contribution from each species to this average was determined (Simper Procedure in Primer, Primer-E Ltd.). We used nonmetric multi-dimensional scaling, based on a Bray-Curtis similarity matrix, to illustrate spatial and temporal groupings in community structure, averaging across time for each site for overall spatial groupings, and averaging across sites for each region and date to examine spatial-temporal patterns (Clarke and Warwick 1994). Finally, we used canonical Mantel tests to

examine whether community structure variation in space and time (Bray-Curtis similarity matrix) was correlated with water depth, floating mat volume, stem density, and days post-dry-down using standardized Euclidian distance matrices for habitat data. All community structure analyses were conducted using the Primer statistical software package (Primer-E Ltd. 2001).

## RESULTS

# Habitat Trends

Dry-down events were more severe and widespread in 2000, 2001, and 2002 (water depth  $\leq 10$  cm at 9 sites) compared to 1998 and 1999 (water depth  $\leq 10$ cm at 5 sites; Figure 2). Across time, mean water depth among sites ranged from 34.0 cm at site 37 in Shark River Slough to 78.9 cm at site 4 in WCA-3A. Peak water levels occurred in October 1999 when Hurricane Irene moved through South Florida (Figure 2). Averaged across time, mean floating mat volume among sites ranged from 1048 ml/m<sup>2</sup> at site 37 in Shark River Slough to 4466 ml/m<sup>2</sup> at site 4 in WCA-3A. Floating mat volume decreased dramatically in Shark River Slough and site 3 in WCA-3A following the 2001 spring dry-down event (Figure 3). Averaged across time for each site, stem density of emergent vegetation ranged from 56 stems/m<sup>2</sup> at site 1 in WCA-3A to 356 stems/m<sup>2</sup> at site 37 in Shark River Slough. Density of emergent vegetation increased consistently through the time series at sites 4 and 5 in WCA-3A, and decreased consistently at site CP in Taylor Slough.

### Variation in Abundance

The most pronounced and consistent patterns in the abundance of large fishes occurred at the regional scale through time. We found significant variation in total CPUE for all species among regions ( $F_{3, 260} = 14.44$ ;  $P \leq 0.0001$ ) and a significant decrease in abundance through time ( $F_{1,323} = 23.96$ ;  $P \le 0.0001$ ). Abundance of all species combined was consistently greater in both WCA-3A and Shark River Slough compared to Taylor Slough (Tukey's P < 0.05; Figure 4a). Trends in abundance through time varied among regions (F<sub>2.244</sub> = 4.91; P = 0.0081, with significant (P < 0.05) negative trends occurring in WCA-3A and Shark River Slough (Figure 4a). Additionally, there was significant  $(F_{1, 422} = 6.86; P = 0.0091)$  and positive covariation in abundance with the number of days post-dry-down. Variation in abundance among sites within regions and the interaction between site and time were not significant ( $F_{8,229} \le 1.12; P \ge 0.2816$ ). Covariation in abundance was not significant for floating mat volume or stem density ( $F_{1, 367} \le 0.59$ ;  $P \ge 0.4412$ ).

As with the abundance of all species combined, patterns in the abundance of all predators were most pronounced among regions through time (Figure 4b). Significant variation occurred among regions (F3, 240 = 13.90;  $P \leq 0.0001$ ) and among sites within regions  $(F_{8,208} = 2.78; P = 0.0061)$ . We found a significant decrease in the abundance of predators through time  $(F_{1,305} = 20.90; P \le 0.0001)$ , and trends through time varied significantly among regions ( $F_{2,223} = 4,68$ ; P =0.0102) and sites within regions ( $F_{8, 208} = 2.66; P =$ 0.0084). Abundance of predators varied significantly (Tukey < 0.05) among the three regions, with CPUE greatest in WCA-3A and lowest in Taylor Slough (Figure 4b), and trends through time were significant for WCA-3A and Taylor Slough (P < 0.05). Covariation of predator abundance with the number of days postdry-down was not significant ( $F_{1,435} = 0.16$ ; P =0.6872).

For the seven most abundant species, variation among regions, variation through time and covariation with the number of days post-dry-down were the most common patterns observed (Figure 5; Table 1). Abundance of lake chubsucker, Florida gar, largemouth bass, warmouth, and Mayan cichlids all varied significantly among regions and through time (Table 1). Of those species, lake chubsucker abundance decreased through time in WCA-3A and Shark River Slough, and trends through time were also negative in WCA-3A for Florida gar, largemouth bass, and warmouth (Figure 5). Mayan cichlid abundance increased through time in Taylor Slough (Figure 5). Covariation of abundance with the number of days post-dry-down was positive and significant ( $F_{1,435} \ge 8.36$ ;  $P \le 0.0041$ ) for lake chubsucker, Florida gar, spotted sunfish, and Mayan cichlids. Variation among sites within region was only significant for Florida gar and warmouth (F1, 435  $\geq$ 2.44;  $P \leq$  0.0151). Interactions between time and region, or time and site within region, were only significant for two of the seven species (Table 1).

Of the two spatial scales examined, the regional scale appeared to be more relevant to abundance of large fishes compared with the intra-regional scale. Effect size for region was greater than site nested within region for all species combined (region effect = 3.15; site(region) effect = 2.15), all predators combined (region effect = 3.02; site(region) effect = 2.19), lake chubsucker (region effect = 2.52; site(region) effect = 1.47), Florida gar (region effect = 3.17; site(region) effect = 2.88; site(region) effect = 1.72), largemouth bass (region effect = 3.15; site(region) effect = 2.97; site(region) effect = 1.79), and Mayan cichlid (region effect = 3.53; site(region) effect = 1.96).



Figure 2. The predicted time series of mean water depth (cm) for all sites within the WCA-3A, Shark River Slough, and Taylor Slough of the Florida Everglades. The dashed line indicates water depth of 10 cm. Dry-down events that lower water depth below 10 cm leave little standing water in the marsh for fishes.

# Variation in Community Structure

In total, we captured 1,928 fish from 17 species (Table 2). Some obvious differences in species composition among regions exist. Both chain pickerel and redfin pickerel apparently reach the southern most extent of their respective distributions in WCA-3A, and these two species are rarely observed within Everglades National Park. Non-native species, including walking catfish, Mayan cichlids, blue tilapia, and spotted tilapia, were more abundant in Shark River Slough and Taylor Slough than in WCA-3A. As with overall abundance, the regional scale was more relevant to variation in community structure of large fishes than the intra-regional scale. The nested analysis of similarity revealed significant variation in community structure among regions ( $\mathbf{R} = 0.59$ ; P =0.001), whereas differences among sites within regions were not significant ( $\mathbf{R} = -0.052$ ; P = 0.859). All pairwise comparisons among regions were significant ( $P \leq$ 0.05), and non-metric multi-dimensional scaling captured the regional groupings in two dimensions (Stress = 0.01; Figure 6). Eight species accounted for

![](_page_6_Figure_1.jpeg)

Date

Figure 3. Time series of mean floating mat volume (ml/m<sup>2</sup>  $\pm$  1 Standard Error) and stem density (#/m<sup>2</sup>  $\pm$  1 Standard Error) for all sites within WCA-3A, Shark River Slough, and Taylor Slough.

more than 80 % of the dissimilarity between Shark River Slough and WCA-3A. Lake chubsucker, spotted sunfish, yellow bullhead, and Mayan cichlids were all more abundant in Shark River Slough, whereas Florida gar, largemouth bass, warmouth, and bowfin were more abundant in WCA-3A (Figure 6). Abundances of all species were lower in Taylor Slough compared to both Shark River Slough and WCA-3A. Number of days post-dry-down had the greatest correlation (Mantel r = 0.482; P = 0.001) with community structure of fishes, whereas floating mat volume, stem density, and water depth did not improve the Mantel correlation. Non-metric multi-dimensional scaling also revealed temporal shifts in community structure that followed variation in days post-dry-down when averaged across sites for each region and year (Figure 7).

# DISCUSSION

We found substantial variation in large-fish abundance and community structure at the regional scale, significant trends through time, and significant covariation with hydroperiod. This has important implications for management and restoration of the Everglades because the regional scale is an artifact imposed on this system through habitat alterations and water management. Differences among regions were significant even though the number of days post-dry-down

![](_page_7_Figure_1.jpeg)

Figure 4. A) Mean CPUE (number of fish/5 min electrofishing;  $\pm 1$  Standard Error) of large fishes (SL > 8 cm) captured by airboat electrofishing in WCA-3A, Shark River Slough, and Taylor Slough. B) Mean CPUE (number of fish/5 min electrofishing;  $\pm 1$  Standard Error) of all predators captured by airboat electrofishing in WCA-3A, Shark River Slough, and Taylor Slough. Lines are the predicted relationship between abundance and time for each region (only shown when significant) after adjusting for autocorrelation.

was included as a covariate. This indicates that factors beyond the immediate effects of hydoperiod (i.e., drydown events) are influencing the abundance and community structure differences among the three regions. We cannot be certain which environmental factors are responsible for the patterns we observed because this was an observational study. Large-scale experiments would be needed to ascertain cause and effect. Additionally, it is possible that environmental conditions prior to anthropogenic alterations to Everglades marshes may have led to similar spatial patterns in the abundance and community composition of large fishes. Nevertheless, simulations of historical Everglades hydrology suggest that marshes within the three regions studied, particularly Shark River Slough and WCA-3A, were more similar to each other in terms of hydrology and vegetation communities prior to anthropogenic changes (Davis 1994, Gunderson 1994)

Compared to the other two regions, Taylor Slough's large fish community had the lowest abundance and the most variable species composition. High variability and low population levels in this region likely reflect more frequent and extreme dry-down events that Taylor Slough experiences compared to Shark River Slough and WCA-3A (Figure 2). Extreme dry downs are known to cause substantial mortality of fishes in the Everglades (Kushlan 1974, Nelson and Loftus 1996). Spring dry-down events occurred in several of our sites in 1999, 2000, 2001, and 2002. These drydown events appear to have caused substantial mortality of lake chubsucker in Shark River Slough, where mean abundance decreased substantially after February 2001, and in Taylor Slough where only one specimen was captured after February 2000. Of the four habitat variables examined in this study, only days post-drydown correlated with the abundance patterns or community structure of fishes, suggesting that dry downs had a strong influence on large fishes in Everglades marshes.

Water-level fluctuations likely affect Everglades fishes through indirect pathways, in addition to direct mortality from dry-down events. We documented sig-

![](_page_8_Figure_1.jpeg)

Figure 5. Mean CPUE (number of fish/5 min electrofishing;  $\pm 1$  Standard Error) of the seven most frequently captured species of large fishes (SL > 8 cm) in WCA-3A, Shark River Slough, and Taylor Slough. Lines are the predicted relationship between abundance and time for each region (only shown when significant) after adjusting for autocorrelation.

nificant decreases in abundance of fishes in WCA-3A despite the fact that this region had a greater proportion of long-hydroperiod marshes compared to Shark River Slough and Taylor Slough. Of the four sites studied in WCA-3A, only site 3 consistently had water depth  $\leq 10$  cm during spring dry downs. Therefore, direct mortality associated with dry-down events was unlikely to be responsible for the decreasing abundance patterns observed in this region. The patterns we observed in WCA-3A may reflect movements of large fishes out of this region, possibly to deep-water

refugia, such as canals, alligator ponds, or deeper marshes in other regions of the Everglades, in response to reduced water depth. For large fishes to locate deepwater refugia successfully, they likely would have to move to these areas before water depth fell below 10 cm. Recent telemetry studies in WCA-3A have documented movements of large fishes from central marshes to outer canals and intra-regional movements of over 10 km in response to sudden decreases in water depth (J. Trexler, unpublished data). Alternatively, other habitat changes associated with the onset of drier 0.0030

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years may have influenced large fish abundance. We observed a substantial increase in stem density of emergent vegetation at sites 4 and 5 in WCA-3A over the course of this study. These are long-hydroperiod sites, and the onset of drier conditions likely promoted growth of emergent vegetation. Both vegetation density and composition can affect distribution patterns of fishes (Chick and McIvor 1994, 1997), but variation in abundance and community structure of large fishes did not correlate with vegetation density in this study.

Our results suggest that regional variation of watermanagement practices can have major influences on the abundance and community structure of large fishes in Everglades marshes. The low abundance of large fishes in Taylor Slough and near extirpation of lake chubsuckers after February 2000 suggest that frequent dry downs may be the primary factor limiting fish populations within this region. WCA-3A has the longest hydroperiod marshes and greatest abundance of predators among the three regions studied. The onset of more severe and consistent dry-down events in 2000, 2001, and 2002 provided a natural experiment to examine hydroperiod effects on large fish community structure. If hydroperiod is a critical factor affecting fish community structure, we should have observed substantial changes in the large fish community during this study. In fact, we did observe significant shifts in community structure of large fishes in all regions during this time. These shifts did not seem to be random because community structure in Shark River Slough and WCA-3A during the driest years of this study (2001 and 2002) displayed similar shifts in our NMDS plots. Changes in community structure of large fishes, especially with regards to the abundance of predators, may influence other biota in Everglades marshes.

Alternative hypotheses have been presented regarding the influence of large fishes on small fish communities of the Everglades ecosystem. Kushlan (1976) presented a top-down view of Everglades community structure, suggesting that large piscivorous fishes limit population growth of small fishes during extended periods of high water. However, more recent publications contradict Kushlan's (1976) top-down view and suggest that Everglades marshes function as "predator refuges" for small fishes (Loftus and Eklund 1994, Jordan 1996). Aquatic macrophytes are known to reduce foraging success of piscivores (Heck and Crowder 1991, Chick and McIvor 1997), and populations of piscivorous fishes in seasonally-flooded wetlands can be limited by dry downs and hypoxia (Lowe-Mc-Connell 1987, Batzer 1998, Turner et al. 1999). Furthermore, standing stocks of large fishes in Everglades marshes are low relative to other wetland and littoral systems (Turner et al. 1999). Our data suggest that the precise ecological role of large fishes in Everglades

Species	Common Name	3A	SRS	TS	Species Total
Lepisosteus platyrhincus De Kay	Florida gar	215	134	49	398
Amia calva Linnaeus	Bowfin	96	45	14	155
Esox americanus Gmelin	Redfin pickerel	35	1	0	36
Esox niger Lesueur	Chain pickerel	15	0	0	15
Erimyzon sucetta Lacepede	Lake chubsucker	200	367	23	590
Ameiurus natalis Lesueur	Yellow bullhead	11	54	14	79
Ameiurus nebulosus Lesueur	Brown bullhead	1	0	0	1
Clarias batrachus Linnaeus	Walking catfish	4	14	8	26
Centropomus undecimalis Bloch	Snook	0	3	0	3
Micropterus salmoides Lacepede	Largemouth bass	80	42	9	131
Lepomis gulosus Cuvier	Warmouth	69	43	10	122
Lepomis punctatus Valenciennes	Spotted sunfish	43	84	9	136
Lepomis macrochirus Rafinesque	Bluegill	28	16	6	50
Lepomis microlophus Gunther	Redear	17	5	9	31
Cichlasoma uropthalmus Gunther	Mayan Cichlid	13	34	25	72
Oreochromis aureus Steincachner	Blue Tilapia	1	20	9	30
Tilapia mariae Boulenger	Spotted Tilapia	6	41	6	53
Total individuals		834	903	191	1928
Species Richness		16	15	13	17

Table 2. Total number of individuals caught electrofishing during this study for each species in WCA-3A (3A), Shark River Slough (SRS) and Taylor Slough (TS) from October 1997 to December 1999.

marshes is intimately tied to hydroperiod. Predator abundance was consistently greater in WCA-3A than Shark River Slough from October 1997 to October 1999, whereas predator abundance in WCA-3A decreased and became similar to that found in Shark River Slough after the dry-down events in 2000, 2001, and 2002. Loftus and Eklund (1994) suggested that regulation of small fishes by large predatory fishes was

		Stress: 0.01	Lake chubsucker				Spotted sunfish			
à à			\$3 <sup>1</sup>		TS		<b>\$</b> 3 <sup>1</sup>		Τ̈́S	
. <sup>. जु. न</sup>		a a SRS a Taylor	37 B8	М́D	C	Ρ	37 88	ŴD		СР
Yellow bullhead			Mayan cichlid				Florida gar			
<i>≱</i> 53 <sup>9</sup>	-9-	ŤS	<i>4</i> β <sup>3 1</sup>		ŤS		£31	_	τs	
37 68	MD	ĈP	37 <sup>88</sup>	MD	Ĉ	Ρ	37 <sup>88</sup>	MD		ĈP
Largemouth bass			Warmouth				Bowfin			
<b>\$3</b> <sup>1</sup>		TS	<b>\$</b> 31		ŤS		53 1		ΤS	
37 88	MD	ĊP	37 58	М́D	c	P	37 88	ŴD		СР

Figure 6. Two dimensional non-metric, multi-dimensional scaling ordination of community structure. Mean CPUE data were square-root transformed and Bray-Curtis similarities were used. 3A = WCA-3A, SRS = Shark River Slough, TS = Taylor Slough. Circle size is scaled to the mean CPUE for the specified species. Numbers and letters designate specific sites within each region (see Figure 1).

![](_page_11_Figure_1.jpeg)

Figure 7. Two dimensional non-metric, multi-dimensional scaling ordination of regional community structure through time. Circle size is scaled to the natural log of the number of days post-dry-down (i.e., since mean water depth < 10 cm). Mean CPUE data were square-root transformed and Bray-Curtis similarities were used.

more likely in the impounded areas of WCA-3A than in the southern Everglades. Our results are consistent with this hypothesis and suggest that regional differences in water management may have important effects on abundance of predatory fishes.

During the past two decades, ecologists have focused more explicitly on the importance of scale to ecological patterns and processes (Turner 1989, Wiens 1989, Levin 1992, Peterson and Parker 1998). In this study, we opted to examine the relevance of two spatial scales on large fish abundance and community structure, one scale being an artifact imposed on the system by anthropogenic habitat alterations and water management. We suggest that this approach provided greater insights into the potential influence of anthropogenic activities than traditional correlative approaches alone. Finding a significant covariation of fish abundance and/or community structure with hydroperiod does not present a complete picture of the differences in fish communities we found among the three regions. For example, although hydroperiod at site 3 in WCA-3A was similar to short-hydroperiod sites in Shark River Slough and Taylor Slough, site 3 grouped closely to the long-hydroperiod sites in WCA-3A in our analysis or fish community ordinations. This suggests that conditions within the entire region were more relevant to fish community structure than differences in local hydrology among sites. The fact that the regional scale was more relevant to large fish communities during this study is especially interesting given that previous studies have found that intra-regional scales are more important to abundance and community structure of small fishes in Everglades marshes (Trexler et al. 2002). This highlights the observation that different groups of organisms often respond uniquely to environmental factors operating on different scales (Martinez and Dunne 1998).

Everglades restoration efforts will provide the ultimate test to determine whether the regional scale patterns in large fish abundance and community structure we observed resulted from anthropogenic disturbances. Restoration and water-management activities for freshwater marshes of the Everglades should be planned as adaptive management/large scale experiments with adequate monitoring to allow insights into the population and community responses of fishes and other biota (Trexler and Busch 2003). Given sufficient time, regional-scale changes to water management should result in predictable shifts in the abundance and community structure of large fishes. For example, increasing water delivery to Taylor Slough likely would increase the survival and, ultimately, the overall abundance of large fishes in this region. Community structure of large fishes in this region might begin to resemble the community in Shark River Slough. Delivering more water from WCA-3A to other areas of the Everglades likely would reduce the survival and abundance of predators in this region, also shifting community structure to resemble that in Shark River Slough.

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