

Final Report

Cooperative Agreement CA5280-8-9003

Between Everglades National Park and Florida International University

Analysis of Relationships of Everglades Fish with Hydrology Using Long-Term Databases from the Everglades National Park

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EXECUTIVE SUMMARY

Fishes provide one of the longest, most spatially extensive records of monitoring information about the environmental integrity of wetland habitats in Everglades National Park (ENP). Monitoring of fish communities in ENP began in the 1960s, was expanded in the 1970s, and presently includes sampling sites in both Shark and Taylor Sloughs. A standard protocol using the 1m² throw trap was developed in the 1970s and has been consistently applied at a number of locations in the Park since late 1977. With funding from the South Florida Management District and the US Army Corps of Engineers, the ENP network was expanded in the 1990s to include more ENP sites and habitats north of the Park in the Water Conservation Areas. The data gathered by this landscape-scale network have provided information critical to a variety of management efforts including: development of performance measures and simulation models to evaluate alternative management plans in the Everglades Restudy; documentation of effects of hurricanes and other environmental disturbances; and interpretation of patterns of wading-bird foraging and nesting. In this report, we provide a history of the aquatic-animal research effort, and we describe the results of our analyses of long-term data (1978 through 1999) collected by throw trap from three of the study sites.

Data gathered at three of the long-term research sites permitted analysis of temporal patterns over a 22-year period. A major finding was the effect that changes in water delivery in Northeast Shark River Slough (NESS) had on fish density and community composition. Starting in 1985, under Experimental Water Delivery Iteration 1, more water was diverted into the NESS from area north of Tamiami Canal. This increased the annual water-depth minima at our NESS study site (Site 23). A drought in 1989 and 1990 reduced densities of fishes at all of our study sites, and was followed by local fish population growth and community succession. After

correcting for system-wide high water conditions in the 1990s, we found evidence that the density of fishes in NESS (Site 23) converged on the density at the long-hydroperiod site in western Shark River Slough (Site 6), near NP-203. Fish density at Site 23 moved away from previous patterns of similarity to the naturally short hydroperiod site at Shark Valley (Site 50). Community composition at Site 23 displayed similar trends toward a more long-hydroperiod fish community at the same time. These results provide evidence that the Experimental Water Delivery Program successfully recovered aspects of longer-hydroperiod fish communities in NESS, that the recovery was manifested over approximately 3 years, and that minimum water depth (not average water depth) was a critical parameter in the ecosystem recovery process.

Other important findings from our analyses of the empirical hydrological and animal data include:

1. Rainfall at the sites did not explain much variation in water depth at the study sites, while flow from the S-12 structures, particularly C and D, were correlated with water depth in Shark River Slough. In NESS, rainfall, flow from the culverts running beneath the Tamiami Trail, and water flow from structures S-12C and D explained water-depth patterns.
2. The sites varied in hydroperiod, frequency of drying, and maximum water depth. Site 6 had the longest hydroperiod and the lowest drying frequency, while Site 50 had the shortest hydroperiod and most frequent dry-downs. Site 23 was intermediate in these parameters.
3. Monthly mean water depths and annual minimum water depths were consistently greater at Site 6 than Site 50. Site 23 was drier than Site 50 for much of the period between 1978 and 1984, then became intermediate in both measures after 1984. The change at Site 23

is correlated with a change in water delivery instituted in 1985 (Water Delivery Iteration 1).

4. There was little consistency in seasonal fish densities among years of the study.

Maximum fish density could occur in any month of the year, though minimum density generally was found from January through September; the density in October was never lower than the density in April. Marked concentration of fishes during the dry season was not evident in most years. Fish density was greatest at Site 6 and least at Site 50 throughout the study. Site 23 had intermediate level of density that was similar to Site 50 between 1985 and 1989, and converged on Site 6 over a number of years following a drought in 1989 and 1990. The drought had a marked effect on fish density, particularly at sites 6 and 23. Hydrology was correlated with fish density through inter-site and inter-year differences. All sites increased in density during the relatively wet years following 1991, though Site 23 increased relatively more than Site 50.

5. Seasonal patterns of fish community composition were detected that divided the year into 4 increments: December through March, April, May through June, and July through November. Those compositional patterns primarily reflected seasonal patterns of recruitment in different species. The drought years of 1989-1990 produced the greatest effect on fish community composition of any time interval of the study. Patterns of relative abundance were recovered most quickly at Site 50 and most slowly at Site 6; from three to four years passed before community composition was re-gained at Site 6. Community composition at site 23 converged on that at site 6 after 1992. The number of days since the last dry-down explained the most variance in density of several fish

species at sites 6 and 23, while minimum water depth in the month prior to sampling explained the most variance at Site 50.

Continued monitoring will be necessary to guide assess the recovery process in NESS and elsewhere in the system. We provide a series of recommendations for future aquatic-animal monitoring during the CERP program.

PART 1. History of Fish Monitoring in Everglades National Park

INTRODUCTION

Everglades National Park (EVER) is located at the downstream end of the southern Florida regional water-distribution system (Fig. 1). Water-management actions and land-use changes have affected hydrological and ecological conditions both outside the park and within it (Davis and Ogden 1994). Regional water management, helped by the construction of the Central and Southern Florida Project (C&SF), has changed the timing, distribution, quantity, and quality of water delivered to EVER. The regional water-conveyance network of canals and levees built for the C&SF Project has divided the once-continuous wetland system into isolated pools. Increasing agricultural and urban development on the park borders has reduced the area of wetland buffer in the southern Everglades. Changes in the physical character of the southern Everglades region have adversely affected the vibrant animal and plant communities that made this area unique. Some of these changes, particularly in alligator and wading bird nesting success and numbers, have been widely publicized (Davis and Ogden 1994), and have helped demonstrate the need for regional restoration of the system. Other ecological changes have been more subtle, yet have played a role in the decline of the charismatic Everglades animals. For example, as we discuss below, the long-term fish study program at EVER has documented changes in fish-community structure resulting from water management in the park and its contiguous wetlands (Loftus et al. 1990, Loftus and Eklund 1994). In the past two decades, introduced fishes have colonized Everglades habitats, particularly those modified by water management and its associated infrastructure of canals and ditches (Loftus and Kushlan 1987,

Trexler et al. 1996a,b, in press-b). Both of those changes in the fish community have the potential to affect prey availability and abundance for fish predators.

To reverse the trend in declining and changing biotic communities, the Comprehensive Everglades Restoration Plan (CERP), a scientifically based restoration program for the entire ecosystem, has been authorized. The restoration requires the restructuring of the physical and operational aspects of the C&SF Project. Ongoing studies of fishes that build on the long-term data set can provide information to guide and evaluate the restoration process. Small-bodied marsh fishes are easy to sample with our standard protocols, and that their short-life spans and rapid turnover rates make them responsive to both short- and long-term environmental changes. In this report, we describe the structure and results of the long-term sampling program, and we discuss how the expanded program of regional monitoring is assisting in Everglades restoration.

LONG-TERM FISH RESEARCH

Everglades Aquatic-Animal Sampling Program

The objective of the long-term sampling program has been to provide a quantitative understanding of the short- and long-term responses of small-fish and macroinvertebrate communities to natural and anthropogenic environmental changes. We have followed a process of empirical data collection and simulation modeling to apply the site-specific information gathered on the fish community to restoration planning and evaluation. We are describing present-day community responses to environmental conditions across the landscape. The empirical data are helping to build and refine simulation models from which to estimate fish-community parameters under modeled pre-management conditions. This will allow scientists and managers to agree on established restoration targets. By applying the fish models to

restoration projects to predict fish-community responses, we can choose the actions that result in biotic characteristics that approximate historical conditions. The models will help assess changes in food-web structure, persistence, and resilience, important process in predicting effects (Moyle 1994). Assessments and evaluations within the adaptive-management model proposed for CERP will demand that fish communities continue to be monitored within and outside of ENP to test predictions and guide the restoration.

History of aquatic-animal sampling in the southern Everglades

Freshwater fishes and invertebrates are abundant animals in the Everglades, and as such, are critical in the transfer of energy through the system. Fish and invertebrate species operate at several trophic levels in the wetlands, as primary consumers of plant material and detritus to predators and scavengers. Some species, such as the crayfish and the apple snail, are major prey for fishes and other predatory species, including characteristic or endangered animals like the Snail Kite, White Ibis, and American Alligator. Fishes are the major prey for most wading birds, the decline of which is attributed to changes in fish abundance and availability. Factors that influence fish and invertebrate numbers, biomass, and composition therefore affect energy flow through the wetlands. The ecology and life histories of these animals are intimately tied to the hydrology of the marsh, which is determined mainly by rainfall, but increasingly by water-management practices. Water management through flood releases, diversions, and impoundment of water can adversely affect aquatic animal stocks and distribution. Such direct effects of water management may be compounded by the subtle impacts of drying on marsh ecology, in particular the reduction of wetland productivity (Loftus et al. 1990). Disturbances, such as hurricanes, floods, and

droughts can also result in dramatically reduced standing stocks, sometimes for more than a year after the event (Trexler et al. 1996a,b).

Scientific collections of Everglades marsh fishes and invertebrates are relatively recent and, prior to the 1950s, entirely qualitative. The first in-depth studies of southern Florida freshwater animals were made by University of Miami staff between the early 1950s-1960s (Hunt 1952; Reark 1960, 1961). Hunt (1952) studied the food habits of large and small fishes from the Tamiami Canal along U.S. Highway 41 and presented information on the abundance of Florida gar. Reark (1960, 1961) was the first to collect fish and invertebrate density and biomass data with relation to vegetation cover. He compiled the only database, albeit very limited, from Shark Slough before the construction of the S-12 water-control structures (Fig. 1) in 1962. Those flood gates placed control of southern marsh hydro patterns in the hands of water managers, resulting in significant departures in the timing and quantity of natural water flows and spatial distribution. All subsequent data from the southern Everglades (south of U.S. Highway 41) were collected after marsh hydrology was disturbed by the construction of the Central and Southern Florida Project (C&SF) (Rose et al. 1981). Thus, very little information, almost none of which was published in peer-reviewed literature, exists from the pre-C&SF Project period.

From 1965 to 1972, the USGS was contracted by EVER to collect data on community composition and population variability related to hydrology in Shark Slough (Higer and Kolipinski 1967; Kolipinski and Higer 1969). The fish data were published later (Kushlan 1976,1980). Data from the pull traps for apple snails (*Pomacea paludosa*) (Kushlan 1975), the crayfish (*Procambarus* spp.) (Kushlan and Kushlan 1979), and the freshwater prawn (*Palaemonetes paludosus*) (Kushlan and Kushlan 1980) have also been published. In 1976, the Research Division of EVER began a long-term commitment of study on the aquatic ecosystem that included several

of the USGS pull traps but expanded on that program. EVER supported an eight-year investigation of fish dynamics with relation to hydrology, using the more accurate one-square meter throw trap developed and tested by Kushlan (1981). Although fish-community data were collected with throw traps at 13 marsh sites, results have been published for only two, as part of a comparison with simultaneously collected data from the pull traps (Loftus and Eklund 1994). Information generated by the eight-year throw-trap study was used to design the next study that ran from October 1985 to 1992 (Loftus et al. 1990). In that study, a new sampling design was initiated to test hypotheses about the effect of marsh hydroperiod on community parameters. Collections at two of the long-term sites (6 and 23) were continued in this study, and a new site (50) added (Fig. 1).

Following Hurricane Andrew in 1992, the original NPS-funded program was supplemented with support from the U. S. Army Corps of Engineers and the South Florida Water Management District. These new funding sources related to Everglades restoration projects, and the transfer of program personnel to the newly formed National Biological Service in 1993, resulted in major changes to the monitoring program. They also provided the first opportunity to build a regional sampling program by expanding the ENP throw-trapping program into a larger, regional program of aquatic-animal community study (Fig. 1). The increased funding enabled the inclusion of sites in EVER and the Water Conservation Areas (WCA) that had been previously sampled but dropped during lean budget years. A collaboration of NPS, FIU, and USGS-BRD personnel shared the sampling responsibilities, and this cooperative effort continues today. The most important aspect of the expanded program is that it employs a standardized and consistent sampling design to enable data comparisons across the region. Several papers

resulting from this long-term program have been published or are in press (Trexler et al. 1996a, 1996b, in press a, b; Loftus et al. 1997; Turner et al. 1999).

METHODS AND PROTOCOLS

The long-term study sites were located mainly in the central core of Shark River Slough, the major drainage channel of the southern Everglades, in ENP (Pull trap sites 1-10, throw-trap sites 6-8). Hydrological data for Shark River Slough were collected at Gages P-33, NP-203, P-36, and P-35, continuous-recording instrumentation platforms near the biological stations. Continuous hydrological data for short-hydroperiod marshes at Shark Valley (Site 50) were obtained from NP-201, for Northeast Shark Slough (NESS – Site 23) using Gage NE-1, and for Taylor Slough (sites 20-22) using Gage P-37 (Fig. 1).

The *Eleocharis* habitat comprising the wet prairies of the southern Everglades is an important habitat for fish and wading bird activity, although it is not as spatially extensive as the sawgrass marsh. Emergent plant stem densities are lower than in sawgrass habitats, and the *Eleocharis* prairies retain standing water longer into the dry season. Major plant species in the wet prairies are spikerushes (mainly *Eleocharis cellulosa*), maidencane (*Panicum hemitomon*), beakrush (*Rhynchospora tracyi*), and arrowheads (*Sagittaria* spp.). Floating mats of bladderworts (*Utricularia* spp.), sometimes covered by thick periphyton, grow among the emergent stems. Organic peat soils are found in the long-hydroperiod wet prairies of the central Everglades, while marls or calcium carbonate sediments occur in marshes with shorter flooding periods (Gleason et al. 1984). The hydrology of the marsh system is complex, with rainfall and water levels varying greatly both seasonally, annually, and interannually. Water depths in wet prairies are usually shallow (<0.75 m) and the period of flooding each year depends on antecedent conditions, water-

management actions, and the local topography. During the dry season from November to May, some or all wet prairies may dry. This forces small fishes into deeper pockets of water where they are vulnerable to resident piscivorous fishes or other predators. Those fishes remaining in the drying marshes are exposed to wading-bird predation or desiccation. The severity of the dry season is the major abiotic factor determining the composition of the fish community and its abundance during the following year (Loftus and Kushlan 1987). Because the wet prairies support large fish populations and attract feeding wading birds, and because the habitat is amenable to long-term quantitative sampling, studies of Everglades fishes have been concentrated within that habitat.

The original pull-trap study, from 1965-1972, utilized ten pull traps in northern Shark Slough, sampled on two consecutive nights each month ($n = 20$ per month). Unfortunately the database has many missing months, especially towards the end of the sampling period when collections apparently ceased. Each trap consisted of sheets of three-mm bar nylon mesh affixed to a metal frame measuring 1.5 m by 3.0 m, sampling an area of 4.5 m². Operators at each end of the trap pulled on lines that lifted the net from the water, capturing animals swimming on or above the net. Two of the original ten pull traps, known as sites 3 and 4, were retained on site in Shark Slough and have been sampled monthly after 1972 to monitor the fish community. Because Kushlan (1974) discerned the biases inherent in the stationary pull traps, he devised and tested the one-square meter throw trap (Kushlan 1981) that we have adopted as the standard method for our sampling protocol. The 80 cm-high metal frame trap was enclosed by 3.2-mm nylon netting and weighed approximately 9 kg. Aquatic animals are cleared from the trap using dip nets and a bar seine. Subsequent studies have confirmed that throw traps are effective and efficient devices for sampling shallow vegetated wetlands (Jacobsen and Kushlan 1987, Chick et al. 1992, Jordan et al.

1997). The data sets for the pull-trap and throw-trap sites were placed by WFL on the Share directory of the SFNRC server under NBS/Loftus/Throtrap.

The first throw-trapping program began in November 1977, at three long-hydroperiod sites in central Shark Slough (sites 6, 7, 8). Between seven and 15 traps (sub-samples) were collected at each site each month, the sample size calculated according to the procedure outlined by Kushlan (1981). Fishes were removed by using a rigid-frame seine (3.2-mm bar mesh), and small-mesh (0.8 mm bar) and large mesh (5.5 mm bar) dip nets until 10 consecutive sweeps produced no more animals. Data on vegetation cover, stem counts, periphyton/bladderwort volume, and soil type were also collected at each trap. Water depths collected at each trap were averaged and regressed against same-day data from a nearby continuous recorder to estimate continuous daily depths at each site. Throw-trap sampling data were also collected from other locations for shorter periods: in Northeast Shark Slough (Site 23) from 1978-1985, and Site 43 from 1983-1984; in Water Conservation Area 3-A (Site 10) and 3-B (Site 12) from 1979-1981; from Taylor Slough (sites 20, 21, and 22) from 1978-1979; and at Rookery Branch (Site 37) from 1983-1985. The data sets for these sites were placed on the Share directory of the SFNRC server under NBS/Loftus/Throtrap.

When the first throw-trapping program ended in August of 1985, fish monitoring continued under a new study that examined the role of marsh hydroperiod in structuring food webs. Results of the first program indicated that reductions in hydroperiod in NESS (Site 23) and other short-hydroperiod sites diminished animal standing stocks and affected the species composition of that area. The new study that began in October 1985 proposed to test the hypothesis that the density and biomass of aquatic animals in Shark Slough marshes with shorter hydroperiods are lower than in those with long hydroperiods. A corollary hypothesis stated that as the hydroperiod in NESS is increased during restoration activities, the densities, biomass, and species richness should also

increase. The proposed mechanism was a bottom-up limitation in short-hydroperiod marsh food webs related to the dominant cyanobacterial community and the reduction in detritus. Three sampling grids were laid out in each of three plots within a naturally long hydroperiod area (Site 6), a naturally short hydroperiod area (Site 50), and an area (Site 23) where hydroperiod had been reduced by water diversions. Within each plot, seven randomly selected grid cells were chosen for sampling by throw trap prior to visiting the plot. Samples were collected five times per year to capture the seasonal dynamics of the marshes – in February, April, July, October, and December. Collections at the three Shark Slough sites continued until December 1992.

Beginning in 1993, EVER personnel continued to collect samples at the three Shark Slough sites, while a cooperative agreement between FIU and EVER following Hurricane Andrew resulted in FIU personnel sampling former sites in Shark Slough that were discontinued in 1985 (7, 8, and 37). Additionally, a contract with the South Florida Water Management District funded FIU to sample new sites in Water Conservation Areas (WCA) 3A and 3B. In 199, the U.S. Army Corps of Engineers funded FIU to continue the WCA sites and to expand into Taylor Slough. The present design of the program includes an identical sampling protocol using the 1-m² throw trap in spikerush habitats. Samples are collected in February, April, July, October, and December to capture seasonality within the year in areas likely to be affected by restoration to gather baseline and post-action data.

EARLY PROGRAM RESULTS

From his analysis of the USGS program data, Kushlan (1976, 1980) concluded that, during a 2.25-year period without a dry-down, fish densities decreased, but fish biomass, mean fish size, species diversity and species richness increased. In examining the fish community composition,

Kushlan (1976) described a functional shift in the trophic structure of the community during the wet period, from one dominated by small, omnivorous livebearers and killifishes to a large-fish community of carnivorous sunfishes and catfish. The wet period presumably fostered the survival of larger fishes. Kushlan (1976) concluded that the Everglades fish community moves between opposing tendencies of species domination, depending on the degree of water-level stability. He invoked increased predation by larger fishes when the environment is stable as the mechanism behind those community shifts. The pull-trap data suggested that the greatest numbers of small prey fishes would be produced if the Everglades marsh were managed for frequent dry-downs (Kushlan 1987).

The first throw-trap study coincided with an eight-year period of prolonged flooding. If the conclusions of the pull-trap study were correct, this prolonged flooding period should have produced even more dramatic shifts towards larger species. The two pull traps sampled during the second study did produce results similar to those of the earlier study. For example, the densities of sunfishes (*Lepomis* spp.) and other large fishes increased as the high-water period progressed. However, small fish densities also increased significantly, and the species composition, biomass, and size data provided no evidence for a shift in community dominance towards larger species. Because the small fish densities remained rather stable over time, there was also no evidence for a functional shift in the marsh food web. The differences between the sampling programs may be explained by the biases inherent in the pull-trap method (Loftus and Eklund 1994), and in the analytical methods used in the early study (Kushlan 1976).

MANAGEMENT APPLICATIONS

The EVER program has produced some major achievements. The analysis of simultaneously collected throw-trap and pull-trap data resulted in a revision of the older paradigm of fish community dynamics (Kushlan 1976, 1987) based on the biased pull trap method (Loftus and Eklund 1994). Subsequent analyses of EVER and other Everglades marsh data sets have supported the view that fish communities in sloughs thrive when hydroperiods are not shortened by drainage nor prolonged by impoundment. In both situations the fish communities may be changed. The results provided evidence for community changes caused by water management in areas east of EVER, helping lead to acquisition of NESS and a call for hydrologic restoration (Loftus et al. 1990, Loftus et al. 1992, Loftus and Eklund 1994). Analyses of community responses to the availability of sub-surface refugia (Loftus et al. 1992), to drought and hurricane disturbances (Trexler et al. 1996a), to high-water events (Nelson and Loftus 1996, Trexler et al. 1996b), and to presence of artificial deep-water pools in wetlands (Howard et al. 1995) have led to better understanding of the community and application to CERP. The empirical data helped in construction of a fish-community simulation model for use in restoration evaluations (DeAngelis et al., 1997). The long-term data from both the pull traps and the throw traps provided a time series through which the appearance and cycles of introduced fishes at the sampling sites were able to be studied (Trexler et al. In press-b).

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PART II. Analysis of a 22-Year Record of Fish Communities from Shark River Slough: The Role of Hydrology in Regulating Everglades Fish Communities

INTRODUCTION

Understanding and predicting the dynamics of populations and communities is a major goal of ecology that has proven to be elusive. At the population level, debates have raged over dichotomies such as the role of density-dependent and density-independent mechanisms of regulation (Andrewartha and Birch 1954, Nicholson 1958) or of the supremacy of competition, predation, or other biotic interactions (Strong et al. 1984, Diamond and Case 1986). Community ecology has also focussed on simplifications such as the balance of disturbance and biotic factors (Menge and Sutherland 1976; Huston 1994), or the dominance of top-down or bottom-up effects (Power 1992). The complexity of ecological systems that has emerged from these debates can seldom be revealed by any single sampling or experimental approach conducted at a single place or time. Increasingly, consideration of ecological dynamics over time and space is seen as critical to capture the range of processes shaping communities. Time lags and non-linearity are pervasive in ecological processes, and render temporal and spatial "snapshot" studies of limited use in revealing the ultimate factors of community regulation.

Understanding and predicting community dynamics is of more than academic interest for managers of the Florida Everglades. The modern Everglades ecosystem is much smaller than the historical one, has experienced a history of drainage, and has been infused with nutrient-enriched runoff (DeAngelis 1994; DeAngelis and White 1994). Managers seek to retain or regain the characteristics and function of the historical ecosystem through manipulation of water quantity and quality in the face of anthropogenic activities that have altered ecosystem function and resilience (Davis and Ogden 1994; Gunderson 1999; Gunderson 2000). However, choosing the

preferred plan out of the myriad possibilities requires predicting the outcome of each hydrologic alternative on biotic resources (DeAngelis et al. 1998; USACOE and SFWMD 1999). Making such predictions and interpreting the results requires an understanding of the mechanisms that drive ecosystem change.

We report the analysis of a 22-year time series of fish samples collected at three Everglades National Park (ENP) sites that experienced different hydrological conditions. Those data provide unique insights into the role of abiotic factors shaping fish communities and the scale of time lags in fish-community response to environmental fluctuation. The results have direct and immediate application to assessment and management tools already under development (e.g., Gaff et al. 2000). This study also provides rare data on the range of organismal density and species composition from several areas in ENP that may be used as reference values for evaluation of future ecosystem conditions. We report our results in four sections: analyses of hydroperiod, fish density, and fish community composition at the study sites, and an analysis of statistical relationships of fish communities and measures of hydroperiod.

METHODS

Study Sites and Sampling Design

We sampled fishes at three sites located in northern Shark River Slough (Sites 6, 23, and 50; Fig. 1). The study sites were located in wet-prairie slough habitats dominated by spikerushes, primarily *Eleocharis cellulosa* (Busch et al. 1997). Other common plant species were maidencane (*Panicum hemitomon*), beakrush (*Rhynchospora tracyi*), and arrowheads (*Sagittaria* spp.). Floating mats of bladderworts (*Utricularia* spp.), sometimes covered by thick

periphyton, grew among the emergent plant stems. The soils at these sites varied with hydroperiod (Gleason et al. 1984). Organic peat soils occurred at the site with the longest hydroperiod (Site 6), while marls or calcium carbonate sediments predominated at the shorter hydroperiod sites (sites 23 and 50). Each study site included three 100m x 100m replicate plots (plots A, B, and C) that were separated by distances of approximately 1 km; the plots were not visible from each other because tall sawgrass-dominated ridges (*Cladium jamaicense*) separated the deeper prairies. There is typically a 10 to 25-cm difference in elevation between the wet-prairie slough and adjacent ridge habitats (personal observation). Two of the study sites (6 and 23) were visited regularly between 1977 and 1999, with sampling at the third (50) beginning in 1985. Only plot A at sites 6 and 23 was sampled between 1977 and 1985. The study was expanded to 3 plots per site, and to include site 50 in 1985 with fewer visits to each plot each year.

Fishes were collected monthly from January 1978 to August 1985 at plot A at sites 6 and 23. Beginning in October 1985, samples were taken five times per year at plots A, B, and C of sites 6, 23, and 50. The five sampling events were in February, April, July, October, and December; February and April within south Florida's dry season, July and October are in the wet season, and December is in a transition period. The number of samples taken per sampling event varied over the course of the study; from 1978 through 1984, the numbers varied from 5 to 21 based on an estimate of the inter-sample variance following Kushlan (1974). After 1984, 7 samples were taken at each sampling event. The location of each throw trap sample within a plot was determined by choice of X and Y coordinates within each plot from a random number table. Thus, each plot had approximately 10,000 possible sampling locations and the chances of re-sampling the same 1-m² area were minimal.

We collected fishes with a 1-m² throw trap following standard methods (Kushlan 1981; Chick et al. 1992; Jordan et al. 1997). Our trap was 0.8-m tall and had 2-mm mesh. When the trap was deployed, all fish were removed using a standardized netting protocol. A bar seine that spanned the width of the throw trap was passed through the trap until no fish were collected in three consecutive passes. After that time, two dip nets, one with 1-mm mesh and one with 5-mm mesh, were used to locate any remaining fish. Dipping was alternated between the two nets until five consecutive sweeps from each net were completed without collecting a fish. All fishes collected were euthanized by immersion in a concentrated solution of MS-222 following animal use guidelines (Anon., 1988), preserved in 10% formalin, and then returned to the laboratory. Before identification and measurement, fishes were transferred to 70% ethanol.

Hydrological information about each site was obtained from water-depth measurements taken simultaneously with each fish sample and were calibrated to a common water-surface plane with data from nearby continuous hydrological recording stations. The calibration, which generated R² values in excess of 0.90 in most cases, permitted us to make daily estimates of water depth at each plot. Those data were used to estimate the mean, minimum, and maximum water depths and the amplitude of fluctuation on a monthly timescale. With those data, we related descriptions of fish community to hydrological conditions at each plot at the time samples were collected, and at several past times, to test for time-lag effects.

The design of this study permits analysis of temporal patterns of fish communities. The dataset includes a hydrological alteration in the 8th year of sampling that we treated as an uncontrolled field experiment. In 1985, during Iteration 1 of the Experimental Water-Delivery Program, water managers changed the schedule for opening gate S-333 in the Tamiami Canal (Fig. 1), permitting more water to enter the Northeast region of Shark River Slough and altering

hydrology at Site 23 (Fig. 2). Beginning late in 1991 (Fig. 3), the entire study region experienced a series of years with high rainfall that increased water depths and decreased frequencies of drying at all three study sites (Fig. 2). After 1992, the marsh surface at both sites 6 and 23 did not dry while it dried once in 1995, at Site 50. Thus, comparisons of sites 6 and 23 before and after 1985, and Site 23 to sites 50 and 6 before and after 1992, permitted an additional test of the role of hydrology in shaping Everglades fish communities.

Statistical Methods

We analyzed hydrological data using backward stepwise multiple regression to identify the role of upstream flow and precipitation in determining water depth at our study sites. This permitted us to identify those fish community parameters most correlated with the hydro pattern experienced at each site, and the relative impact of management actions and climatic variation on hydro pattern. Precipitation records were obtained from the Tamiami Ranger Station (formerly Forty-Mile Bend; Fig. 1) because it was the closest rain gauge to our study sites that was continuously monitored between 1977 and 1999.

We used statistical techniques for the analysis of time series to identify re-current patterns and time lags in the hydrological and fish data. The length of a time series limits the ability of statistical techniques to detect a cycle to less than half the duration of the time series (Legendre and Legendre 1998), and as the length of the cycle approaches this limit, the power to detect it decreases because of diminishing sample size. We identify two types of events that may produce time lags or cycles in our data: seasonal environmental fluctuations in water depth that result from seasonal patterns of rainfall; and infrequent disturbances caused by dry-down events when the marsh surface is exposed and only fish that find infrequent aquatic refuges survive to

repopulate the habitat. The former patterns can be detected by time-series analysis of our data, while the latter occur too infrequently and irregularly to be examined with such methods. However, both types of time lags affect our ability to predict fish communities following hydrological manipulations. Time-series analysis is inappropriate with data displaying long-term trends. We used seasonal differencing to remove multi-year trends in the data by subtracting each value from the value n time units previous, where n is the number of time steps per year. We used cross-correlation analysis on the seasonally detrended data (Legendre and Legendre, 1998) to test for lag effects of four years or less in fish density and hydrological parameters. The effect of dry-down events was examined by analysis of fish density relative to the number of days since a dry-down event occurred. We also used partial autocorrelation analysis (Legendre and Legendre 1998) to test for temporal autocorrelation in water depth.

We analyzed fish density (sum of all species per unit area) and community composition separately to differentiate between patterns of abundance and community structure of fishes. The square root of fish density was analyzed to fulfill the assumptions of our analytical techniques. The distributions of all species-level data ($\#/m^2$) were highly non-normal with many zeros. We found that a negative binomial model was necessary to effectively estimate variances for hypothesis testing of these data (Power and Moster 1999). We will report those analyses elsewhere. In this paper, we have used non-parametric analyses where possible in analyzing species compositional data to avoid distribution-related artifacts in the results. Repeated-measures analysis of variance comparing monthly data, and time-series techniques, yielded little indication of temporal autocorrelation in either fish or hydrological data collected more than three months apart. This surprising result, reported in detail later, resulted from marked intra- and inter-year variation in the onset and severity of the annual wet-dry weather cycles, and was

probably exacerbated by temporal changes in the actions of water managers. Thus, repeated-measures analysis of variance was not needed in analyses of inter-annual variation.

We standardized fish density estimates to a 0 to 1 scale by converting them to relative abundance (number of specimens of each species divided by the number of all fish collected in a sample) to study the spatial and temporal dynamics of community composition. Previous analyses of Everglades fish data indicated that throw-trap samples are dominated by four to five species that are highly influential in ordination results. To create a more balanced view of the total fish community, we transformed the data by taking double square-roots of counts of each species from each sample (Clarke and Warwick 1994). Our analyses used this intermediate scaling of relative abundance instead of the extremes of untransformed numbers or presence-absence values. We calculated the Bray-Curtis dissimilarity index from the transformed data to create a matrix of pairwise comparisons of all samples for analyses of community change by a non-parametric analysis of variance (Clarke 1993). Permutation tests were used to determine the probability that any n groups of matrices differed by chance alone. Following Clarke (1993), we calculated a test statistic R and compared it to estimates derived from 1,000 random permutations of the original matrices. The test statistic is defined as:

$$R = \frac{(\bar{r}_B - \bar{r}_W)}{(n(n-1)/4)}$$

where r_W is the average of all rank similarities among replicates within a treatment (e.g., site or time period) and r_B is the average of rank similarities of all pairs of replicates between treatments. R ranges between 0 and 1, with 0 indicating that similarities within and among treatments are the same while 1 indicates that all replicates within treatments are more similar

than any replicates from different treatments. We followed this analysis with a breakdown of the dissimilarity matrices to determine which species were contributing most to differences observed (Clarke and Warwick 1994).

Separately, we used nonmetric multidimensional scaling (NMDS) to ordinate the Bray-Curtis dissimilarity indices (Kruskal 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 (Kruskal and Wish 1978). NMDS was chosen because it is robust to non-linearities in the patterns of density among species (Faith et al., 1987; Minchin, 1987; Legendre and Legendre 1998: 413).

We used analysis of variance (ANOVA) with type III sum of squares (Wilkinson 1997) to partition the variance attributable to selected hydrological variables. Our study sites were chosen to represent different hydrological conditions such that inter-site variation is confounded with hydrological variation. For example, average water depth was consistently different among the study sites so that analysis of the effects of water depth variation on fish density confounds local temporal variation from sources other than hydroperiod (e.g., demographic cycles, piscivore abundance, etc.) with inter-site variation. Also, our hydrological measures are inter-correlated (e.g., water depth in one month and depth in the previous month). The type III sum of squares identifies the variance uniquely attributable to each factor, i.e., those patterns in the dependent variable that can only be explained by that particular factor in the model. Thus, we must consider both the effects of particular factors in our model and the total variance explained

by the model. Inter-site and inter-year variation can be attributed to any number of factors beyond our control (Table 1). Arguably, hydrological variation is the preeminent factor in shaping communities of the Everglades not receiving anthropogenic nutrient enrichment, but descriptive data alone cannot prove this (James and McCulloch 1990). Analysis of the effects of the hydrological change at Site 23 after 1985 provided a supplemental test of hydrological effects that excludes non-hydrological interpretations because the role of human intervention was known.

RESULTS

Hydrological Patterns

Hydrological variation at the study sites was primarily the result of actions of water managers through manipulation of flow from the Tamiami Canal. Control structures S-12A, B, C, and D permit water to enter the Shark River Slough upstream of sites 6 and 50, while water enters Northeast Shark River Slough through a series of about 20 culverts (Fig 1). Average monthly water depths at Sites 6 and 50 could be predicted best by water flow through structures S-12C and S-12D, while regional rainfall yielded little indication of an influence (Multiple regression results, **Site 6**: Precipitation $t_{1,263} = 0.796$, $P = 0.427$; S-12A $t_{1,263} = -0.732$, $P = 0.465$; S-12B $t_{1,263} = -0.940$, $P = 0.348$; S-12C $t_{1,263} = 6.473$, $P < 0.001$; S-12D $t_{1,263} = 4.630$, $P < 0.001$; $R^2 = 0.525$; **Site 50**: Precipitation $t_{1,263} = -0.257$, $P = 0.797$; S-12A $t_{1,263} = 0.014$, $P = 0.989$; S-12B $t_{1,263} = -1.323$, $P = 0.187$; S-12C $t_{1,263} = 6.919$, $P < 0.001$; S-12D $t_{1,263} = 4.227$, $P < 0.001$; $R^2 = 0.559$). Average monthly water depth at Site 23 was influenced by regional rainfall, water flow through the NESS culverts, and also flow through structures S-12C and S-12D (Multiple regression results, **Site 23**: Precipitation $t_{1,262} = 2.620$, $P = 0.009$; S-12A $t_{1,262} = -0.455$, $P = 0.650$; S-12B $t_{1,262} = -0.944$, $P = 0.346$; S-12C $t_{1,262} = 5.092$, $P < 0.001$; S-12D $t_{1,262} = 3.562$, $P <$

0.001; NESS $t_{1,262} = 8.541$, $P < 0.001$; $R^2 = 0.546$). Though the amount of variance explained by these regressions is only moderate (R^2 between 0.5 and 0.6), these models could be improved by adding several months of time lags in water flow into the model (Fig. 4A). However, it appears that adding time lags to the rainfall data would have a much less beneficial effect (Fig. 4B). Rainfall affected water level at the study sites, but primarily through its influence on flows from the north. Low rainfall years (annual total $< 1\text{m}$) occurred in 1984 and 1989 (Fig. 3A), and water flow into the Park was low from all sources in 1989 and 1990 (Fig. 3B). Rainfall and water flow into the Park were relatively high (for this study period) from 1992 through 1999 (Fig. 3B). Water flow into Northeast Shark River Slough, relative to the sum of flows through the S-12 structures into Northwest Shark River Slough, increased after 1983 (Fig. 3B).

The three study sites differed in the average hydroperiod, frequency of drying of the marsh surface, mean water depth, and maximum water depth over the years between 1977 and 1999 (Table 1; Fig. 2a,b). Site 6 had the longest hydroperiod and dried the least, Site 50 had the shortest hydroperiod and dried the most frequently, and Site 23 had a hydroperiod intermediate between the two other study sites, with an intermediate frequency of drying. Monthly average water depths and annual minimum water depths were consistently greater at Site 6 than at Site 50. Site 23, in northeast Shark River Slough, was drier than Site 50 for much of the period between 1978 and 1984, and then was usually intermediate in both measures of water depth after 1984 (Fig 2A,B).

Annual cycles of water depth fluctuation were most consistent at Site 23 and least at Site 6. It was necessary to remove multi-year trends in the water-depth data to record patterns of autocorrelation (Fig. 5). Differencing by 12 months proved most successful in removing a trend of increasing depth seen after year 15 (1989) in all three series. After differencing, we observed

significant, but diminishing, partial autocorrelation of monthly mean water depth for up to three years at Site 23, up to two years at Site 50, and only one year at Site 6 (Fig. 6). This indicated that adjacent years tended to have similar patterns of water depth at all three sites, and that this similarity could extend for up to three years at Site 23.

There were three hydrological events during the 22-year study that affected the pattern of relative hydrology at the three study sites. In 1989 and 1999 there was a two-year drought when all three sites dried for over a month and the annual average water depth was near or below zero at sites 23 and 50 (Fig. 2A). Also, the four years preceding the onset of fish sampling (1974-1977) were relatively dry ones when compared to the next 20 years (Fig. 2A,B). The second important event began in 1985 when water management practices in the Tamiami Canal were changed, leading to more water entering the Northeast Shark River Slough and altered hydrological patterns at Site 23. The third important event was the unusually wet period in much of the 1990s (Fig. 3A). In the mid to late 1990s, water depths were typically higher than the preceding 20 years at all three study sites, and each experienced less frequent marsh-surface drying during this period (Fig. 2A,B). The pattern of relative water depths at our three study sites was not altered during these wet years, and Site 6 remained consistently deeper than sites 23 or 50; the annual means at sites 23 and 50 were well within one standard error of each other from 1994 to 1999 (Fig 2A). However, the minimum water depth at Site 23 converged on the minimum at Site 6 during this period, and was greater than at Site 50 from the late 1980s onward (Fig. 2B).

Fish Density

Seasonality - There was remarkably little consistency in the seasonal pattern of fish density over the 22-years of this study (Fig. 7). Repeated-measures analysis of variance comparing the five sampling months (February, April, July, October, and December), indicated that only October and December consistently differed in average fish density (Table 2). There were very few instances when high fish density was noted in the dry season, as water level receded. Possible exceptions were in 1985, 1989, 1990, 1992, and 1995 at Site 6, but never at sites 23 or 50. The more typical pattern was for fish density to be lowest during February and April, and then to increase to a maximum in October or December. This pattern was noted at Site 6 in 1986, 1991, 1993, 1996, and 1997, and at sites 23 and 50 in 1985, 1986, 1989 - 1993, 1996, and 1997. No seasonal pattern was observed at any sites in 1994, 1995, 1998, and 1999. Gaps in the data made it difficult to identify patterns in 1987 and 1988. Only limited statements can be made about seasonal patterns of density, such as that maximum fish density was usually observed in October in these marsh habitats, though comparable densities were possible in any month of the year. Dry years tended to create the "typical" pattern of low fish density following the dry season with an increase in summer months to a maximum late in the wet season in the winter. Also, this pattern was most typical at the sites with relatively shorter hydroperiods, sites 23 and 50. Little evidence of a marked concentration of fishes in the dry season was observed over the 22-year study at these marsh sites, with possible exception of Site 6 in 1988. Unfortunately, no data were collected from July through December that year because of budget cuts.

Inter-annual Patterns - Fish density was greatest at Site 6 and least at Site 50 throughout the study, while density at Site 23 fluctuated at intermediate levels relative to sites 6 and 50 (Fig.

8). Site 6 averaged 18.4 fish/m² for the study period, while Site 23 averaged 7.3 fish/m² and Site 50 averaged 2.4 fish/m² (Table 3). The drought years of 1989 and 1990 had a marked effect on fish density, especially at sites 6 and 23, and served to divide the study period into two intervals. The average density of fishes at Site 6 in 1988 was unusually high (Fig. 8) because of a very high density of fish in the February collection and missing data, so we excluded 1988 from these analyses. Overall, fish density did not differ before and after the drought years (treatment: 1985 – 1987 before drought, 1995 – 1999 after drought: $F_{1,24} = 0.476$, $P = 0.476$) but the variation among sites did change (treatment x site: $F_{2,48} = 5.21$, $P = 0.007$); density at Site 6 did not change before and after the drought (Site 6 before $\bar{x} = 20.8$ fish/m², after $\bar{x} = 20.1$ fish/m²) while both sites 23 and 50 increased (Site 23 before $\bar{x} = 3.2$ fish/m², after $\bar{x} = 11.5$ fish/m²; Site 50 before $\bar{x} = 2.0$ fish/m², after $\bar{x} = 4.2$ fish/m²). The relative increase over this time period was greatest at site 23 (259%) compared to site 50 (110%).

Correlations with Hydrology - Hydrological parameters had major effects on fish density at these study sites over the 22 years of study. Our statistical model explained over 77% of the total variance in fish density (analysis limited to plot A at all three sites to make replication comparable through time). Variation among sites uniquely explained 2.7% of the variance ($F_{2,226} = 13.14$, $P < 0.001$), among years explained 9.1% of the variance ($F_{19,226} = 4.71$, $P < 0.001$), and variation among years in the difference among sites explained an additional 7.9% (site x year interaction; $F_{35,226} = 2.22$, $P < 0.001$). Water depth in the preceding month was the only hydrological parameter to remain in the statistical model after the backwards stepping procedure and it uniquely explained only 0.5% of the total variance ($F_{1,226} = 4.63$, $P = 0.03$). In summary, over 60% of the variance explained by the statistical model could not be uniquely attributed to any one parameter considered.

There were significant correlations between fish density and water depth with various time lags at sites 23 and 50, but no significant correlations were noted at any time lag at Site 6 (Fig. 9). Seasonal detrending by differencing on a one-year time scale yielded the most interpretable correlations, and indicated that time lags of up to three months, but not six months, were present at both sites 23 and 50. This was validated when no significant time lags remained at either site after differencing by three months (Fig. 9, only illustrated for Site 23).

Community Composition

Seasonality - The clearest pattern of seasonality in fish relative abundance was observed at Site 6 where 3 axes were needed to describe the seasonal variation. Community composition varied among months (Permutation test: Global R = 0.09, P = 0.006). Three groups of months emerged as distinct, and April was different from all three of those groups (Fig. 10a). The three groups are December through March, May to June, and July through November. Generally, the permutation tests indicated $P < 0.05$ for comparisons of adjacent months within these groups, and $P > 0.05$ for comparisons among these groups; April was different from all other months in most comparisons (Table 4). This was supported by the repeated-measures analysis of variance of NMDS Axis 2, which differed between April and July samples for all sites (Table 2B). The seasonal patterns could best be explained as reflecting patterns of five taxa (Table 5). Lake chubsucker (*Erimyzon sucetta*) and spotted sunfish (*Lepomis punctatus*) relative abundance peaked in April, while flagfish (*Jordanella floridae*) peaked in April through June. Sailfin mollies (*Poecilia latipinna*) displayed low relative abundance in December through February. Finally, Everglades pygmy sunfish (*Elassoma evergladei*) displayed low relative abundance in April through November.

There was evidence for a seasonal pattern at Site 23 similar to that noted at site 6. Patterns of relative abundance in November through May plotted in one portion of the ordination graph, while those from June through September in another (Fig. 10B). January through May differed from June through September (Permutation test: $R = 0.152$, $P = 0.018$), but not from October through December (Permutation test: $R = 0.83$, $P = 0.059$). June through September did not differ from October through December (Permutation test: $R = 0.067$, $P = 0.084$). The difference between January to May and June through September resulted from a decrease in the relative abundances of bluefin killifish (*Lucania goodei*), least killifish (*Heterandria formosa*), and sailfin mollies, and an increase in marsh killifish (*Fundulus confluentus*) and flagfish. When individual months were compared in all possible combinations, February and March differed from the summer months of June and July, and May through July differed from January and February (Table 5, 6).

Inter-annual Patterns.- The drought years of 1989 and 90 displayed the greatest deviation in fish-community composition of all the years studied. The effects of the drought on fish community composition persisted for at least two years at Site 6, but less at Sites 23 (Fig. 11). Of the three study sites, these two dry years affected the fish community composition least at Site 50 (Fig. 11).

We divided the time sequence into four increments based on the drought years: pre-drought 1978 through 1988, drought years 1989 and 1990, drought-recovery years 1991 and 1992, and wet years 1993 through 1999. Permutation tests indicated that community composition differed between each successive time interval at Site 6 (Global permutation test, $R = 0.475$, $P < 0.001$; pre-drought vs. drought, $R = 0.699$, $P < 0.001$; drought vs. recovery, $R = 0.210$, $P = 0.034$; recovery vs. wet, $R = 0.587$, $P < 0.001$). Though composition converged back

to a similar mix in the pre-drought and wet intervals (Fig. 11A), they were not identical (Permutation test: pre-drought vs. wet, $R = 0.226$, $P < 0.001$). The relative abundance of eastern mosquitofish (*Gambusia holbrooki*) (30% of all fish) and flagfish (25%) were high in the drought years, while bluefin killifish (6%) and least killifish (9%) were relatively infrequent (Table 7). In the pre-drought years, mosquitofish (22%) and flagfish (5%) had been less abundant while bluefin killifish (20%) and least killifish (21%) were present at higher relative abundance. A decrease in the relative abundance of mosquitofish (24%) and flagfish (16%) and a relative increase in bluefin killifish (20%) and least killifish (13%) characterized the post-drought years compared to the drought years. Bluefin killifish had a higher relative abundance in the wet years (22%) than they did in the pre-drought years, while mosquitofish (19%) and least killifish (18%) had slightly lower relative abundances.

The drought years had a smaller and less persistent effect at Site 23 than at Site 6, and little effect at Site 50 (Fig. 11B, C). Species composition varied over the study period at Site 23 (Global permutation test: $R = 0.428$, $P < 0.001$). There, the pattern of relative abundance changed between the pre-drought and drought years (Permutation test: $R = 0.78$, $P < 0.001$) but not between drought and post-drought years (Permutation test: $R = 0.068$, $P = 0.232$). However, species composition in the post-drought and wet years did differ (Permutation test: $R = 0.859$, $P < 0.001$), and the pre-drought and wet years differed (Permutation test: $R = 0.137$, $P < 0.001$). At site 23, the relative abundances of bluefin killifish, least killifish, golden topminnow (*Fundulus chrysotus*), and mosquitofish decreased between the pre-drought and drought years, while flagfish, sailfin mollies, marsh killifish, and sheepshead minnows (*Cyprinodon variegatus*) increased (Table 7). In general, the pattern of species change was reversed between the post-drought and wet years at this study site. Notably, bluefin killifish and least killifish increased

substantially in the wet years at Site 23, and were more abundant at that time than in the pre-drought years. Species composition also changed at Site 50 (Permutation test: $R = 0.330$, $P = 0.001$), but there were no significant changes in the fish community between the pre-drought and drought years (Permutation test: $R = 0.249$, $P = 0.122$) or the drought and post-drought years (Permutation test: $R = -0.086$, $P = 0.643$). Species composition did change between the post-drought and wet years (Permutation test: $R = 0.480$, $P = 0.003$). Also, the pre-drought and wet years had different species composition at Site 50 (Permutation test: $R = 0.200$, $P = 0.042$). Bluefin killifish, least killifish, sheepshead minnows, golden topminnows, and mosquitofish all increased in relative abundance in the wet years, while marsh killifish and flagfish decreased in relative abundance (Table 7).

NMDS ordination revealed two patterns in community composition at the three study sites that explained approximately 86% of the total variation in relative abundance (axis 1: 33%; axis 2: 53%). The first axis did not differ among study sites (Fig. 12A; $F_{2,205} = 0.084$, $P = 0.920$), while the second axis did (Fig 12B; Site: $F_{2,205} = 3.714$, $P = 0.026$; Site x Year: $F_{35,205} = 1.848$, $P = 0.005$). The first axis was positively correlated with the relative abundance of mosquitofish ($r = 0.295$) and negatively correlated with the relative abundance of bluefin killifish ($r = -0.255$) and sheepshead minnows ($r = -0.220$) (Fig. 11A). This axis increased in value during 1989 and was lowest in the wet year of 1994. Axis 2 differed among sites and years and was positively correlated with bluefin killifish ($r = 0.627$), least killifish ($r = 0.406$), golden topminnows ($r = 0.328$), sailfin mollies ($r = 0.270$), and spotted sunfish ($r = 0.364$), but negatively correlated with marsh killifish ($r = -0.342$), flagfish ($r = -0.289$), and sheepshead minnows ($r = -0.197$) (Fig. 11B). Site 23 was generally intermediate in value for this axis,

though it converged on Site 50 during the drought years before shifting to similar values as Site 6 in the wet years.

Correlations with Hydrology.- We used NMDS to analyze species composition separately at each study and test for correlations with hydrological parameters. Two axes were adequate to describe the fish community at Site 6 from 1978 to 1999. In a multiple analysis of variance, both axes were significantly correlated with days since the last dry-down event (Fig. 13; Wilks' $\lambda = 0.609$, $P < 0.001$, full model axis 1 $R^2 = 0.256$ and axis 2 $R^2 = 0.634$). There was a significant non-linear component to the relationship of axis 2 with days since dry-down that explained 7.5% of the variance in that variable, but not axis 1 (axis 1: $F_{1,97} = 0.552$, $P = 0.456$; axis 2: $F_{1,97} = 21.090$, $P < 0.001$). Minimum water depth one month before sampling explained an additional 5% of variance in axis 1 ($F_{1,98} = 6.125$, $P = 0.015$) and 15.4% in axis 2 ($F_{1,98} = 19.041$, $P < 0.001$), while amplitude of water depth fluctuation in the month before sampling explained less than an additional 1% of variance in axis 2 ($F_{1,96} = 3.820$, $P = 0.054$). Axis 1 was negatively correlated with marsh killifish, flagfish and mosquitofish, while axis 2 was positively correlated with mosquitofish, marsh killifish, flagfish, and spotted sunfish but negatively correlated with sailfin mollies, least killifish, and bluefin killifish. Plots of the density of selected species versus days since the last dry-down illustrate the origins of these results. There is a significant negative slope to this regression for flagfish, but positive slopes for least killifish, bluefin killifish, and golden topminnows, and little slope for mosquitofish (Fig. 14). Sailfin mollies, flagfish, and bluefin killifish displayed significant non-linear components to this relationship.

Similar patterns of compositional change were noted at sites 23 and 50 to that observed at Site 6. At Site 23, two axes were produced from NMDS that were correlated to days since the

last dry-down event (Fig. 15; Wilks' $\lambda = 0.629$, $P < 0.001$, full model axis 1 $R^2 = 0.316$ and axis 2 $R^2 = 0.328$). There were significant non-linear aspects to the relationship with days since last dry-down for both axes (axis 1: $F_{1,76} = 16.971$, $P < 0.001$; axis 2: $F_{1,76} = 6.263$, $P = 0.014$). Axis 1 was negatively correlated with marsh killifish and flagfish relative abundance, while axis 2 was positively correlated with mosquitofish, sailfin molly, least killifish, bluefin killifish, and golden topminnow relative abundance. At site 50, NMDS produced only one axis that was significantly related to any hydrological parameter (Fig. 16). That axis was correlated with the minimum water depth in the month prior to sampling ($F_{1,48} = 11.175$, $P = 0.002$, $R^2 = 0.210$). There was a significant non-linear component to this relationship as well ($F_{1,48} = 6.529$, $P = 0.014$). This axis was negatively correlated to mosquitofish ($r = -0.391$), least killifish ($r = -0.399$), and bluefin killifish ($r = -0.305$) relative abundance, though none of the correlations were significant at the $P = 0.05$ critical level.

DISCUSSION

This time-series study demonstrated that the fish community in the Shark River Slough was strongly influenced by hydrological variation and was highly resilient to hydrological disturbances such as the drought of 1989 and 1990. The management alteration at Site 23, coupled with the wet years in the last third of the study provided a "natural experiment" (Diamond 1986) that demonstrated the ability of this community to respond to a purely hydrological change in a predictable manner. The density of fishes and community composition at Site 23 converged on those at Site 6 when the hydroperiod of NESS was manipulated to become longer, like that at Site 6. The driest study site, Site 50, displayed similar change in the wet years, though less marked than at Site 23. Further, this study revealed a multi-year time lag

in the response of the fish community to hydrological events that resulted from inter-specific variation in the time of population response to hydrological changes. Natural cycles of dry and wet years that affected all three sites explained the majority of variation in these fish communities, though relatively dry years had their most persistent effect on the wettest of the three sites, Site 6. The results suggested that fish community responses to longer hydroperiod and deeper water were slower to accumulate than the dramatic and persistent effect of marsh drying. These results have important implications for both understanding and predicting fish community dynamics in this ecosystem and for planning and anticipating the effects of management activities in freshwater marshes of the Everglades.

Control of Hydrology at the Study Sites

The environmental factors controlling water depth at our three study sites differed between the northwestern and northeastern sections of Shark River Slough. Water depth at sites 6 and 50 was correlated with flow from water delivery structures S-12C and S-12D. While it would be desirable to have precipitation data from gauges closer to the sites, we found no evidence that such information would alter our finding that precipitation affected these sites largely or solely through its influence on management of flow through the water control structures. Northeast Shark River Slough differed in this regard, where our measure of regional rainfall did improve our regression model of water-depth fluctuation. That analysis also indicated management actions that changed flows through the culverts upstream of Site 23 affected water fluctuations there. The additional influence of water deliveries from S-12C and S-12D must have been through groundwater or from back-flow around the L-67E levee. The combined flow through the S-12 structures greatly exceeded the combined flow through the

culverts for most of the study, with the possible exception of 1985 through 1987. Flow into Northeast Shark River Slough was increased after 1984 as a result of the Experimental Water Delivery Program, and its primary effect in our data was manifested as increasing the minimum water depths at Site 23.

Community Dynamics

Our data indicated that the Everglades fish community is both resilient and sensitive to hydrological variation. Community composition at the relatively short-hydroperiod sites converged toward that of the long-hydroperiod site during periods of wet years. A hydrological manipulation created a similar effect. The drought years changed fish community composition quickly and dramatically for obvious reasons of habitat loss, predation, and desiccation (Kushlan 1976, 1980). More interesting patterns included the small effect of the drought on mosquitofish, the short-lived increase in flagfish and marsh killifish that followed, and the relatively slow recovery of bluefin killifish and least killifish. Presumably, this resulted from inter-specific variation in survival through the drought in local aquatic refuges, long-distance dispersal ability from distant refuges, and population growth rate in the post-drought environment.

Mosquitofish are well known for their dispersal and colonization ability (Brown 1985, 1987; Congdon 1994; Snodgrass et al. 1996), so their rapid recovery following the drought may be not particularly surprising. However, the short-lived increase in flagfish in the post-dry-down environment seen in our analyses confirmed a similar pattern reported by Loftus and Eklund (1994). It is not clear whether flagfish decrease in abundance as the time since dry-down increases because environmental conditions become less suitable or because other fishes, perhaps piscivores, become more abundant. The marsh killifish also briefly increased in relative

abundance following the dry-down at Site 6. The eggs of that species have been shown to tolerate desiccation in other south Florida habitats (Harrington 1959), which may explain their quick reappearance at our study sites. Unlike flagfish, its absolute density did not decline as time following the drought increased. They simply never reached high densities at any study sites, and their relative abundance declined as the rest of the community increased at site 6.

These data provide strong support for the thought that marsh drying events regulate fish population density and community composition in Everglades marshes when they recur at frequencies of less than three years, or when the most recent dry-down is less than three years in the past (Kushlan 1976; Loftus and Eklund 1994). In the latter case, a fish community in a long-hydroperiod marsh is in a recovery or successional stage for at least three years following the infrequent but inevitable dry-down events that characterize the central sloughs. Our analyses provided indirect evidence that the role of biotic interactions become more critical in regulating community composition when the last dry-down event was more than two or three years in the past. A potentially surprising result of our analyses was the relative absence of concentrations of fish density during the dry season. We believe that this has two origins: first, if concentrations occur in this ecosystem, they are very ephemeral and may be missed by a sampling routine not aggressively targeted to observe them (they also occur when access to the marsh is most difficult); secondly, fish concentrations in the Everglades are of smaller magnitude and possibly more localized than in tropical river-floodplain ecosystems (Turner et al. 1999; Trexler et al., in press). In the natural Everglades habitats, dry-season fish concentrations are most evident in alligator ponds (Kushlan 1979) not sampled by this study.

Management Implications

Our findings provide direct evidence that water-management actions that manipulate water delivery can have relatively quick and predictable effects on aquatic communities in Everglades marsh habitats. The goal of the Experimental Water Delivery Program was to increase the hydroperiod of NESS because soil data (Gleason and Stone 1994), simulation models (Fennema et al. 1994), and historical accounts (Loftus et al. 1990; e.g., Willoughby 1898) indicated that this region was historically a long-hydroperiod community. Our data indicate that restoration of relatively long-hydroperiod conditions in NESS was begun successfully by the water delivery schedule initiated in 1984 that led to less frequent dry-downs in the vicinity of Site 23. Also, our data indicate that the average water depth at this site was not much affected by the change, so any modifications of the aquatic community were the result of less frequent marsh dry downs (we treat any marsh water depth below 5 cm as dry from the perspective of fishes).

Other lessons from this analysis include the benefit of multiple study sites with long-term data collection for use as reference sites in analysis of management activities. Interpretation of the "natural experiment" presented by the change in water delivery in 1984 depended on the availability of shorter and longer hydroperiod sites in areas unaffected by the alteration. The historical and ongoing data collection at these sites render this study a tremendous resource for assessment of management in Shark River Slough, and interpretation of data from studies of shorter length in other areas of the Everglades.

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Table 1. Description of the study sites. Values in parentheses are standard errors. * All hydroperiod data are for the period 1977-1999 at plot A. Water depth averages include negative numbers for depth below ground surface. ** Soil samples are means from the three study plots and standard errors reflect inter-plot heterogeneity. *** Data reprinted from Busch et al. (1998).

Description	Site 6	Site 23	Site 50	
Latitude (N)	25° 38.22'	25° 41.25'	25° 41.46'	
Longitude (W)	80° 44.05'	80° 37.06'	80° 45.58'	
Hydroperiod (days)*	358	322	259	
Frequency of dry-down*	4/23	10/23	16/23	
Mean water depth (cm)*	46.9 (1.2)	26.8 (1.3)	17.4 (1.8)	
Max water depth (cm)*	98.9	68.8	90.4	
Soil total phosphorus ($\mu\text{g/g}$)**	385.6 (86.6)	128.0 (42.9)	207.8 (21.8)	
Soil total nitrogen (%)**	3.2 (0.2)	0.5 (0.2)	0.9 (0.1)	
Soil organic carbon (%)**	41.5 (2.9)	16.1 (1.5)	15.9 (0.7)	
Plant Cover (species, common name, stems/m ² unless otherwise noted)***				
<i>Eleocharis cellulosa</i>	spikerush	137.9	55.9	46.1
<i>Rhynchospora tracyi</i>	Tracy's beakerush	14.4	37.2	44.5
<i>Cladium jamaicense</i>	sawgrass	2.9	3.8	15.8
<i>Panicum hemitomon</i>	maidencane	12.9	2.5	5.8
<i>Utricularia</i> spp. (% cover)	bladderwort	24.9	18.1	19.1
Float mat volume (ml/m ²)	1,689	3,415	2,555	

Table 2. Results from repeated measures analysis of variance of monthly data taken at 3 study sites in the Everglades National Park. Years within sites are replicates. This analysis permits no missing data, so cells were estimated in cases where only one month was missing from a year. When two or more months were not sampled in a year, that year was omitted. Contrasts were used to compare means from adjacent months. A. Analysis of fish density. Superscripts indicate means that differ: ^a $F_{3,47} = 4.118$, $P = 0.011$. B. Analysis of NMDS Axis 2. There is no relative abundance when density = 0, so there were more missing cells in this analysis than for density. Identical superscripts indicate means that differ: ^a $F_{6,34} = 2.183$, $P = 0.069$; ^b $F_{6,34} = 2.517$, $P = 0.040$.

A. Fish Density

<i>Between Subjects</i>	df	F	P
Site	2,44	4.275	0.020
Average Water Depth	1,44	9.778	0.003
Site x Water Depth	2,44	1.640	0.206
<i>Within Subjects</i>			
Time	4,176	3.273	0.013
Time x Site	8,176	2.073	0.041
Time x Water Depth	4,176	3.072	0.018
Time x Water Depth x Site	8,176	2.105	0.038

	February	April	July	October	December
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Fish Density (#/m ²)	9.02	8.95	11.202	12.09 ^a	10.01 ^a
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B. NMDS Axis 2

<i>Between Subjects</i>	df	F	P
Site	2,34	0.121	0.836
Average Water Depth	1,34	24.381	<0.001
Site x Water Depth	2,34	0.801	0.457
<i>Within Subjects</i>			
Time	4,136	3.735	0.006
Time x Site	8,136	0.386	0.927
Time x Water Depth	4,136	2.502	0.045
Time x Water Depth x Site	8,136	0.417	0.909

	February	April	July	October	December
NMDS score Axis 2	0.292	0.255 ^a	-0.006 ^{a, b}	0.147 ^b	0.183

Table 3. Summary of fishes collected at the three study sites. Data reported from site 6 were obtained from 2,461 throw-trap samples, from site 23 were from 2,051 samples, and from site 50 were from 1,435 samples. Sites 6 and 23 were sampled from 1978 through 1999, while site 50 was sampled from 1985 through 1999. Sum indicates the total number of specimens of each species collected during the study period, max is the maximum number collected in a single m² sample, and mean is the average number per m² for the study period.

Species	common name	Site 6			Site 23			Site 50		
		sum	max	mean	sum	max	mean	sum	max	mean
<i>Lepisosteus platyrhincus</i>	Florida gar	2	1	<0.01	1	1	<0.01	2	1	<0.01
<i>Amia calva</i>	bowfin	1	1	<0.01						
<i>Notemigonus crysoleucas</i>	golden shiner	2	1	<0.01						
<i>Notropis maculatus</i>	tailight shiner	3	1	<0.01	2	1	<0.01			
<i>Notropis petersoni</i>	coastal shiner	24	8	0.01	2	1	<0.01	3	3	<0.01
<i>Erimyzon sucetta</i>	lake chubsucker	81	4	0.03	7	2	<0.01			
<i>Ameiurus natalis</i>	yellow bullhead	13	1	<0.01	3	2	<0.01	10	1	<0.01
<i>Noturus gyrinus</i>	tadpole madtom	15	2	<0.01	3	1	<0.01	16	1	0.01
<i>Cyprinodon variegatus</i>	sheepshead minnow	76	11	0.03	143	6	0.07	225	9	0.16
<i>Fundulus chrysotus</i>	golden topminnow	3,199	16	1.30	991	6	0.48	376	7	0.26

<i>Fundulus confluentus</i>	marsh killifish	120	4	0.05	229	5	0.11	246	4	0.17
<i>Fundulus seminolis</i>	Seminole killifish				2	1	<0.01			
<i>Jordanella floridae</i>	flagfish	2,348	141	0.95	1,182	15	0.58	469	10	0.33
<i>Lucania goodei</i>	bluefin killifish	11,341	28	4.61	3,582	15	1.75	1,190	21	0.83
<i>Belonesox belizanus</i>	pike killifish	11	2	<0.01	3	1	<0.01	3	1	<0.01
<i>Gambusia holbrooki</i>	eastern mosquitofish	13,059	109	5.31	4,564	44	2.23	2,052	112	1.43
<i>Heterandria formosa</i>	least killifish	11,373	83	4.62	2,959	35	1.44	413	18	0.29
<i>Poecilia latipinna</i>	sailfin molly	2,632	81	1.07	923	21	0.45	381	24	0.27
<i>Labidesthes sicculus</i>	brook silverside	11	6	<0.01				4	4	<0.01
<i>Elassoma evergladei</i>	Everglades pygmy sunfish	165	8	0.07	53	3	0.03	4	1	<0.01
<i>Emmeacanthus gloriosus</i>	bluespotted sunfish	16	1	0.01	40	3	0.02	2	2	<0.01
<i>Chaenobrytus gulosus</i>	warmouth	11	1	<0.01	22	2	0.01	1	1	<0.01
<i>Lepomis macrochirus</i>	bluegill	5	1	<0.01	2	1	<0.01			
<i>Lepomis marginatus</i>	dollar sunfish	83	4	0.03	68	3	0.03	4	1	<0.01
<i>Lepomis microlophus</i>	redear sunfish	15	2	<0.01	11	1	<0.01	5	1	<0.01
<i>Lepomis punctatus</i>	spotted sunfish	474	7	0.19	179	5	0.09	41	3	0.03
<i>Lepomis spp</i>	unidentified sunfish	39	3	0.02	13	2	<0.01	8	1	<0.01
<i>Micropterus salmoides</i>	largemouth bass	1	1	<0.01	3	1	<0.01	5	1	<0.01
<i>Etheostoma fusiforme</i>	swamp darter							1	1	<0.01

<i>Astronotus ocellatus</i>	oscar	2	3	<0.01															
<i>Cichlasoma bimaculatum</i>	black acara				2	1	<0.01												
<i>Cichlasoma urophthalmus</i>	Mayan cichlid	12	3	<0.01	45	7	0.02	40	2	0.03									
<i>Tilapia mariae</i>	spotted tilapia	1	1	<0.01	1	1	<0.01	1	1	<0.01									
Unidentified fish		55	20	0.02	11	1	<0.01	22	5	0.02									
Total fish		45,191	292	18.36	15,046	70	7.34	3,472	50	2.42									

Table 4. Seasonal variation in relative abundance of fishes at site 6A from 1978 through 1984.

Each row displays the result of pairwise comparisons of the month indicated on that row versus the month indicated at the top of each column. Horizontal lines connect months not different at $P < 0.05$ as determined by permutation tests, while dotted lines indicate months not different with $P < 0.10$. The down pointing arrows indicate the month being compared. Arrowheads at the ends of rows indicate that neither December nor January is different from the month being compared in that row.

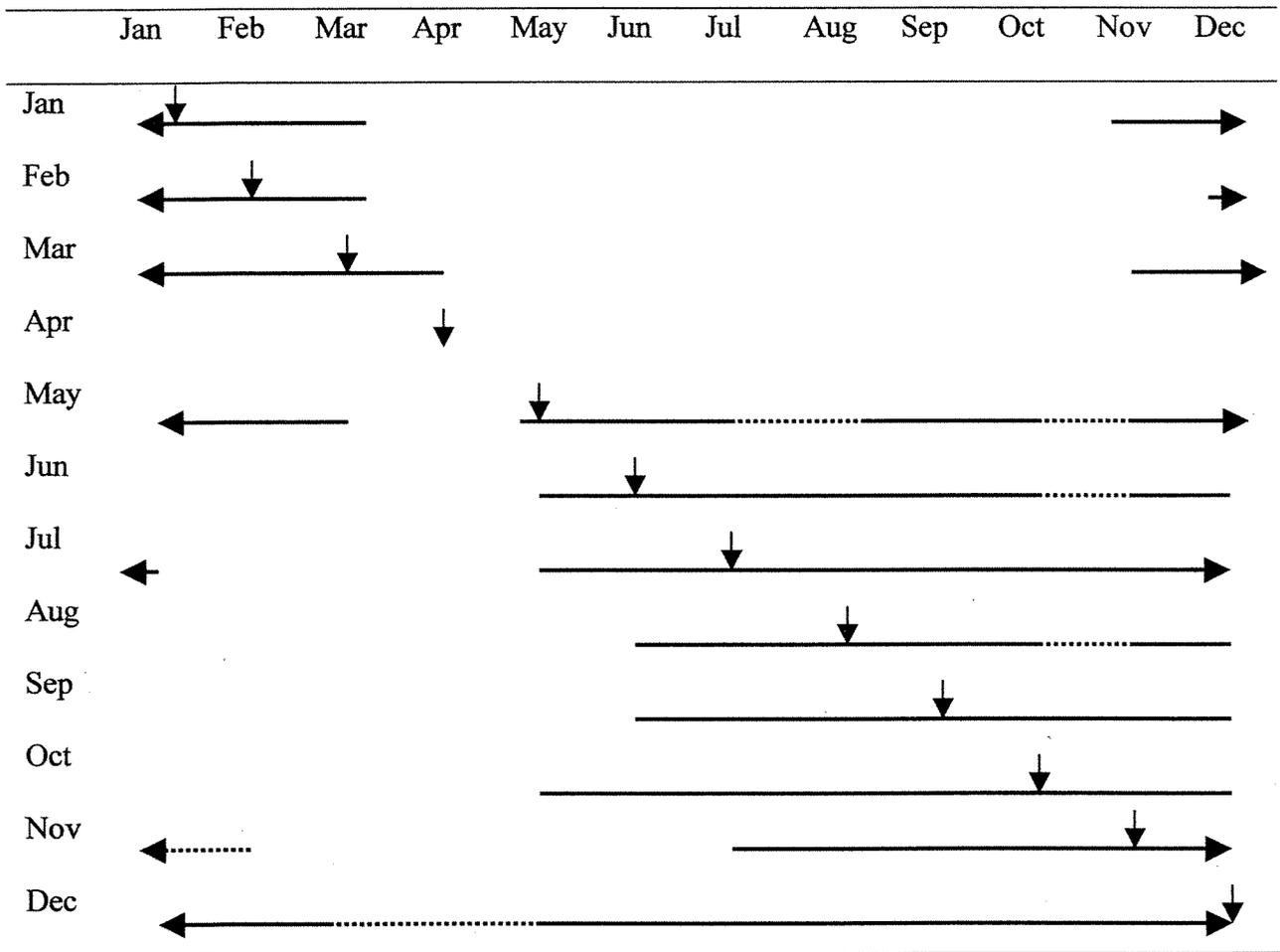


Table 5. Breakdown of similarity matrices for analysis of seasonal patterns in species composition. Data were collected monthly between 1978 and 1984. Average Density indicates the average #/m² of each species during the specified months, and contribution indicates the % of the total dissimilarity contributed by each species. Only species contributing > 10% are listed.

Species	Average Density 2	Average Density 1	Contribution (%)
Site 6			
<i>Dec to March (1) vs April (2)</i>			
flagfish	0.39	0.21	13.95
lake chubsucker	0.19	0.01	13.73
Ev. pygmy sunfish	0.04	0.13	12.04
spotted sunfish	0.46	0.13	11.94
<i>April (2) vs May to June (2)</i>			
flagfish	0.26	0.39	14.43
spotted sunfish	0.15	0.46	14.01
lake chubsucker	0.06	0.19	12.87
Ev. pygmy sunfish	0.19	0.04	12.41
<i>May to June (1) vs July to November (2)</i>			
flagfish	0.17	0.26	15.57
Ev. Pygmy sunfish	0.06	0.19	13.48
spotted sunfish	0.10	0.15	12.72

Species	Average Density 2	Average Density 1	Contribution (%)
Site 23			
<i>January to May (1) vs June to September (2)</i>			
bluefin killifish	1.19	2.30	11.35
least killifish	0.86	1.92	11.31
sailfin molly	0.15	0.72	10.90
marsh killifish	0.21	0.03	10.25
<i>June to September (1) vs October to December (2)</i>			
bluefin killifish	1.50	1.19	11.54
least killifish	0.85	0.86	10.34
flagfish	0.45	0.71	10.25

Table 6. Seasonal variation in relative abundance of fishes at site 23A from 1978 through 1984.

Each row displays the result of pairwise comparisons of the month indicated on that row versus the month indicated at the top of each column. Horizontal lines connect months not different at $P < 0.05$ as determined by permutation tests, while dotted lines indicate months not different with $P < 0.10$. The down pointing arrows indicate the month being compared. Arrowheads at the ends of rows indicate that neither December nor January is different from the month being compared in that row.

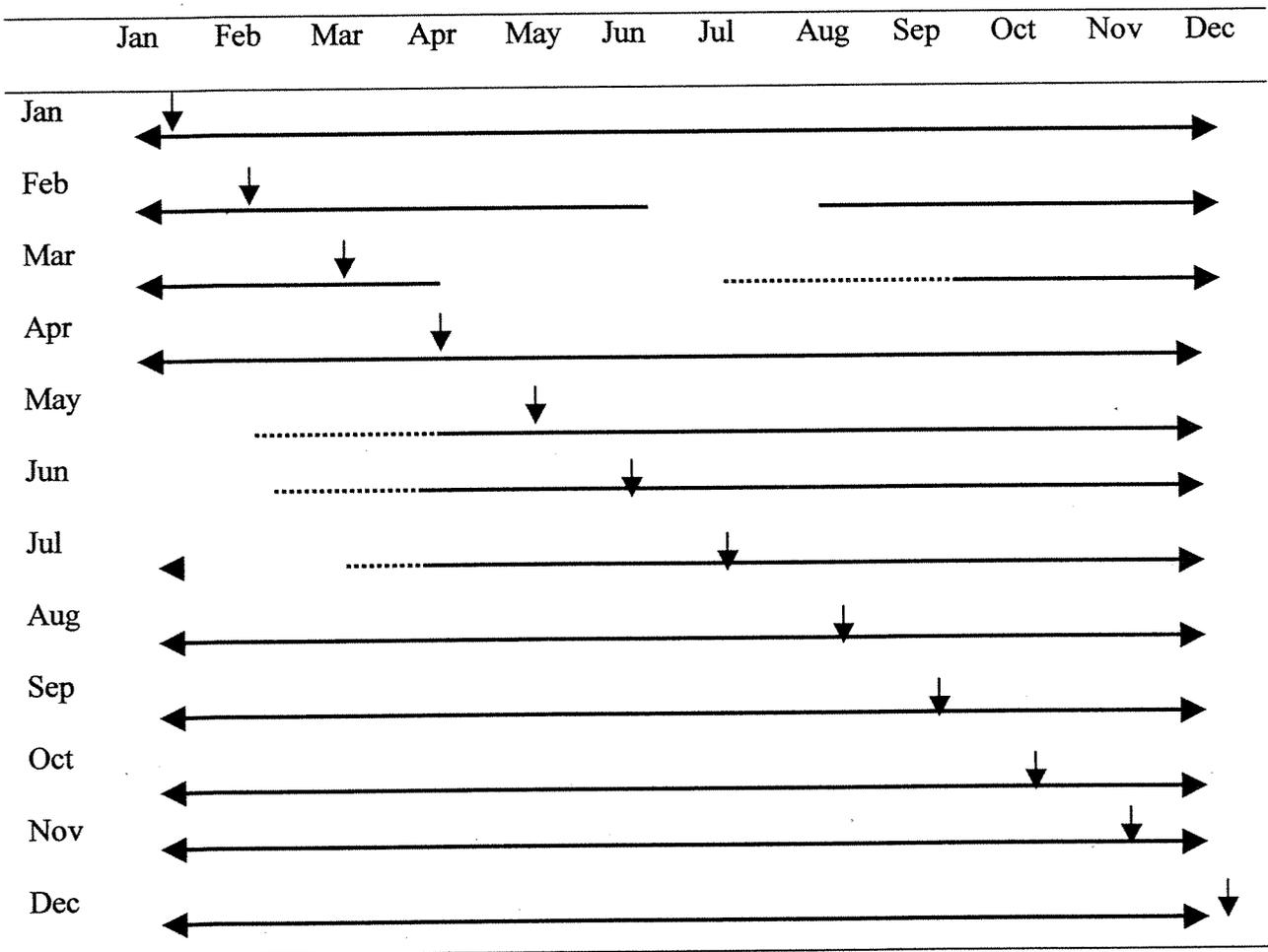


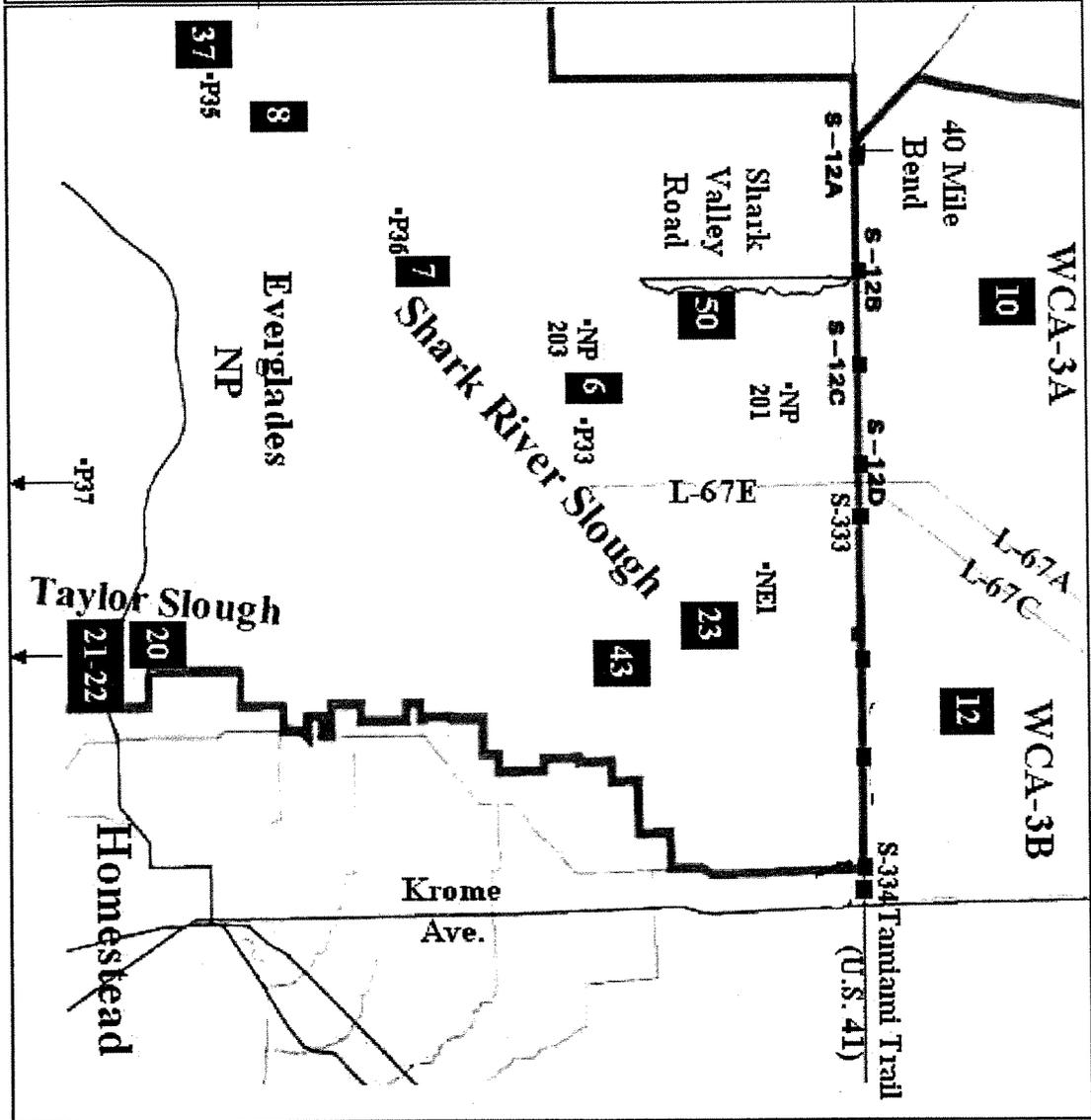
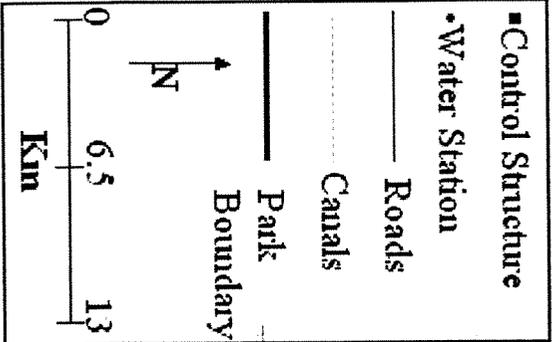
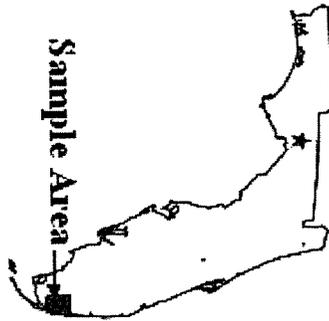
Table 7. Breakdown of similarity matrices for analysis of annual patterns in species composition. Data were collected 5 times annually between 1978 and 1999. Average Density indicates the average #/m² of each species during the specified months, and contribution indicates the % of the total dissimilarity contributed by each species. Only species contributing > 10% are listed.

Species	Average Density 2	Average Density 1	Contribution (%)
Site 6			
<i>1978-1988 (1) vs 1989 - 1990 (2)</i>			
flagfish	4.17	1.04	17.27
bluefin killifish	0.82	4.83	16.20
least killifish	1.84	6.07	13.95
<i>1989-1990 (1) vs 1991 - 1993 (2)</i>			
bluefin killifish	3.65	0.82	10.05
spotted sunfish	0.38	0.02	10.00
<i>1991-1993 (1) vs 1994 - 1999 (2)</i>			
sailfin mollies	1.47	0.12	11.82
Site 23			
<i>1978-1988 (1) vs 1989 - 1990 (2)</i>			
bluefin killifish	0.00	1.78	16.66
least killifish	0.06	1.33	13.76
flagfish	2.51	0.70	11.74
mosquitofish	0.80	2.49	11.05
golden topminnow	0.17	0.63	10.66

Species	Average Density 2	Average Density 1	Contribution (%)
Site 23 continued			
<i>1989-1990 (1) vs 1991 - 1993(2)</i>			
mosquitofish	1.21	0.80	15.16
flagfish	0.75	2.51	14.28
marsh killifish	0.23	0.17	10.32
<i>1991-1993 (1) vs 1994 - 1999 (2)</i>			
bluefin killifish	3.27	0.07	15.63
least killifish	2.70	0.02	12.70
flagfish	0.28	0.75	10.70
golden topminnow	0.71	0.18	10.26
Site 50			
<i>1978-1988 (1) vs 1989 - 1990 (2)</i>			
least killifish	0.00	0.40	18.94
flagfish	0.43	0.79	16.84
marsh killifish	0.29	0.30	16.43
golden topminnow	0.00	0.27	13.87
mosquitofish	0.29	0.94	11.40
<i>1989-1990 (1) vs 1991 - 1993 (2)</i>			
mosquitofish	0.48	0.29	18.51
flagfish	0.76	0.43	16.49
marsh killifish	0.36	0.29	16.11
sheepshead minnow	0.17	0.05	13.62

Species	Average Density 2	Average Density 1	Contribution (%)
Site 50 continued			
<i>1989-1990 (1) vs 1991 - 1993 (2) continued</i>			
pike killifish	0.02	0.00	11.05
<i>1991-1993 (1) vs 1994 - 1999 (2)</i>			
bluefin killifish	1.64	0.02	16.59
flagfish	0.38	0.76	11.24
mosquitofish	2.22	0.48	10.11

Figure 1. Map of the study sites in the Shark River Slough. Study sites are indicated by numbers in black squares. Sites 6, 23 and 50 were the focus of this study. Three plots, not shown, separated by approximately 1-km of marsh habitat were present at each study site.



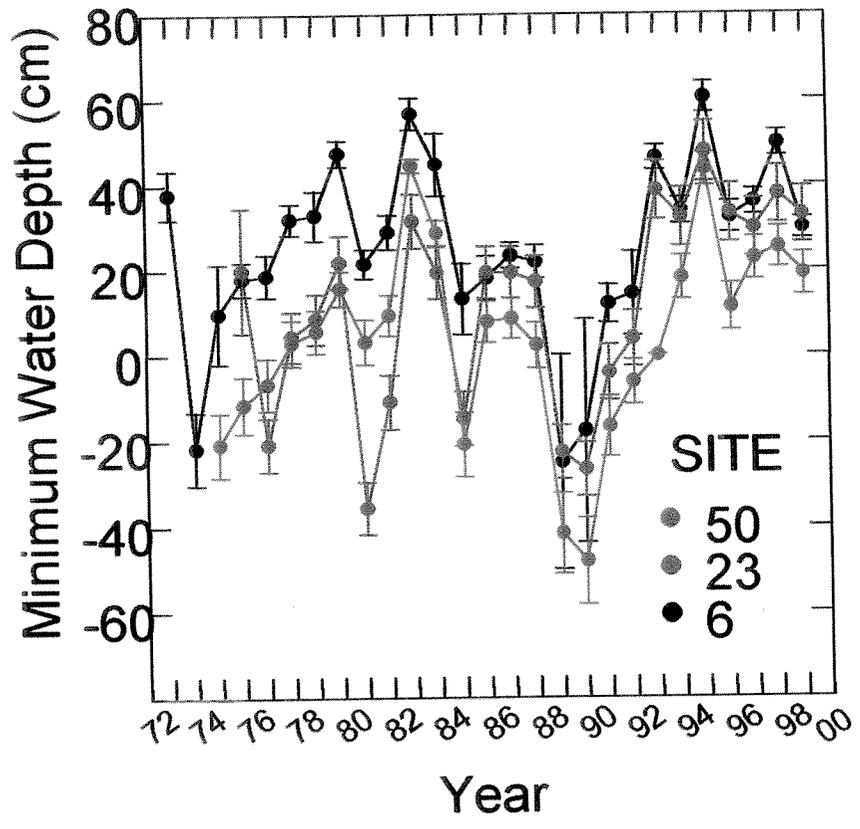
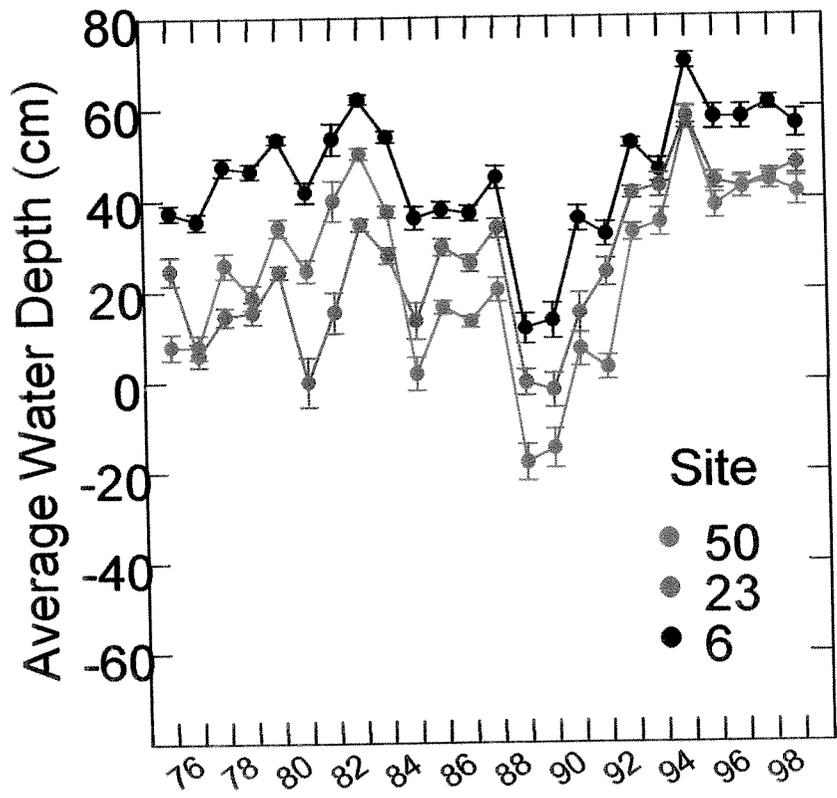


Fig. 3. Regional patterns of precipitation and water flow into the study areas between 1977 and 1999. A. Annual rainfall (summation of daily values) collected at the Tamiami Ranger Station (aka, Forty-Mile Bend) gauging station. This was the closest rain gauge to the study continuously monitored through the study period. B. Average flow of water into Everglades National Park through selected water structures. These sites were chosen because of their influence on the study sites; structures S-12A and S-12B were not plotted to limit the clutter on this graph.

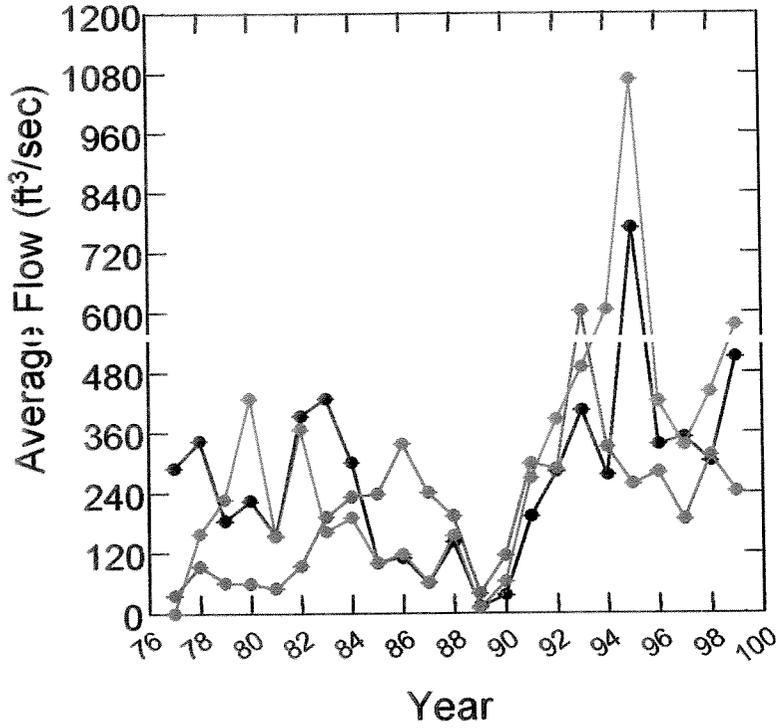
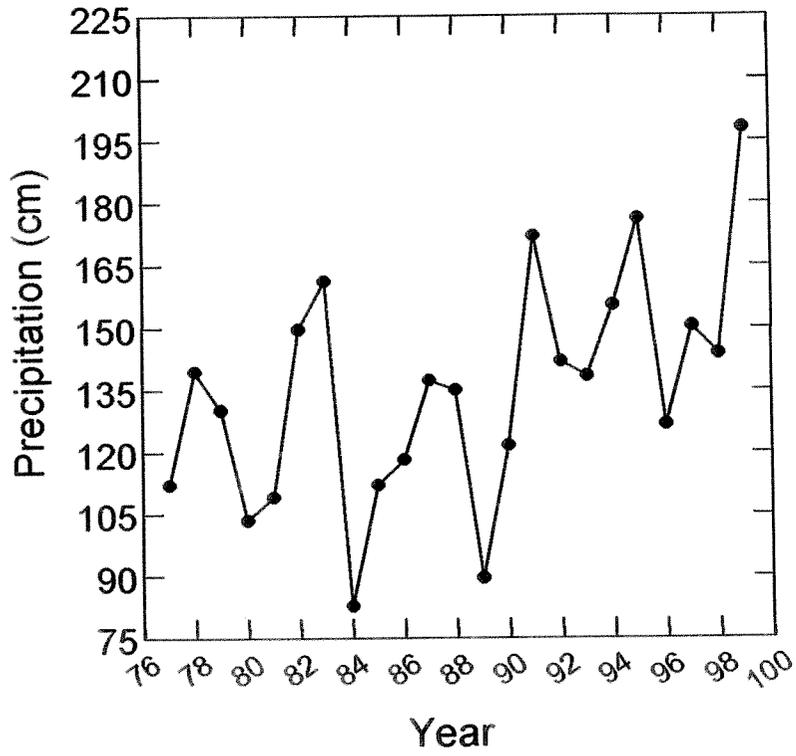
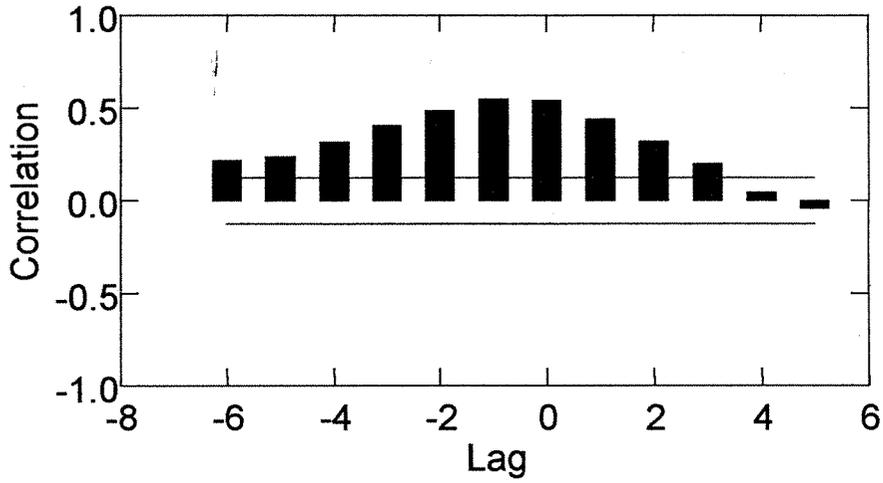


Fig. 4. Cross-correlation plots of monthly average water depth at site 6 versus hydrological parameters. Lags are indicated on a monthly scale. Correlations must exceed the horizontal bars to be different from zero. A. Average water depth versus flow through the S-12C structure. Similar results were observed at S-12D. B. Average water depth versus monthly precipitation at the Forty Mile Bend station.

Cross Correlation Plots
Both variables with 12-month detrending

Ave water depth site 6 vs S-12C flow



Ave water depth at site 6 vs FMB rainfall

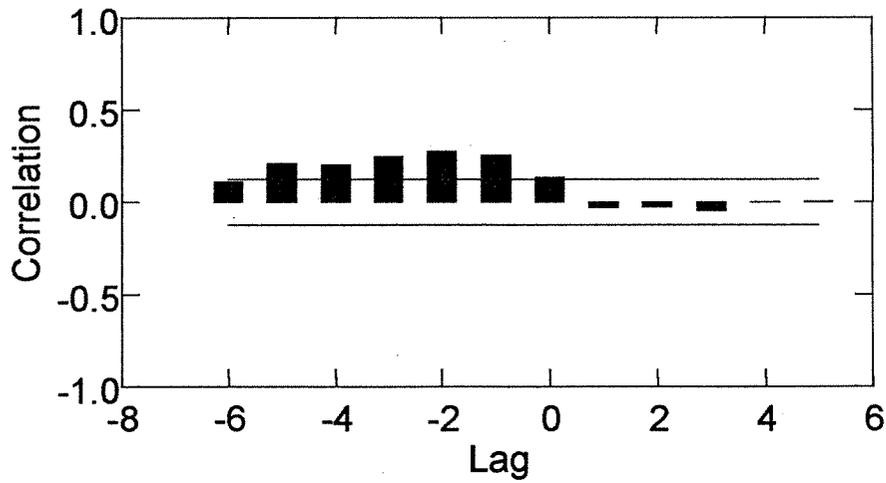
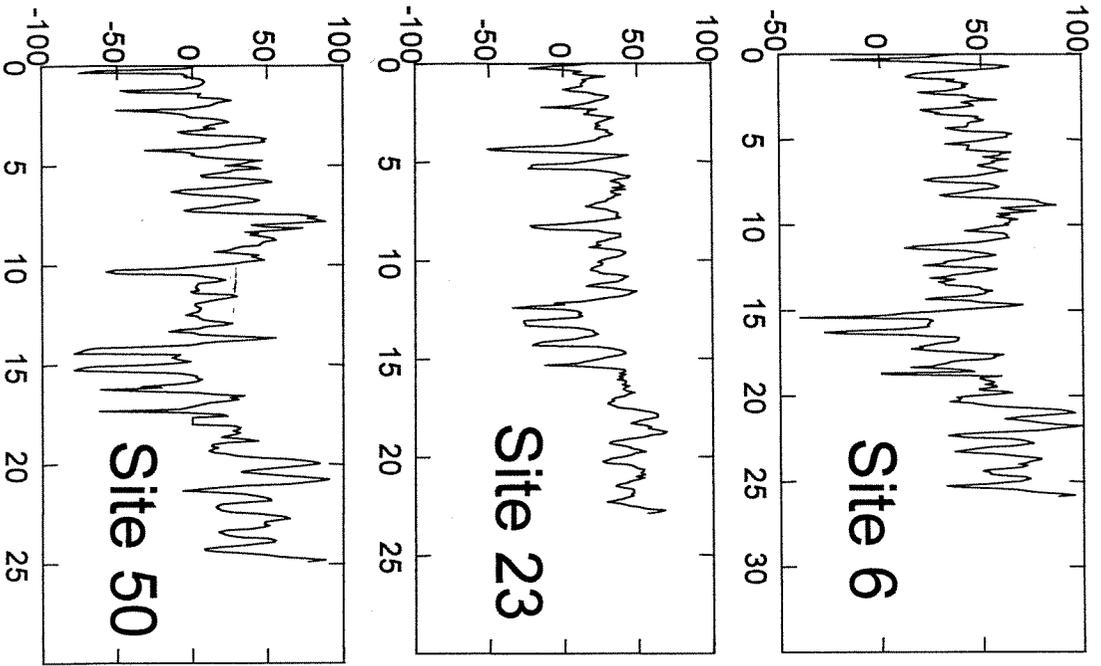


Fig. 5. Time series of average monthly water depth with and without multi-year trends from January 1974 through December 1999. Differencing was used to center the time series and remove trends by subtracting each monthly depth value from the depth observed in the same month one year earlier. Year indicates the number of years since January 1974.

Monthly Average Depth (cm)



Depth After Differencing

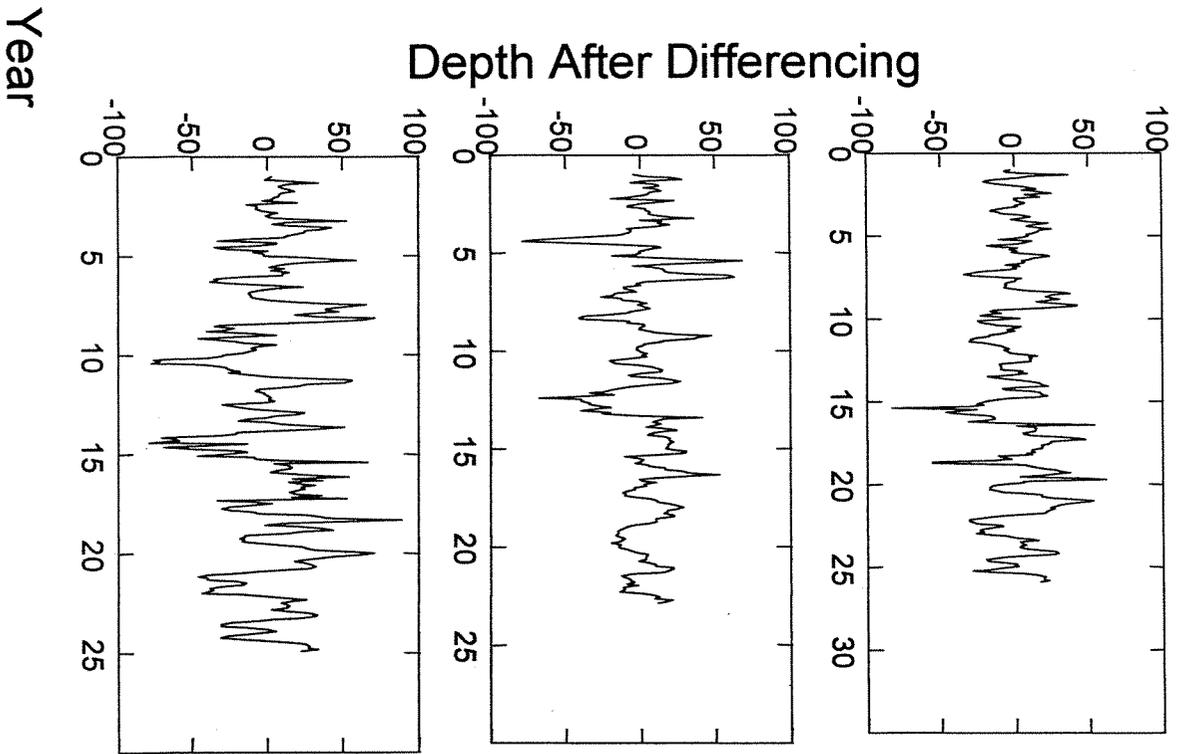


Fig. 6. Partial autocorrelation of monthly water depth for time lags up to 64 months (over 5 years). The horizontal bars above and below 0 correlation indicate the minimum positive and negative correlations that are significantly different from 0. Time lags between a month and the preceding month at multi-year intervals are indicated at lags of 1, 13, 25, 37, 49, and 61 months.

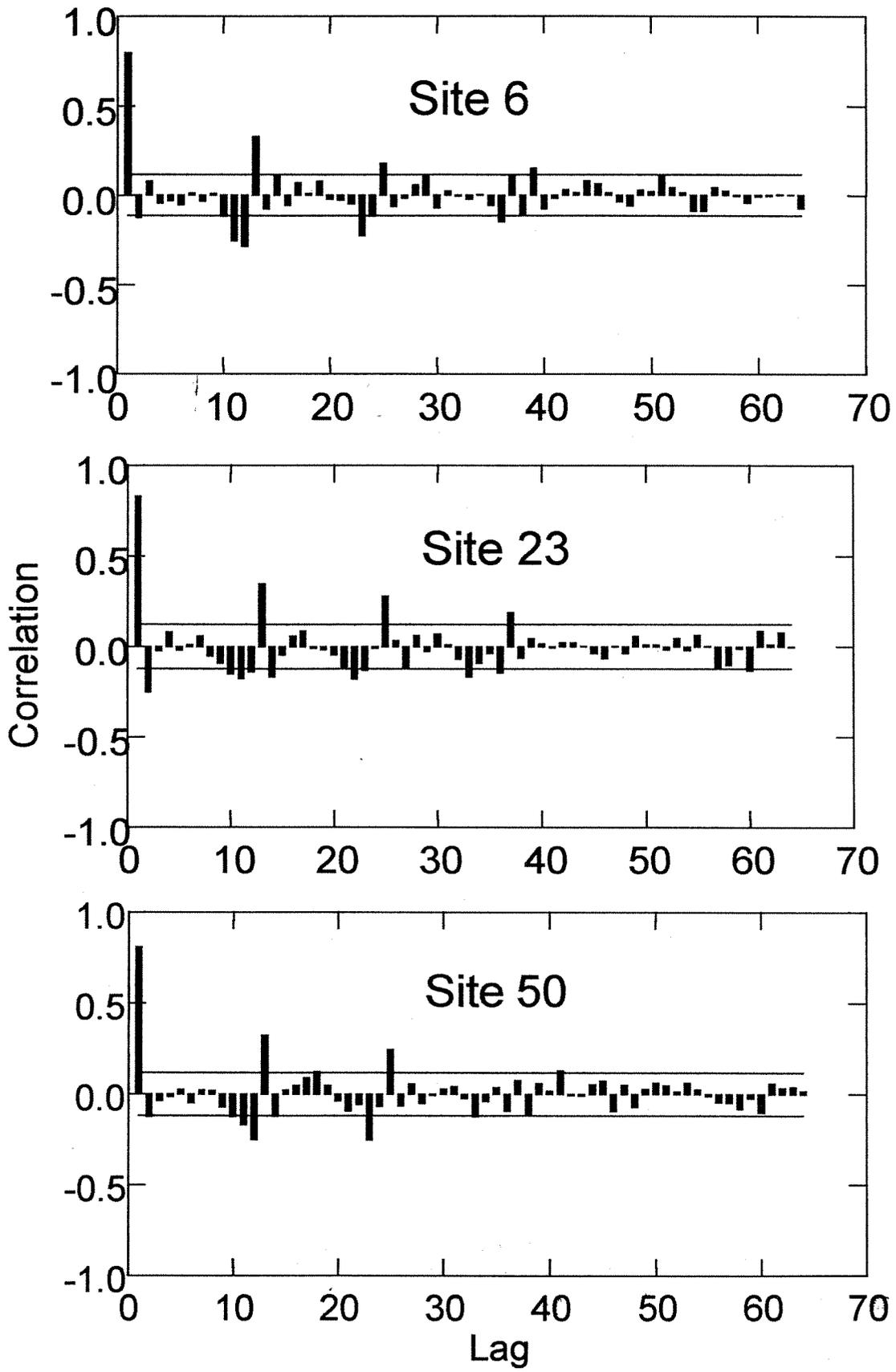
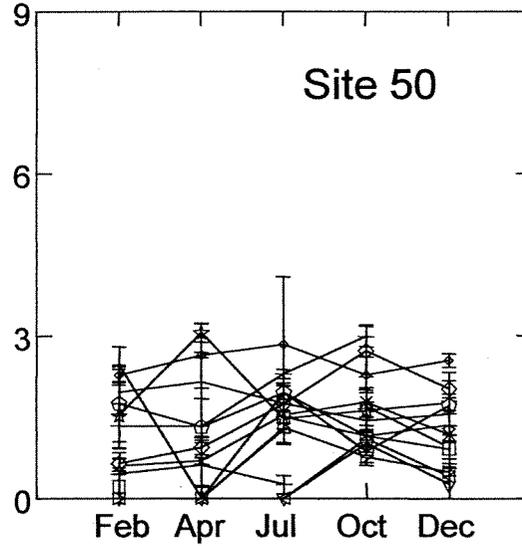
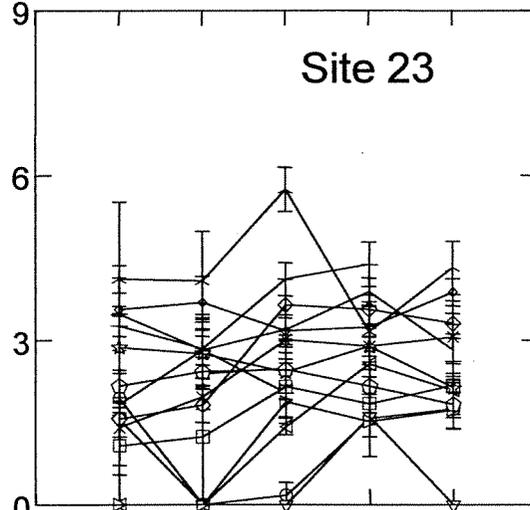
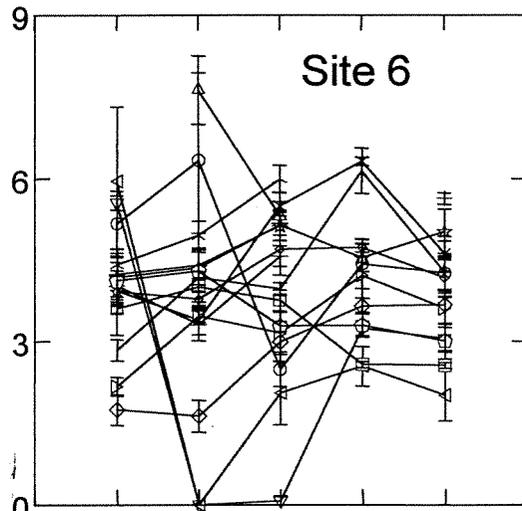


Fig. 7. Average density of fish collected in each month plotted separately by study site. The horizontal lines connect months from the same year. Means with one standard error interval bars are reported based on inter-plot variance, N = 3 plots at each site.

Fish Density (sqrt (#/m²))



Month

Fig. 8. The annual average density of fish at plot A of each study site over the study period plotted separately. Data were limited to single plots in order to equalize the number of replicates over time (plots B and C were not added until 1985). The means for 1988 are based on data from February and April only. The mean ± 1 standard error is plotted; the standard errors represent within-year among-sampling-period variance.

Sqr (Fish Density (#/m2))

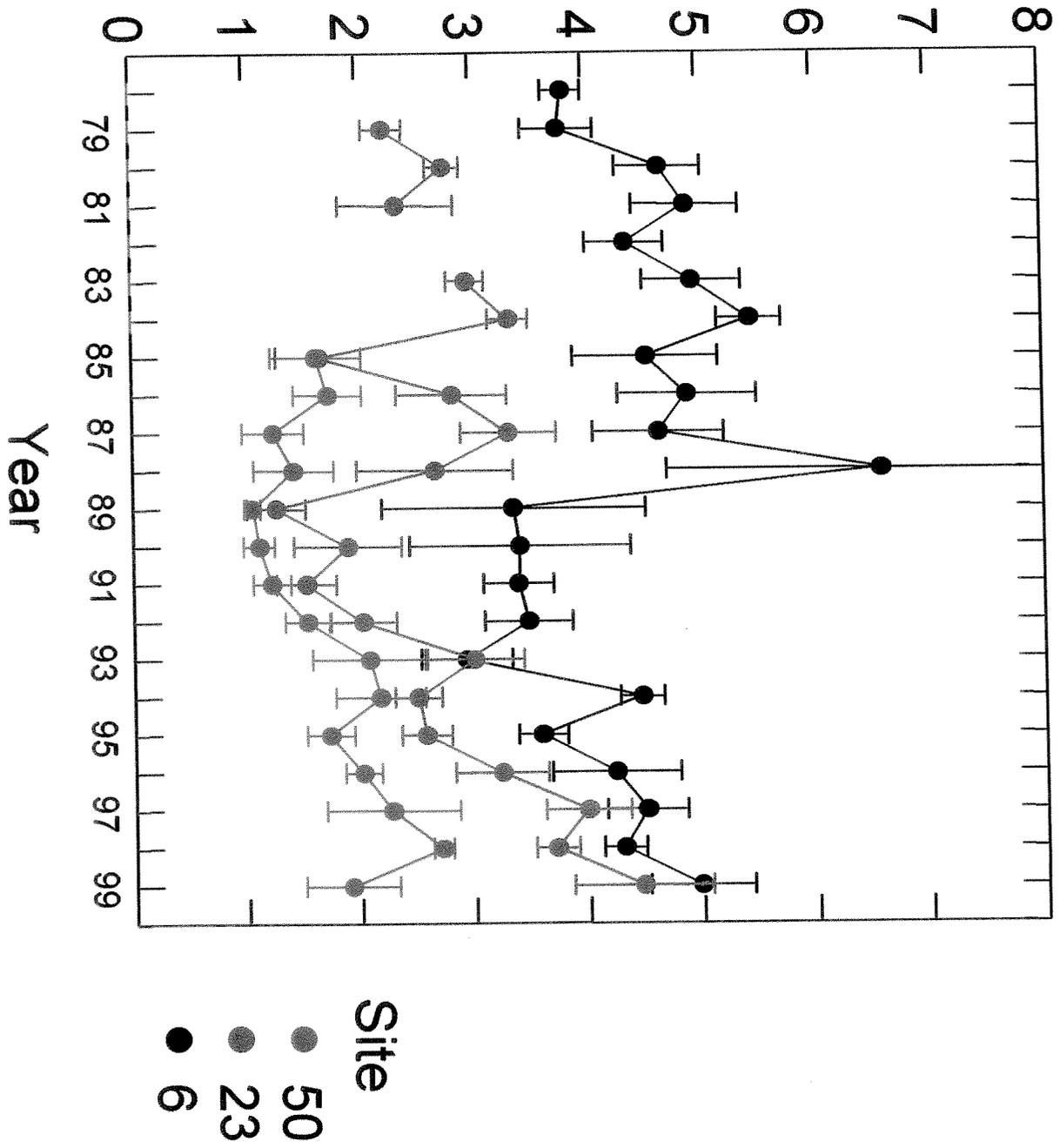
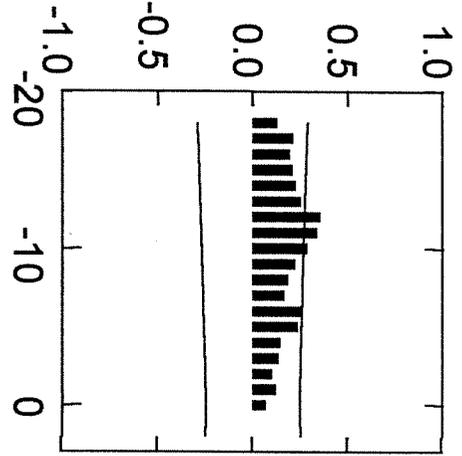


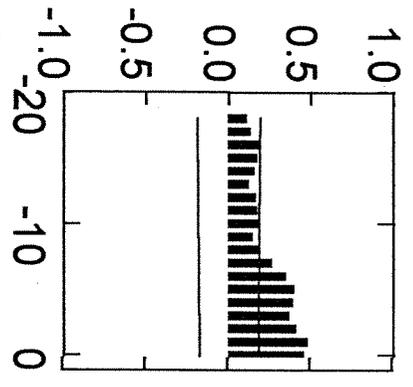
Fig. 9. Plots of cross correlations between square-root transformed fish density and monthly average water depth. Only negative lags are interpretable in these analyses. The correlations must exceed the range of the horizontal bars, negative or positive, to be different from zero. Only data from February, July, and December from each year were included in these analyses in order to minimize missing data. These analyses permit no missing data, so missing data were estimated from adjacent sample months. Differencing refers to the time course of seasonal detrending to remove multi-year trends in the data. Differencing by subtracting means from 3 steps previous compares adjacent years in this analysis.

Correlation

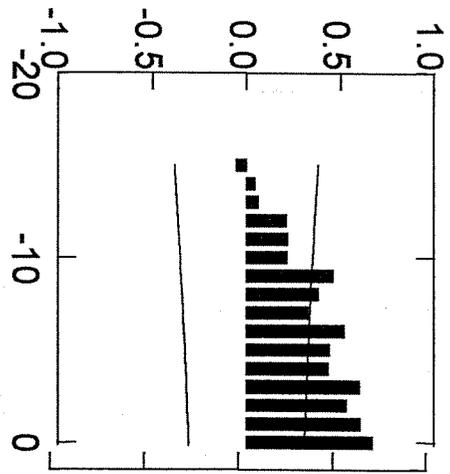
Site 6



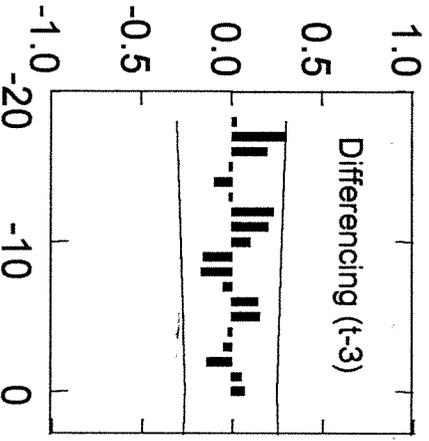
Site 23



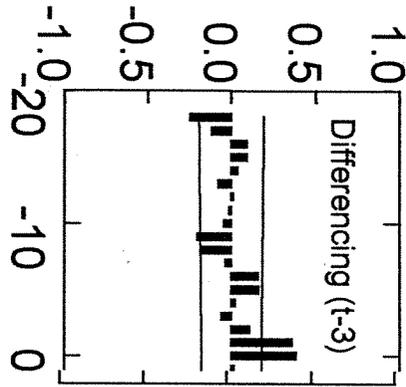
Site 50



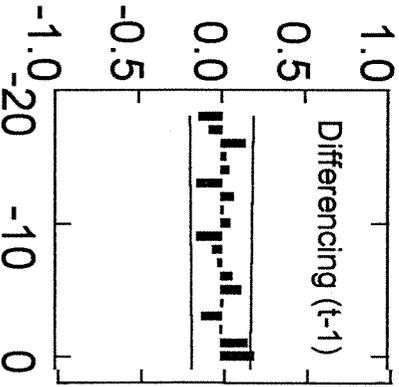
Differencing (t-3)



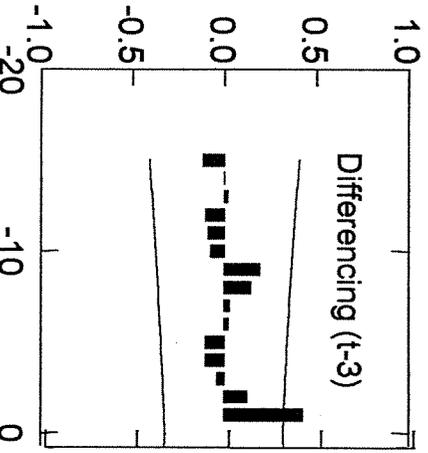
Differencing (t-3)



Differencing (t-1)



Differencing (t-3)



Lag

Fig. 10. Seasonal patterns of species composition illustrated by NMDS plots. Circles enclose months shown to be similar by permutation tests. A. Site 6. B. Site 23.

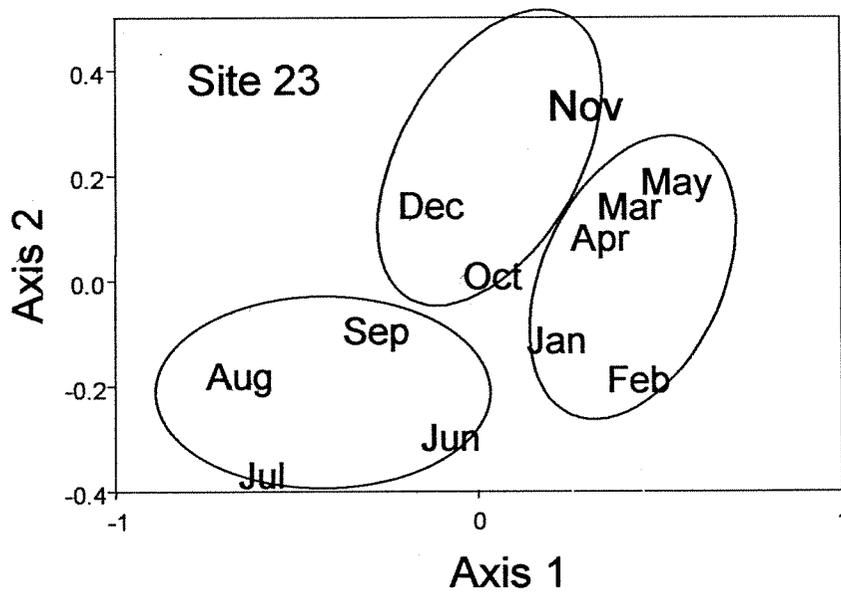
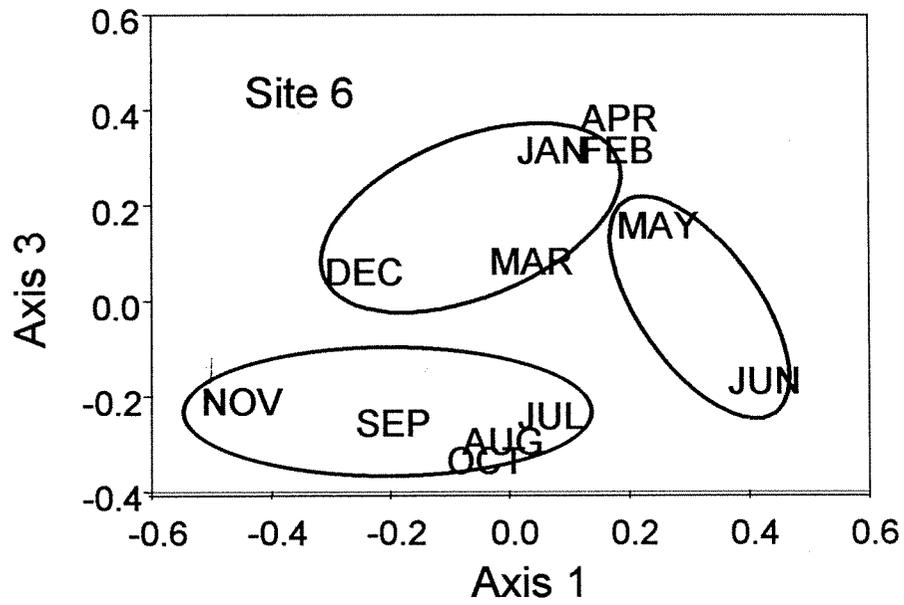


Fig. 11. Inter-annual variation of fish community composition illustrated by NMDS. Circles enclose months before, during, and after the drought years of 1989 and 1990. Arrows connect years from before, during, and after the drought period. Site 23 required a third NMDS axis to fully describe the inter-annual variation, but the first 2 axes illustrate the pattern revealed by permutation tests.

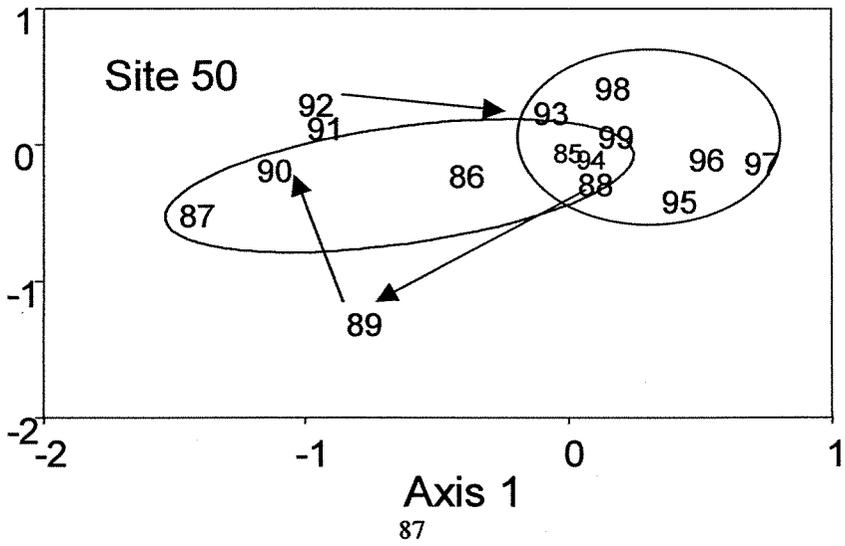
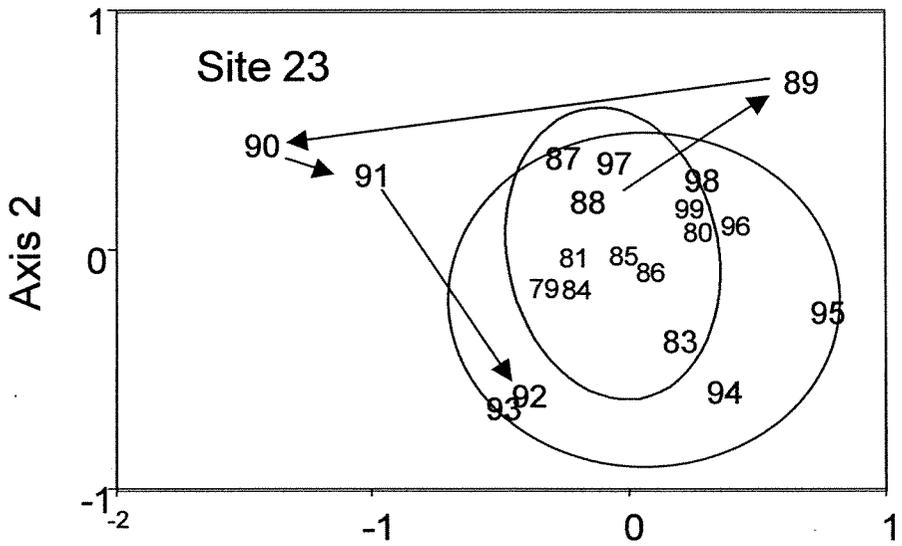
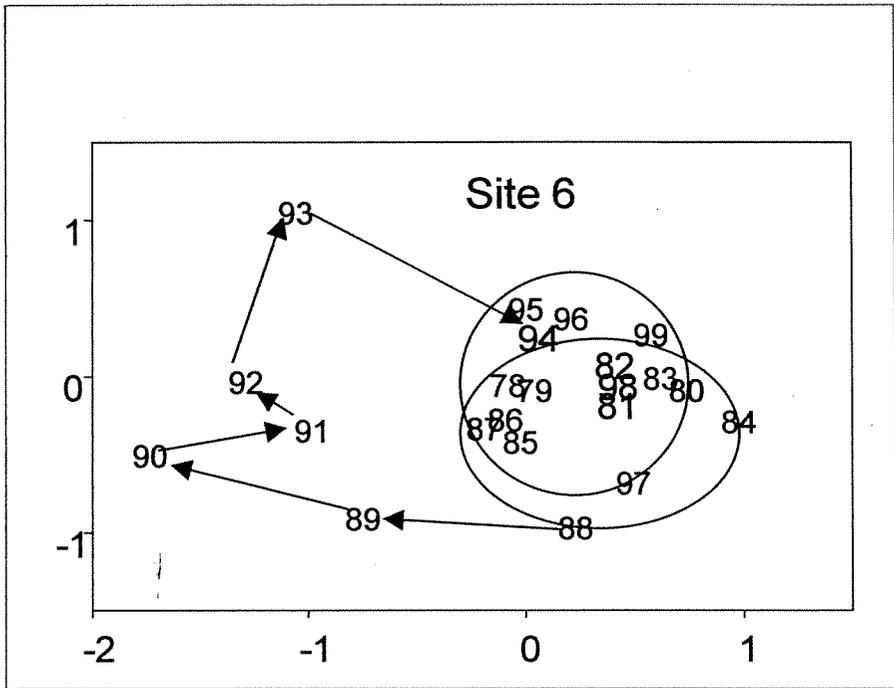


Fig. 12. NMDS scores plotted by year. The mean \pm 1 standard error is plotted; the standard errors represent within-year among-sampling-period variance. Asterisks indicate years where large error bars were omitted to improve the clarity of the graph. A. Scores from Axis 1. B. Scores from axis 2.

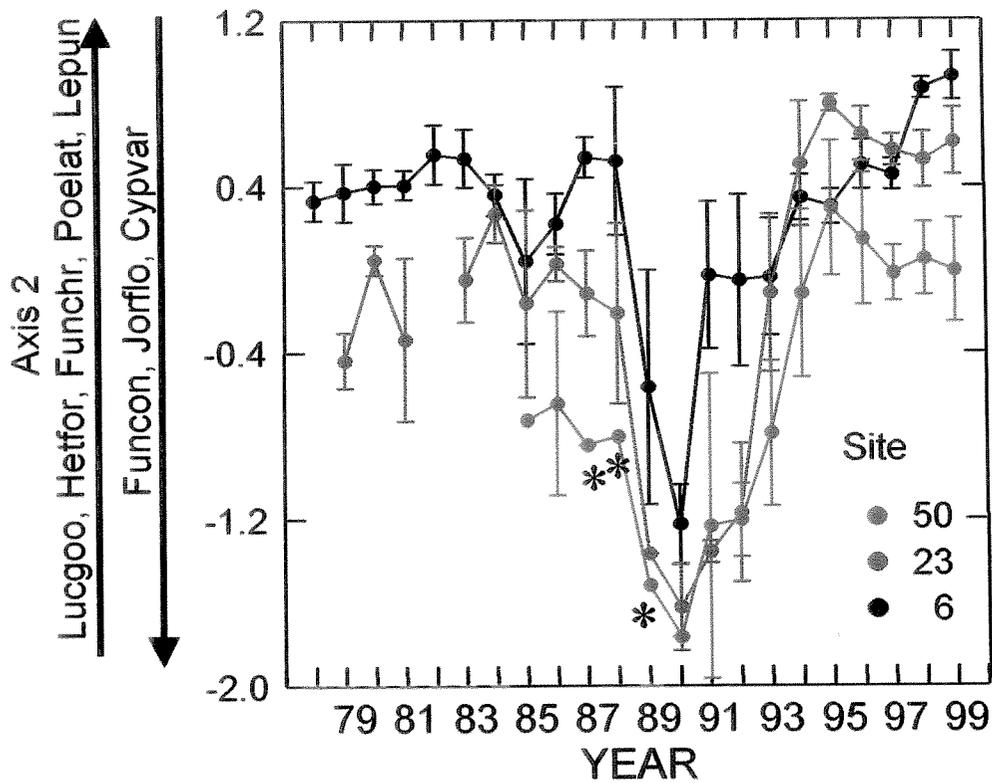
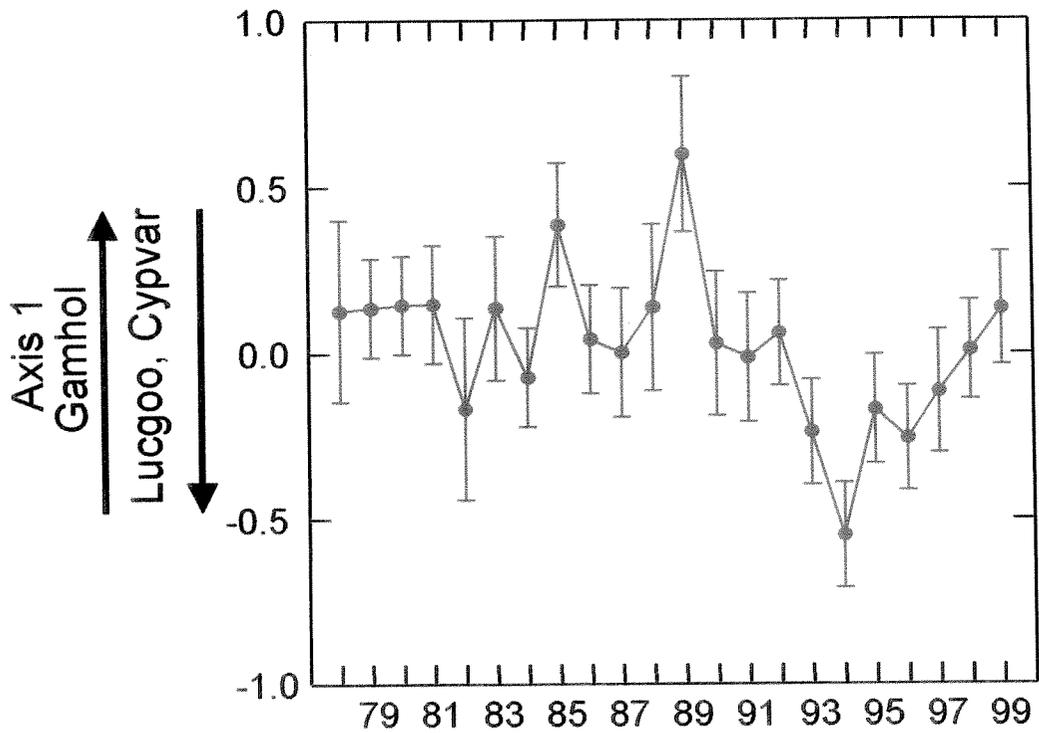


Fig. 13. Plots of NMDS scores relative to days since last dry-down at site 6.

Site 6

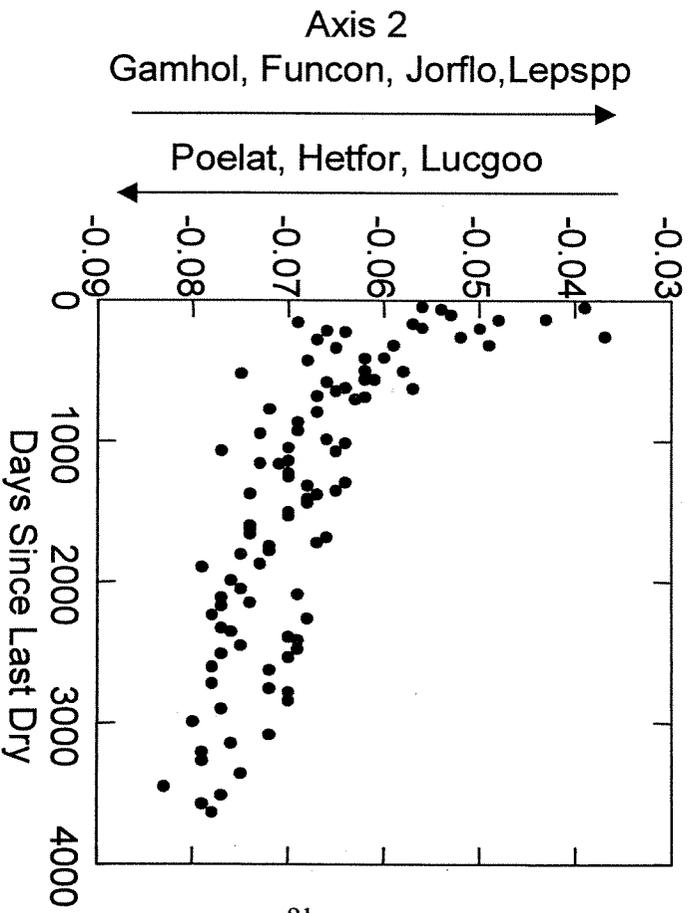
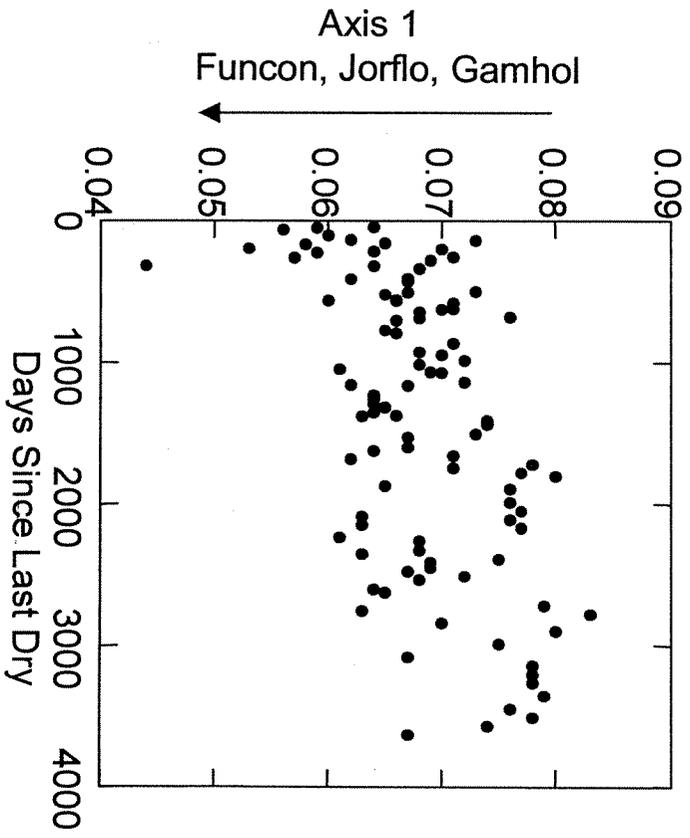
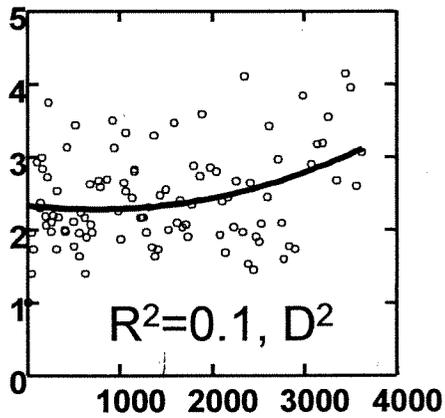


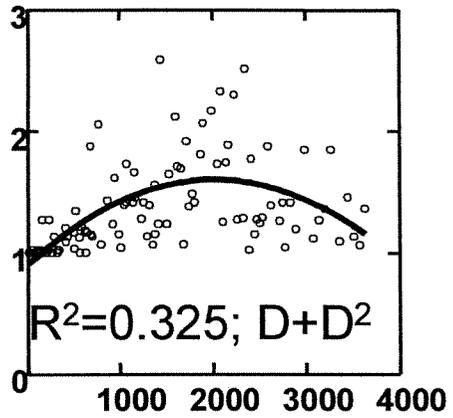
Fig. 14. Fish density (square-root transformed) plotted against days since dry-down for 6 common species at Site 6. The coefficient of determination for each relationship is indicated and the parameters that were significant. D indicates that the relationship is linear, while D^2 indicates that a non-linear term was added to the model.

Fish Density (sqrt(#/m²))

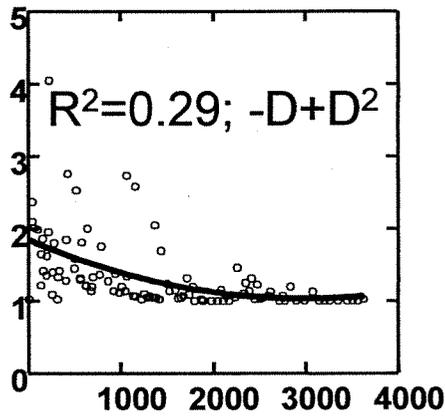
Mosquitofish



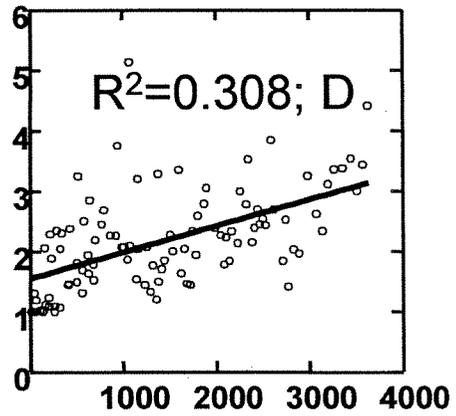
Sailfin molly



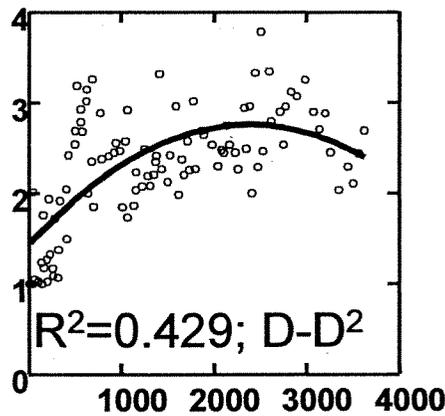
Flagfish



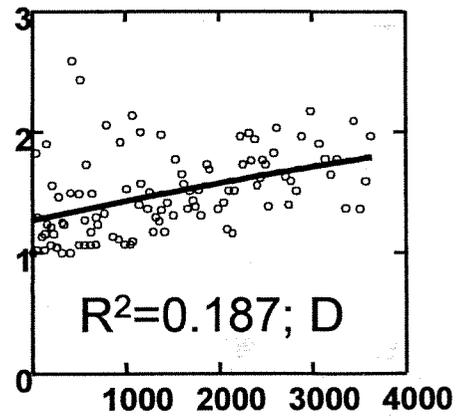
Least killifish



Bluefin killifish

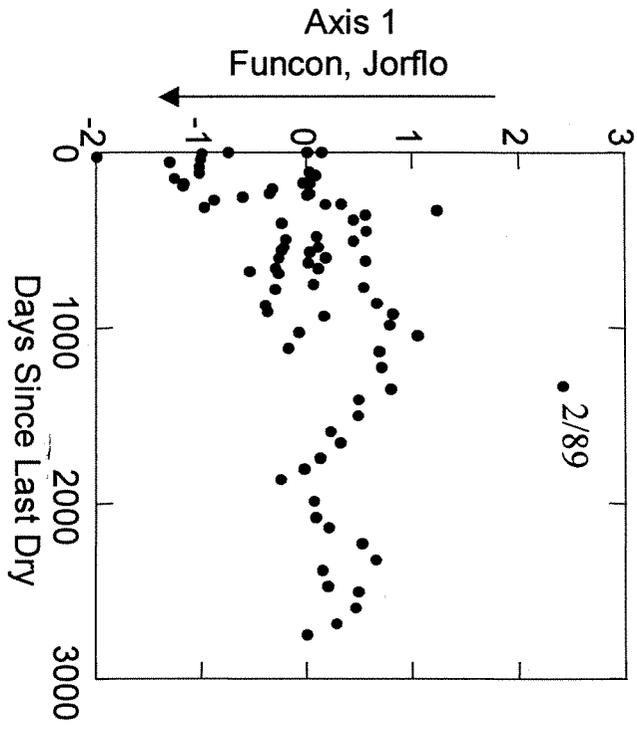


Golden topminnow



Days since dry

Fig. 16. Plots of NMDS scores relative to days since last dry-down at site 23.



Site 23

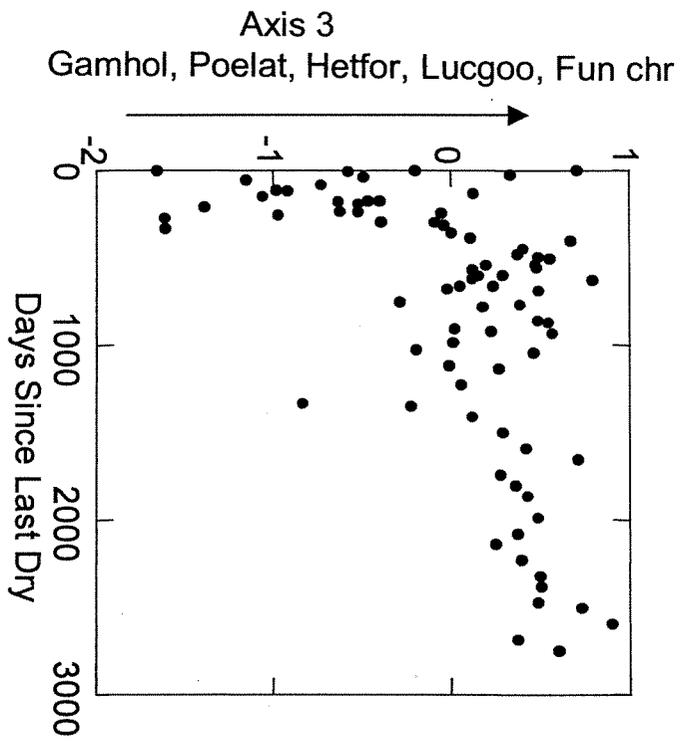
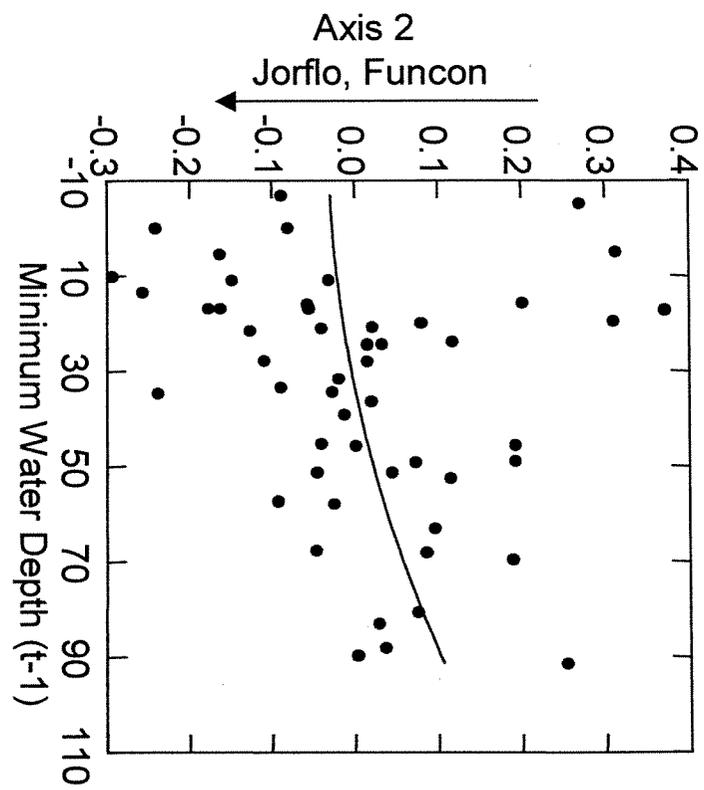
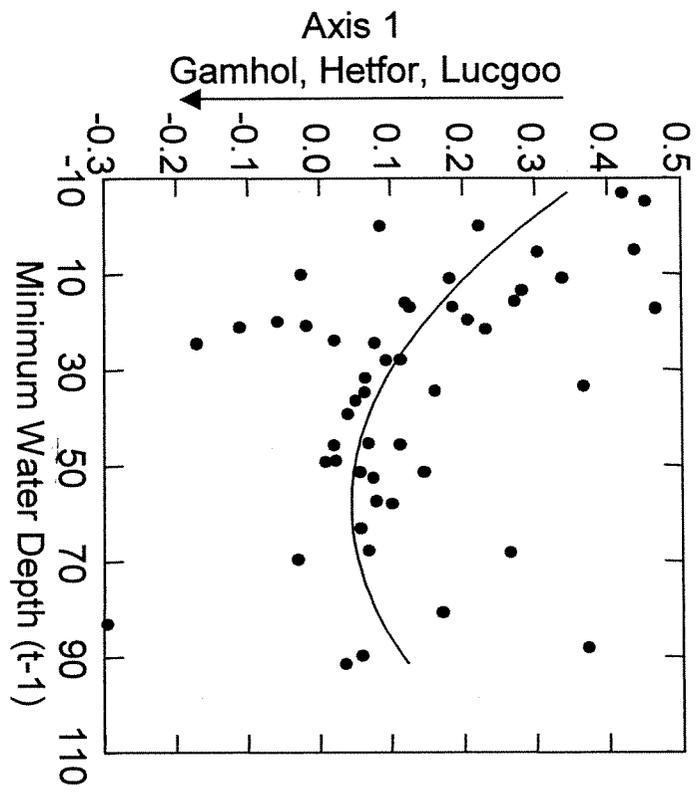


Fig. 17. Plots of NMDS scores relative to minimum water depth, t-1 at Site 50.

Site 50



Part III. RECOMMENDATIONS AND ACKNOWLEDGEMENTS

Recommendations

Need for a Regional Study Program

When regional management activities affect a protected area, restoration actions must focus on the entire ecosystem. Attempts to restore only ENP while ignoring the effects on surrounding marshes would probably fail, particularly in the case of such charismatic fish predators as wading birds, which forage regionally. Wading-bird nesting has been suggested as a measure of restoration success. Proposed water-management changes will affect fishes across the landscape, in turn affecting nesting success because wading birds integrate fish abundance and availability over large areas of marsh. For that reason, we must continue to track changes in fish abundance and availability across the region. Continued support of uninterrupted sampling by the agencies responsible for tracking the progress of restoration is essential to the adaptive-management process.

The major drawback in using fish-community parameters as measures of success is that no fish data were collected before the system was modified. Therefore, restoring fish communities to some pre-modification target is problematic. Unfortunately the same may be said for almost every biotic group - little or no historical data exist. We suggest a process of empirical data collection and simulation modeling that uses the fish community to guide and evaluate restoration project components. By describing present-day community responses to environmental conditions across the landscape, the empirical data are used to build, refine, and validate simulation models with which to estimate fish-community parameters under modeled pre-management conditions. This will allow us to establish restoration targets with well-defined assumptions and scientific bases. By applying the fish models to restoration alternatives and

predicting fish-community responses, we can choose the alternatives that result in biotic characteristics that approximate historical conditions.

Lessons Learned

Several lessons were clear from our work with this data set, particularly things to be avoided in future planning of long-term research. Our analyses were hampered by the absence of pre-manipulation data at Site 50, where collections were begun after the management change was begun. Also, gaps in the data, forced by budget cuts as in 1987 and 1988, precluded the use of time-series analysis and repeated measures designs that are intolerant of missing data. This forces the data analyst to use less powerful analytical techniques, to estimate the missing data, or to lose power to detect pattern because of reduced sample size. Temporary problems in funding, personnel, or vacillation of agency mission can all greatly diminish the benefit of a monitoring data such as those reported here.

Long-term data collection is necessary in a hydrologically variable environment because every year is idiosyncratic and "average" years are rare. Trexler et al. (1996a) showed that if sampling is done over short-time periods, different pictures of the community emerge, depending on the segment of the time series sampled. This is because present fish communities reflect past conditions. Data gaps that result from budget or personnel inconsistencies are detrimental to interpreting time-series data. Events of interest will invariably occur when shortfalls, or other problems, limit the sampling program. For that reason, guaranteed consistent funding and a strong personnel commitment are necessary to a long-term program.

Although Loftus and Eklund (1994) presented evidence for strong bias in pull-trap data to characterize animal population dynamics, this method has been retained as part of the monitoring

program in ENP. The traps act as analogs of alligator ponds (i.e., deeper, open-water habitats in the marshes), thereby providing qualitative information on the presence/absence of large-bodied native and introduced species. Also, the pull traps represent the longest data set for aquatic animals in the entire region. These data have a unique historical record of patterns of invasion by non-indigenous fishes into natural wetlands of the Everglades (Trexler et al. in press-b). The program of data collection should continue to employ the pull-trap method. However, the main emphasis in funding and effort should be focused on maintaining and expanding the throw-trap sampling network because extensive testing has shown that method to have characteristics needed to meet the objectives of a long-term marsh-monitoring program.

These data, and the continuing stream of information from these study sites, are invaluable for assessment of future manipulations of hydrological management in the Shark River Slough. It is, of course, impossible to go back in time and obtain additional data sets of the sort described here. However, these are exactly the kind of data necessary to develop a quantitative assessment of ecosystem health in the context of environmental fluctuation. The Everglades is an oligotrophic ecosystem that historically experiences seasonal and inter-annual variation of hydroperiod. Adding water or nutrients can lead to increases in the density and size of fishes in the ecosystem, but this may not reflect conditions found there at any point in its history before man's influence. Long-term data gathered under the full range of management conditions (especially extremes of wet and dry years), coupled with efforts to better understand and predict historical ecosystem function, are critical to develop management plans unbiased by preconceived notions of Everglades ecosystem characteristics.

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