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Disturbance frequency and community structure in a twenty-five year intervention study

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Abstract Models of community regulation commonly incorporate gradients of disturbance inversely related to the role of biotic interactions in regulating intermediate trophic levels. Higher trophic-level organisms are predicted to be more strongly limited by intermediate levels of disturbance than are the organisms they consume. We used a manipulation of the frequency of hydrological disturbance in an intervention analysis to examine its effects on small-fish communities in the Everglades, USA. From 1978 to 2002, we monitored fishes at one long-hydroperiod (average 350 days) and at one short-hydroperiod (average 259 days; monitoring started here in 1985) site. At a third site, managers intervened in 1985 to diminish the frequency and duration of marsh drying. By the late 1990s, the successional dynamics of density and relative abundance at the intervention site converged on those of the long-hydroperiod site. Community change was manifested over 3 to 5 years following a dry-down if a site remained inundated; the number of days since the most recent drying event and length of the preceding dry period were useful for predicting population dynamics. Community dissimilarity was positively correlated with the time since last dry. Community dynamics resulted from change in the relative abundance of three groups of species linked by life-history responses to drought. Drought frequency and intensity covaried in response to hydrological manipulation at the landscape scale; community-level successional dynamics converged on a relatively small range of species compositions when drought return-time extended beyond 4 years. The density of small fishes increased with diminution of drought frequency, consistent with disturbance-limited community structure; less-frequent drying than experienced in this study (i.e., longer return times) yields predator-dominated regulation of small-fish communities in some parts of the Everglades.

Keywords BACI · Community regulation · Disturbance · Hydroperiod · Succession · Wetland

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Introduction

Disturbance (defined here as a process that removes biomass) plays a central role in several prominent models of community structure (Grime 1977; Menge and Sutherland 1987; Tilman 1988; Huston 1994; Chase and Leibold 2003). A common feature of these models is an inverse relationship between the impact of biotic interactions and disturbance in effecting intermediate trophic levels. Intermediate levels of disturbance may affect predators more severely than their prey, particularly when predators are larger, have longer generation times, or lower fecundity than their prey, while a higher frequency or intensity of disturbance may affect both negatively. Field studies conducted over multigenerational temporal scales that manipulate the frequency or intensity of disturbance to determine these "intermediate" levels are not common (Bell et al. 2003). Wetlands are excellent systems to explore the relationship of disturbance and community dynamics. Wellborn et al. (1996) argued that frequent drying events structure wetland-community dynamics and function through direct mortality and physiological stress. Similar to fire in some terrestrial landscapes, drying events in wetlands maintain a dynamic community structure by re-setting succession with trajectories determined by disturbance history (frequency, temporal sequence, and intensity). Thus, wetlands experience gradients of disturbance that may encompass extremes of community control, and permit documentation of intermediate levels in which control shifts from biotic (density-dependent) to abiotic (density-independent) sources.

A complex picture is emerging to explain the mechanisms through which disturbance shapes communities. The frequency, intensity, and scale of disturbances are often confounded in natural ecosystems and difficult to disentangle (Benedetti-Cecchi 2003). Further, the sequence of disturbance events may change the community composition that emerges (Fukami 2001). For example, 10 years of alternating wet and dry years may yield a different wetland community than a sequence of five dry years followed by five wet years. The spatial scale of disturbance determines the distance colonists must travel to repopulate a disturbed site, also influencing emergent community dynamics (Huston 1994, pp 224–227; McCabe and Gotelli 2000; Magoulick and Kobza 2003). Landscape features may enforce a covariance of disturbance spatial scale with disturbance frequency and intensity. For example, the frequency, intensity, and scale of hydrological disturbance in wetlands are tied to landscape features of topographic relief (Ruetz et al. 2005); short-hydroperiod areas commonly fringe deeper aquatic habitats (e.g., river channels, lakes, slough habitats) and are dried, not only more frequently, but also for longer periods than long-hydroperiod sites. By nature of their arrangement in space, the spatial scale of disturbances that affect long-hydroperiod sites is often larger than those affecting short-hydroperiod ones. Rivers and lakes, with their floodplains, ephemeral feeder streams, or littoral zones, have similar landscape constraints on disturbance characteristics (Benda et al. 2004)—permanent aquatic environments bounded by temporary ones—driving an exchange of organisms between the habitats. While experimental efforts to disentangle disturbance frequency, sequence, intensity, and spatial scale may be impractical in many ecosystems, parsing the covariance of these factors is necessary before a mechanistic understanding from theory and laboratory experiments can be scaled up.

Physiological stress and mortality from hydrological fluctuation has long been the focus of efforts to explain aquatic-community dynamics in the Florida Everglades, USA. Kushlan (1976, 1980) proposed that frequent drydown events limit the abundance of piscivores in the Everglades, releasing small-bodied fish species with annual life cycles to increase in abundance (predator-regulation hypothesis). Loftus and Eklund (1994) demonstrated that short-hydroperiod marshes have lower density of small fish than longer hydroperiod sites, and suggested that direct mortality from drying is the critical factor setting the density of both small and large fish in this large wetland (disturbance-limitation hypothesis). We report the analysis of a 25-year time series of fish samples collected at three sites in the Everglades National Park (ENP) that experienced different hydrological conditions. Hydrological management was changed at one of the three study sites after the start of this study, providing a unique opportunity to test Kushlan's predator-regulation hypothesis. This study design, termed an ''intervention analysis'' rather than an experiment because of the lack of replication of the landscape units (Rasmussen et al. 1993), can be a useful tool to interpret natural processes when analyzed with Before-After-Impact-Control (BACI) models (Downes et al. 2002). Paired intervention analyses (one intervention site and one ''control'') are problematic because they rely on the untestable assumption that the ''control'' site reflects the trajectory of intervention habitats that have not been manipulated (Murtaugh 2000, 2002; Stewart-Oaten 2003). In this study, we employed two areas for comparison that, at the outset of the study, bracketed the conditions of the intervention site. By intervening in the hydrological dynamics at one site to change the frequency and intensity of local droughts over the following 17-year period, we provide a landscape-scale test of the impact of drought frequency and intensity on community structure.

Methods

Study sites and sampling design

We sampled fishes from three plots (A, B, C) at each of three sites located in northern Shark River Slough, ENP (Sites 6, 23, and 50; Fig. 13-1 in Trexler et al. 2003). The study sites were located in wet-prairie slough habitats dominated by spikerushes, primarily *Eleocharis cellulosa* (Appendix 1; Busch et al. 1998). Other common plant species were maidencane (*Panicum hemitomon*), beakrush (*Rhynchospora tracyi*), and arrowheads (*Sagittaria* spp.). Submerged mats of bladderworts (*Utricularia* spp.), sometimes covered by thick periphyton, grew among the emergent plant stems. There is typically a 10- to 25-cm difference in elevation between the wet-prairie slough and adjacent ridge habitats typically vegetated by dense sawgrass (*Cladium jamaicense*). Hydroperiod, mean water depth, and frequency of drying events consistently varied among the sites during the study, leading to a characterization of Site 6 as long hydroperiod and Site 50 as short hydroperiod (Appendix 1). Soil development in the Everglades is a function of hydroperiod (Gleason et al. 1984). Organic peat soils occurred at the site with the longest hydroperiod (Site 6), while calcium carbonate sediments (marls) predominated at the shorter hydroperiod sites (Sites 23 and 50); soil organic matter is a slow parameter to change and a mixed marl and peat character was retained at Site 23 by the end of the study.

Spatial replication was limited for the first 7 years of the study. Fishes were collected monthly from January

1978 to August 1985 at one plot at Sites 6 and 23. The spatial aspects of the sampling design were expanded in October 1985, while the frequency of sampling was decreased; three randomly positioned plots were initiated at Site 50, along with two more at Sites 6 and 23, and the frequency of sampling dropped to five times per year at all three plots at Sites 6, 23, and 50. Distances of approximately 1 km separated the three plots at each study site; the plots were not visible from each other because sawgrass ridges separated the deeper sloughs. The five sampling events were undertaken in February and April (dry season), July and October (wet season), and December (seasonal transition). The number of samples taken per sampling event varied over the course of the study; from 1978 to 1984, the numbers varied from 5 to 21 based on an estimate of the intersample variance following Kushlan (1974). After 1984, seven samples were taken at each sampling event. The location of each throw-trap sample within a plot was determined by choosing seven *X* and *Y* coordinates from a random number table. Each plot had approximately 10,000 possible sampling locations and the odds of resampling the same 1-m^2 area were low; recent studies detected no evidence of habitat alteration by visitor impacts at these sites (Wolski et al. 2004).

We collected fishes with a 1-m^2 throw trap following standard methods (Jordan et al. 1997). Our trap was 0.8-m tall and had 2-mm mesh on a copper-pipe frame. 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 it 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 humane animal-use guidelines (Anonymous 1988), preserved in 10% formalin, and then returned to the laboratory. Before identification and measurement, fishes were transferred to 70% ethanol.

We obtained hydrological information about each site from water-depth measurements taken simultaneously with each fish sample. These were calibrated to a common water-surface plane with data from nearby continuous hydrological recording stations to yield daily estimates of water depth at each plot (R^2 values in excess of 0.90). We also used these regressions to estimate the dates when each study plot was dry, which we defined as any time when water depth was below 5 cm; at this depth, no standing water remains and fishes die submerged in organic floc that clogs their gills (Loftus and Eklund 1994). We calculated the number of days since dry (DSD) for each fish-sampling visit from our estimates of daily water depths at each plot for the length of the study. We also estimated the severity of the most recent drying event as the number of days that water was below 5-cm depth (length dry, or LD) and the minimum depth. Minimum depth never uniquely explained variance in fish density, unlike LD, so it is not discussed further.

The design of this study permitted us to compare temporal patterns of fish-community dynamics among the three study sites over a range of hydrological conditions. The study encompassed a hydrological alteration in the eighth year of sampling that we treated as an unreplicated field experiment. In 1985, water managers changed the schedule for opening a water-control gate (S-333 in the Tamiami Canal), permitting more water to enter the northeast region of Shark River Slough, the location of Site 23. This altered the annual minimum water depth and frequency of drying at Site 23 (Appendix 2). There was a regional drought from 1989 to 1990, which affected all study plots. Beginning late in 1991 (Fig. 1a), the entire study region experienced a series of high-rainfall years that increased water depths and decreased frequency of drying at all three study sites. After 1992, the marsh surface at Sites 6 and 23 did not dry, and Site 50 dried only once (1995). Thus, comparisons of Site 6 with Site 23 before and after 1985, and Site 23 with Sites 50 and 6 before and after 1992, permitted a test of the role of hydrology in shaping Everglades fish communities.

Statistical methods

We analyzed fish density (number of individuals per m^2) and community composition (relative abundance of all species) to differentiate patterns of abundance and community structure of fishes. We used the mean density at each plot for these analyses (mean of throw-trap samples collected in a visit) for several reasons: we were not concerned with intermeter^2 patterns in these analyses, as this level of variance has little (probably no) effect on the outcome of the hypotheses we sought to test, and its inclusion made several analyses intractable. To focus the analysis of treatment effects in an intervention analysis, we divided the 25-year study into five intervals: before (7 years: 1978–1985); after1 (8 years: 1986–1993); after2 (3 years: 1994–1996); after3 (3 years: 1997–1999); after4 (3 years: 2000–2002). The first two intervals are of unequal duration and longer than the last three to accommodate changes in sampling design that occurred prior to 1986 and the system-wide drought event of 1989–1990. Our analyses were designed to test for a treatment-by-site interaction, with the expectation that Sites 23 and 50 would be more similar in the "before" portion of the study and that Sites 23 and 6 would become more similar after the change in management initiated in 1985 (the 'treatment'). We used Tukey-Krammer-adjusted *P* values for pairwise comparisons among sites within the four time increments of the study when omnibus tests indicated significant treatment-by site interaction.

We analyzed the density of all fish (Total = sum of all species per unit area) and the four most abundant

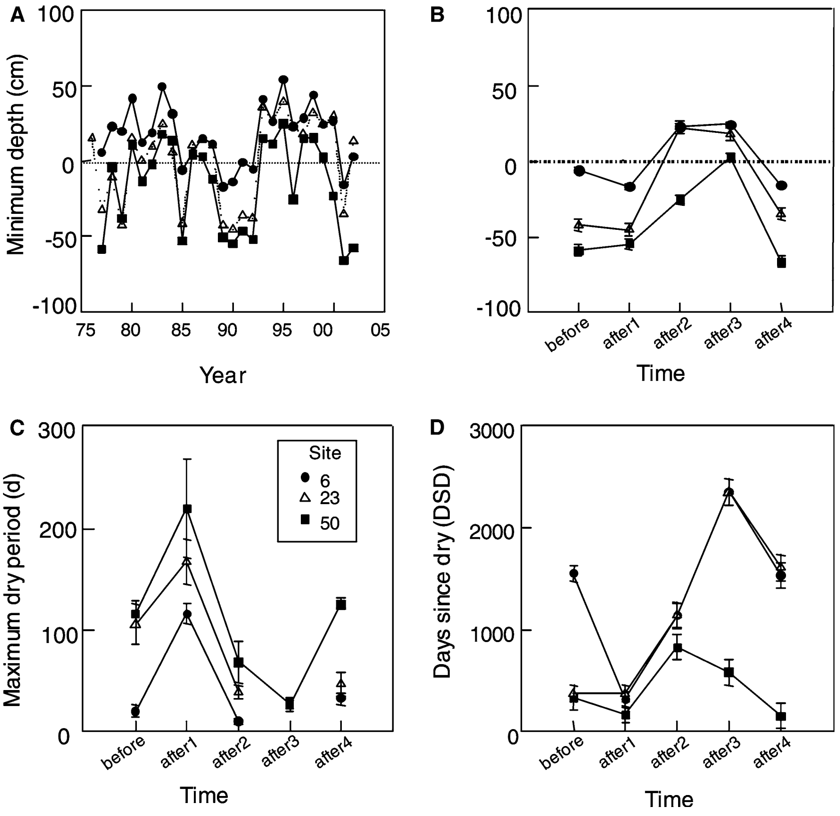

Fig. 1 Hydrographic parameters from the three study sites (6, 23, 50) in northern Shark River Slough, Everglades National Park (means ± SE based on interplot(site) variance). Zero depth indicates ground surface and negative values are estimates of the below-ground water table. Before: 1977–1985; after1: 1986–1993; after2: 1994–1996; after3: 1997–1999; after4: 2000–2002. **a** Annual minimum water depth plotted separately by site. *Error bars* are omitted to reduce clutter. **b** Average minimum water depth plotted for each interval was the annual minimum at the three plots for each site during the interval. **c** Maximum dry period indicates the maximum length in days as one of the plots at each site was continuously dry during the time interval. Subtracting this value from 365 days yields the minimum hydroperiod observed. Sites 6 and 23 did not dry during interval ‘after3’. **d** Average days since dry (DSD) during each interval

species (bluefin killifish, *Lucania goodei*; least killifish, *Heterandria formosa*; eastern mosquitofish, *Gambusia holbrooki*; and flagfish, *Jordanella floridae*), in tests for effects of the management intervention. We found that log transformation ($n+1$ to permit zeros) of density of these abundant taxa was an adequate transformation to meet the assumptions for parametric analysis of normally distributed data (McCullagh and Nelder 1989, p 198). We used Proc Mixed in SAS to model these plot means with reduced maximum likelihood (REML) techniques, and employed an analysis of deviance (ANODE) framework of comparing nested models (Burnham and Anderson 2002) to test our BACI hypotheses. Proc Mixed permits explicit modeling of temporal autocorrelation in time series of the type examined here using a one-step autoregressive model (AR(1)); plot(site) was the repeated-measures factor. We fitted a base model [site + season + treatment + year(treatment) + plot(site)] to our data and compared the sequential improvement in model fit by addition of a site-by-treatment interaction (indicative of management effects) and DSD + DSD^2 + LD + LD-by-treatment (indicative of hydrological effects) with the Akaike’s Information Criterion (AIC). Model selection was based on four comparisons: (1) base model + site-by-treatment versus base model; (2) base model + hydrology parameters versus base model; (3) base model + site-by-treatment + hydrology versus base model + site-by-treatment; (4) base model + site-by-treatment + hydrology versus base model + hydrology parameters. Our data set was large relative to the number of parameters that fit, and no small-sample adjustment was required (Burnham and Anderson 2002). In all cases, we added DSD and DSD^2 simultaneously because other work has demonstrated that density often increases asymptotically over time intervals exceeding 2 years (Ruetz et al. 2005). We report the coefficient of determination (R^2 = observed − predicted mean density) to evaluate the fit of our preferred models to the data. Wald’s test, an approximate F-test for maximum likelihood parameter estimates, is reported for significance tests of parameters in the selected models (Littell et al. 1996).

Our community data were highly non-normal because of many zeros (0 specimens of a particular species at a particular plot visit), as is typical for count data from quadrats (Legendre and Legendre 1998). To resolve this problem, we used techniques robust to sampling distribution for hypothesis testing and descriptive analysis of species-by-sample matrices of fish community composition (Clarke and Warwick 1994). Relative abundances estimated from annual mean density of each species at each plot were used to calculate Bray–Curtis dissimilarity indices (Legendre and Legendre 1998) for all pairs of samples in our species-by-sample matrix. These indices were used to test hypotheses of community change with a nonparametric analysis of community similarity (ANOSIM: Clarke 1993). All community-structure analyses were repeated with double square-root-transformed relative abundance and presence–absence data to document the contribution of dominant (relative abundance) and rare (presence–absence) taxa to the results (Clarke and Warwick 1994).

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 with the 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 plots 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 typically 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 (Philippi et al. 1998). 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). We used a Mantel Test (Mantel 1967, Douglas and Endler 1982) to evaluate correlations between community dissimilarity matrices and matrices of Euclidian distances of environmental parameters.

We used nonmetric multidimensional scaling (NMDS) to ordinate the relativized Bray–Curtis dissimilarity indices (Kruskal and Wish 1978) and to illustrate latent patterns in our species composition data. This technique configures samples along axes based on the proximity of their dissimilarity scores. A stress statistic is produced as a measure of goodness-of-fit of the newly created axes and for the ordering of the dissimilarity matrix (Kruskal and Wish 1978).

Results

Hydrological patterns

The three study sites differed in the hydroperiod, frequency of drying of the marsh surface, mean water depth, and maximum water depth over the years between 1977 and 2002 (Fig. 1; Appendix 1). Throughout the study, Site 6 had the longest hydroperiod and dried the least, while Site 50 had the shortest hydroperiod and dried most frequently. Prior to 1985, Sites 23 and 50 were indistinguishable in most hydrological parameters, while Site 23 converged on Site 6 in all hydrological measures soon after that time (Fig. 1). Hydrological variation among the study sites within a year was primarily the result of actions of water managers through manipulation of flow into the Shark River Slough from the Tamiami Canal by partitioning water flow through the S-12 structures and Northeast Shark Slough (NESS) culverts (Appendix 2).

Three hydrological events during the 25-year study affected the relative pattern of inundation at the three study sites. The first of these was a two-year drought in 1989 and 1990 that dried all three sites for over at least a month each year, and yielded annual-average water depth at Sites 23 and 50 near or below zero for both years. The four years preceding the onset of fish sampling (1974–1977) were also relatively dry when compared to the next 20 years. The second important event began in 1985 when water management practices were changed, leading to more water entering NESS and lengthening hydroperiods at Site 23. The third important event was the unusually wet period in much of the 1990s. In the mid- to late-1990s, water depths were typically higher than the preceding 20 years at all three study sites, and all experienced less-frequent marsh-surface drying during this period (neither Sites 6 nor 23 dried between 1992 and 1999; Fig. 1a, c). Relative water depth did not change among our three study sites during these wet years; Site 6 remained consistently deeper than Sites 23 or 50. However, during this period, the minimum water depth at Site 23 converged on the minimum at Site 6, and the minimum at both was greater than at Site 50 from the late 1980s onward (Fig. 1a, b).

Fish density

Twenty-nine species were collected from the three study sites (Appendix 3). Of these, six species (eastern mosquitofish, bluefin killifish, least killifish, golden topminnow—*Fundulus chrysotus*, flagfish, sailfin molly—*Poecilia latipinna*) comprised 97, 94, and 88% of the fishes collected at Sites 6, 23, and 50, respectively. At Site 6, no other species comprised 1% or more of the fishes collected; at Site 23, not only spotted sunfish (*Lepomis punctatus*) but also marsh killifish (*Fundulus confluentus*) exceeded 1% of the fishes collected; and at Site 50, not only marsh killifish but also sheepshead minnow (*Cyprinodon variegatus*) exceeded 1% (at Site 50, each of these species accounted for approximately 4% of the fishes captured). 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. 2). Density at Site 6 averaged 18.6 fish/m^2 for the study period, while Site 23 averaged 8.1 fish/m^2 and Site 50 averaged 3.4 fish/m^2 (Appendix 3).

For all five dependent variables we examined, statistical models incorporating hydrology (DSD and LD), management (site-by-treat), or both, described our data better than models with only spatial and temporal effects. Models including both hydrology and management best described our observations for fish density (Total) and least killifish density (Table 1). For both of these dependent variables, adding DSD and LD contributed more information to the description than adding site-by-treat (Table 1: ANODE comparisons 2 and 3 vs. 1 and 4). However, both independent variables

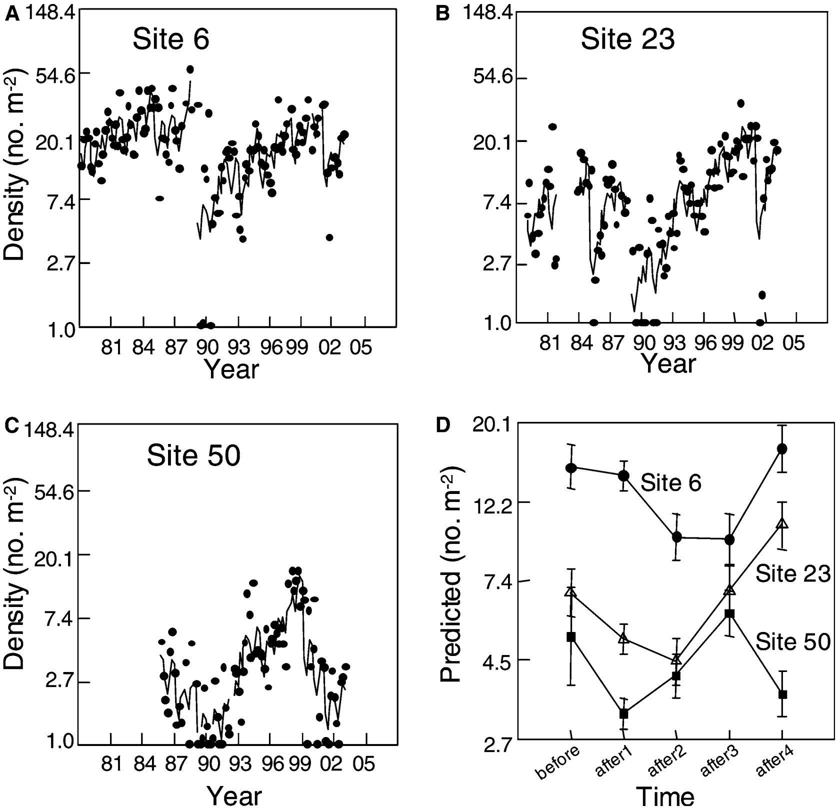

Fig. 2 Observed (*filled circles*) and predicted (*solid lines*) density of all species of fish summed for **a** Site 6, **b** Site 23, **c** Site 50 illustrate patterns revealed by our "best" model for this variable. *X*-axis tick marks indicate the start of each sampling year. No standard errors are reported to minimize clutter. **d** Predicted density (± 1SE) for five time intervals used in ANODE; adjusted grand means for each time interval are plotted. Site 6 ; Site 23 ; Site 50 . Before: 1977–1985; after1: 1986–1993; after2: 1994–1996; after3: 1997–1999; after4: 2000–2002. All panels were plotted on log scale

decreased the AIC statistic by similar amounts when they were added in the presence or absence of the other (comparisons 2 vs. 3 for hydrology and 1 vs. 4 for management). This consistency indicates that these parameters are explaining unique aspects of the data (they are not confounded) for these two dependent variables. The effect of DSD was nonlinear for Total Fish (Table 1: both DSD and DSD^2 were significant) while its effect was linear for least killifish (Table 1: only DSD was significant). Bluefin killifish yielded no evidence of an effect of management (Table 1: ANODE comparisons 1 and 4), but did display a marked effect of hydrology (Table 1: ANODE comparisons 2 and 3); site-by-treat was not indicated as significant by the Wald's test statistic. In contrast, our base models of eastern mosquitofish and flagfish density were not improved by adding DSD, but were improved by adding site-by-treat. Though ANODE did not indicate that DSD improved the models for either species, the Wald's *F*-statistic did indicate significant effects when it was present. Finally, our best models for Total, bluefin killifish, and least killifish fit the data well (Table 1, $R^2 > 0.60$), while our models for eastern mosquitofish and flagfish were more equivocal ($R^2 = 0.54$ and 0.40, respectively).

Total fish, least killifish, and eastern mosquitofish displayed similar patterns of effects in our BACI comparisons: prior to 1986, they were less dense at Site 23 than at 6, the density at 23 was not different from Site 50; however, their density at Site 23 gradually increased and converged on that observed at Site 6, the density exceeding the density at Site 50 by sampling interval after4 (Table 2). We have illustrated the management effect by plotting the predicted density of all fish versus DSD, separately for each sampling interval (Fig. 3). During the first three sampling intervals, Site-23 fish density overlapped with that at Site 50 when comparing over a similar range of DSD. However, in the last two intervals, and especially in the final interval, density at Site 23 overlapped more with density at Site 6 and less with Site 50. This is most clear at low values for DSD. In contrast, the density of bluefin killifish and flagfish were not demonstrated to be different between Sites 6 and 23 in the "before" period of the study (Table 2), and displayed no clear temporal patterns through its course. Generally, though not significantly different by our Tukey-adjusted comparisons, bluefin killifish were consistently denser at Site 6 than at Site 23, and least dense at Site 50, throughout the five time intervals. The density of flagfish was variable and inconsistent among the sites over the five comparisons. Both bluefin killifish and flagfish were more abundant at Site 6 than at Site 23 in the 'after1' interval, but Sites 23 and 50 were not different at that time.

Community composition

We observed marked temporal change in community structure at all three study sites over the course of the study (Fig. 4). Permutation tests were calculated by resampling across both plots and years; the ordination

Table 1 Summary of models for all fish summed (Total) and four most abundant species

Species	Model	AIC	ANODE		R^2 (AIC)	Treat	Site ×treat	DSD	DSD^2	LD	LD ×treat
			C	D							
Total	Base (B)	1624				*	–	–	–	–	–
	B + site × treat	1584.6	1	39.4		*	*	–	–	–	–
	B + hydrology	1611.8	2	12.2		0.052	–	*	*	NS	NS
	Full	1578.3	3	6.3	0.702(1588.7)	0.531	*	*	*	*	0.063
			4	33.5							
Bluefin Killifish	Base (B)	1041.6				*	–	–	–	–	–
	B + Site × treat	1044.5	1	–2.9		*	0.558	–	–	–	–
	B + dsd[b]	1013.6	2	28	0.663(1245.8)	0.019	–	*	*	–	–
	Full[b]	1023.2	3	21.3		0.027	0.993	*	*	–	–
			4	–9.6							
Least Killifish	Base (B)	1121				*	–	–	–	–	–
	B + Site × treat	1092.6	1	28.4		*	*	–	–	–	–
	B + hydrology	1094.1	2	26.9		0.143	–	*	0.271	NS	0.024
	Full	1075.7	3	16.9	0.722(1213)	0.04	*	*	0.484	0.062	NS
			4	18.4							
Mosquitofish	Base (B)	1395				*	–	–	–	–	–
	B + Site × treat	1342.1	1	52.9	0.546(1369.4)	*	*	–	–	–	–
	B +hydrology	1445.5	2	−50.5		*	–	*	*	NS	*
	Full	1407.2	3	−65.1		0.264	*	*	*	*	0.121
			4	38.3							
Flagfish	Base(B)	833.2				*	–	–	–	–	–
	B + Site × treat	802.4	1	30.8	0.404(818.3)	*	*	–	–	–	–
	B + hydrology	881.2	2	−48		*	–	0.076	*	0.022	*
	Full	875.8	3	−73.4		*	*	*	*	NS	NS
			4	5.4							

Analysis of Deviance (ANODE) models increase in complexity from Base (see text) to Full model. Under ANODE, C indicates comparison (1–4 described in text) and D indicates deviance for that comparison. Comparisons (1) and (4) indicate effects of the management manipulation and comparisons (2) and (3) indicate effects of hydrology; for values > 2.0, inclusion of term to the model increases information about the data

R^2 is the coefficient of determination for the best model; AIC for fixed-effects model is reported in parentheses

[b] Inclusion of LD in the model for bluefin killifish decreased fit and was not reported; $^*P < 0.003$; – indicates a term not tested on this model

Table 2 Generalized least-squares (GLS) means (ln[$n+1$]) and effect sizes ([GLS mean Site 6 – GLS mean Site 23] and [GLS mean Site 50 – GLS mean Site 23]) from pairwise comparisons of BACI hypotheses for targeted species

Species/data type	Site	Before (SE) 1978–1985	After1 (SE) 1986–1993	After2 (SE) 1994–1996	After3 (SE) 1997–1999	After4 (SE) 2000–2002
Total fish						
Effect size	6	**0.791**(0.208)	**1.033**(0.128)	**0.787**(0.194)	0.325(0.201)	0.477(0.196)
GLS mean	23	1.928(0.153)	1.636(0.093)	1.493(0.146)	1.938(0.157)	2.359(0.145)
Effect size	50	−0.277(0.339)	−**0.473**(0.129)	−0.091(0.196)	−0.142(0.214)	−**1.072**(0.204)
Bluefin killifish						
Effect size	6	0.613(0.201)	**0.591**(0.133)	0.597(0.188)	0.640(0.194)	0.516(0.197)
GLS mean	23	0.801(0.147)	0.667(0.095)	0.811(0.137)	0.785(0.145)	0.933(0.143)
Effect size	50	−0.363(0.277)	−0.241(0.134)	−0.166(0.190)	−0.144(0.201)	−0.381(0.202)
Least killifish						
Effect size	6	**0.742**(0.191)	**0.769**(0.123)	**0.810**(0.179)	−0.092(0.185)	−0.005(0.185)
GLS mean	23	0.750(0.140)	0.441(0.089)	0.390(0.131)	1.020(0.139)	1.078(0.135)
Effect size	50	−0.319(0.273)	−0.099(0.125)	−0.139(0.180)	−0.497(0.193)	−**0.661**(0.191)
Mosquitofish						
Effect size	6	**1.089**(0.170)	**0.689**(0.108)	**0.782**(0.165)	−0.137(0.172)	0.318(0.167)
GLS mean	23	0.878(0.129)	0.802(0.077)	0.922(0.117)	1.495(0.121)	1.516(0.118)
Effect size	50	−0.354(0.295)	−**0.450**(0.108)	−0.207(0.165)	−0.311(0.170)	−**1.048**(0.166)
Flagfish						
Effect size	6	0.016(0.108)	**0.425**(0.069)	0.142(0.105)	−0.090(0.109)	0.274(0.106)
GLS mean	23	0.355(0.082)	0.445(0.048)	0.084(0.075)	0.309(0.077)	0.258(0.074)
Effect size	50	0.225(0.197)	−0.208(0.068)	0.069(0.105)	−0.069(0.108)	0.032(0.105)

GLS means and effect sizes were estimated from the best model for each species, except for bluefin killifish, which required addition of site-by-treat interaction to produced estimates for this table.

SE is the standard error for the GLS mean or pairwise comparison. Comparisons with Tukey-adjusted P values less than or equal to 0.05 are indicated in bold

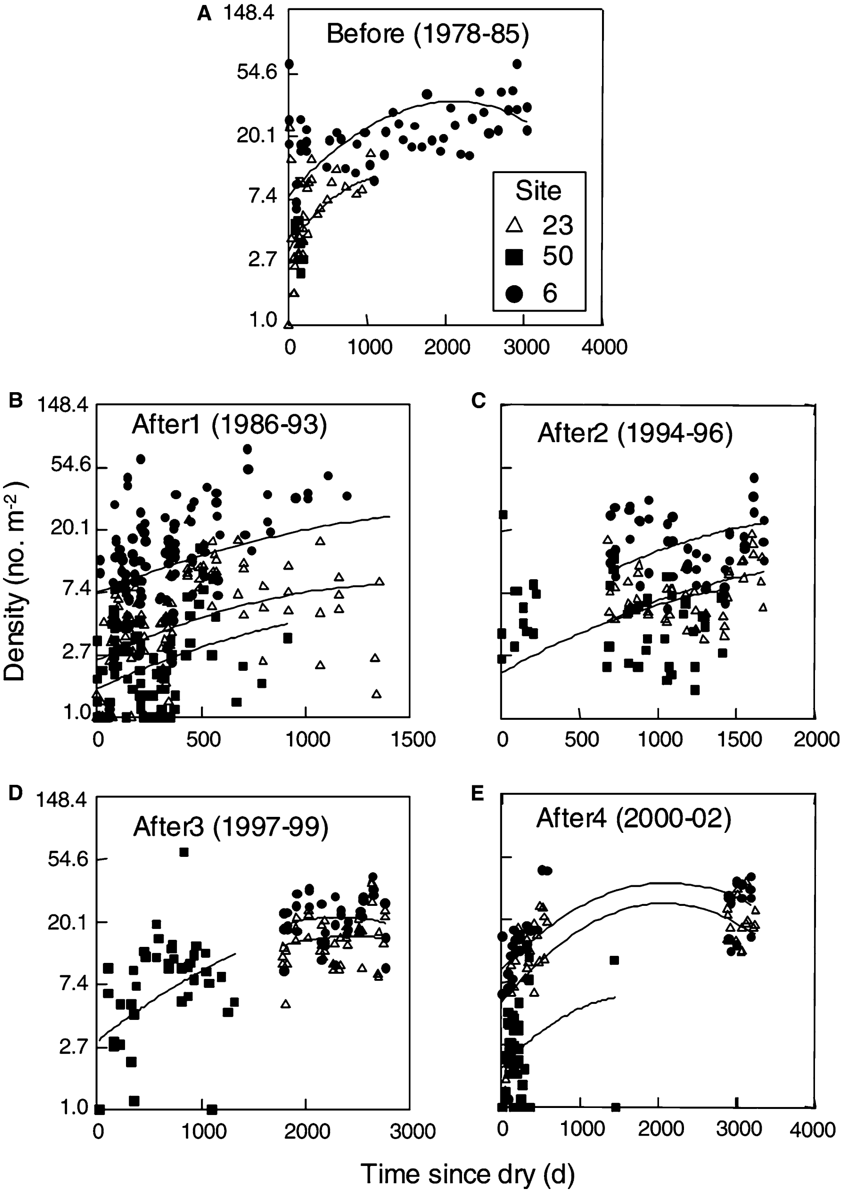

Fig. 3 ANODE-predicted density plotted against time-since-dry for dependent variable total fish; the site-by-time-since-dry interaction is shown on each graph as separate *solid lines* for each site. Three clustered points with the same symbol display results for each plot. The five study intervals are plotted separately. In the after4 panel, the points with low values for time-since-dry were collected after the ones with higher values because the interval started late in a sequence of wet years and continued after a dry-down event

plot was derived by pooling years to create visually interpretable graphs. These tests indicated that community composition differed between all but one pair of successive time intervals at Site 6 (Global permutation test, $R = 0.155$, $P = 0.005$; before vs. after1, $R = 0.182$, $P < 0.009$; after1 vs. after2, $R = 0.029$, $P = 0.318$; after2 vs. after3, $R = 0.343$, $P = 0.005$; after3 vs. after4, $R = 0.280$, $P = 0.004$). The lack of significant change between intervals after1 and after2 is surprising because this corresponds to the 1989–1990 drought and the immediate years afterward. It seems likely that this result derives from high interyear variation within these two intervals, rather than a lack of real change (i.e., the grouping of years used here is obscuring change at a shorter time scale). Though composition converged back to a similar mix in the predrought and wet intervals (Fig. 4a, b), they were distinguishable (Permutation test: before vs. after4, $R = 0.172$, $P = 0.031$). At Site 23, two of the time intervals did not yield significant change (Global permutation test, $R = 0.265$, $P = 0.001$; before vs. after1, $R = 0.089$, $P < 0.089$; after1 vs. after2, $R = 0.262$, $P = 0.009$; after2 vs. after3, $R = 0.774$, $P = 0.001$; after3 vs. after4, $R = 0.146$, $P = 0.044$). Finally, only the difference between time interval after2 and after3 was not significant at Site 50 (Global permutation test, $R = 0.318$, $P = 0.001$; before vs. after1, $R = 0.048$, $P < 0.323$; after1 vs. after2, $R = 0.431$, $P = 0.001$; after2 vs. after3, $R = 0.282$, $P = 0.012$; after3 vs. after4, $R = 0.738$, $P = 0.001$).

After combining the data for fish collected within a single interval, all of the comparisons of the species-by-sample matrices indicated that the study sites were different, with one exception. The pairwise comparison of Site 6 and Site 23 at the final sampling interval indicated that the communities were not distinguishable from 2000 to 2002 (Global permutation test, $R = 0.635$, $P = 0.001$;

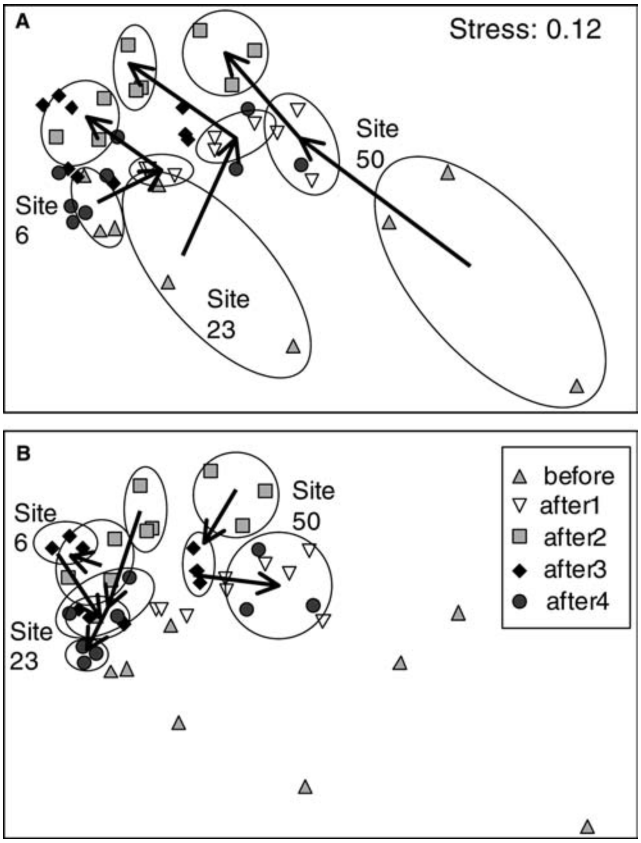

Fig. 4 Twenty-five years of change in fish community composition illustrated by NMDS. The distance separating points is proportionate to relative difference in community composition. Both panels illustrate the same ordination results; circles enclose data from the three plots at each site and sampling interval. Before: 1977–1985; after1: 1986–1993; after2: 1994–1996; after3: 1997–1999; after4: 2000–2002. **a** Lines connect results from the same site during the first three sampling intervals (before, after1, after2). **b** Lines connect results from the same site during the last three sampling intervals (after2, after3, after4)

Site 6 vs. Site 23, $R = 0.054$, $P = 0.210$; Site 6 vs. site 50, $R = 0.990$, $P = 0.001$; Site 23 vs. site 50, $R = 0.944$, $P = 0.001$). The increasing similarity of Sites 6 and 23 over the course of this study was primarily from the changing density of least killifish (Fig. 5) and eastern mosquitofish. The difference between these two sites and Site 50 was not only from differences in density (there were consistently fewer fish at Site 50) but also from differences in relative abundance. Site 50 consistently produced fewer bluefin killifish and least killifish, and more marsh killifish (Fig. 5), flagfish, and sheepshead minnows than Sites 6 and 23. Lake chubsuckers were never abundant enough to be influential in these analyses, but were collected at Site 6 in all sampling intervals, were first collected at Site 23 in the 'after2' interval but then in all subsequent intervals, and were not collected until the final interval at Site 50. We repeated these analyses with standardized (relative abundance) and presence–absence data, and the same pattern of results were obtained.

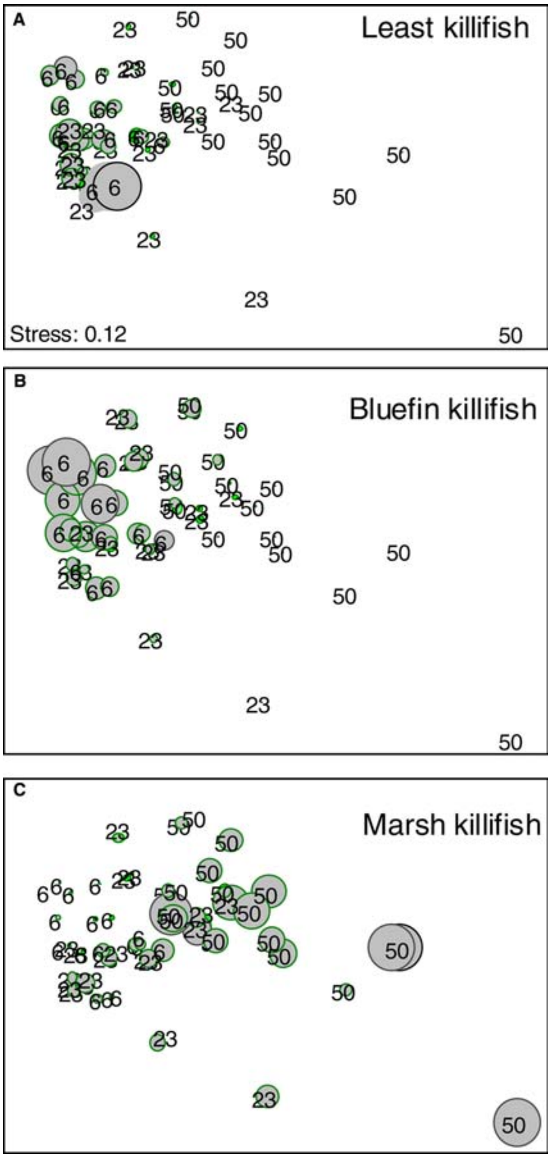

Fig. 5 The relative contribution of three fish species **a** least killifish, **b** bluefin killifish, **c** marsh killifish to temporal and spatial patterns of community dissimilarity. Marsh killifish dominate the short-hydroperiod site (Site 50), while least killifish and bluefin killifish were most abundant at the long-hydroperiod site (Site 6). All three panels illustrate the same NMDS results as shown in Fig. 4; the *size of the circles* indicate the relative density of each species at each site and time

The fish communities at our three study sites displayed a succession of species that unfolded over a multiyear period following a dry-down event if the site was not redried. At all three sites, Bray–Curtis dissimilarity among samples increased as the difference in DSD between them increased. A Mantel test revealed positive correlations between Bray–Curtis dissimilarity and the difference in DSD if data from the same plot and drying event were compared (using fourth-root transformed data; Site 6: Mantel's $r = 0.302$, $P \ll 0.001$; Site 23: Mantel's $r = 0.246$, $P \ll 0.001$; Site 50: Mantel's statistic $r = 0.313$, $P \ll 0.001$). These correlations were not different from zero if different plots and/or events were intermingled in the comparisons.

Discussion

Our intervention study revealed multiyear time lags in the fish community's response to hydrological events that resulted from interspecific variation in population recovery following drought, similar to those seen for aquatic macroinvertebrates in streams (Boulton 2003). The magnitude of this temporal lag was influenced by landscape and environmental history; short-hydroperiod habitats (by definition) seldom remain inundated more than one or two years before a new disturbance resets community composition, while the time lag extended for years at long-hydroperiod sites. The intensity of disturbance (length of a dry period) contributed to explain community variance, though less than the time since the most recent disturbance. Finally, the data suggested that the history of drying prior to the most recent event also affected the impact of disturbance, though our data were not adequate to confidently discriminate this historical effect from the intensity of disturbance.

Our data provide support for Loftus and Eklund's (1994) disturbance-limitation hypothesis when drought events recur every three or fewer years, or anywhere that the most recent dry-down is less than three years in the past. The small fish community in a long-hydroperiod marsh is in a recovery stage for at least 3–5 years following the infrequent but inevitable dry-down events that characterize central sloughs of large wetlands. Following the 1989–1990 drought, small-fish community composition and density at Site 6 stabilized at levels similar to those present before the drought and afterward it remained inundated for over 3 years. An ideal test of our alternative regulation hypotheses would include a manipulation of piscivore density independent of the hydrological manipulation. The density of adult piscicorous fishes was not assessed in this ecosystem until 1995 (Chick et al. 1999), and a manipulation of their abundance is not practical at the scale of this ecosystem. However, we are able to assess Kushlan's hypothesized piscivory release from data collected between 1995 and the present (Trexler et al. 2001; Chick et al. 2004). Piscivore density (and the density of all fishes less than 8-cm standard length) increases as postdrought time increases, and is lower at short-hydroperiod sites than long-hydroperiod ones (Fig. 6a; Chick et al. 2004). Further, the density of piscivorous fishes declined at Sites 6 and 23 in 2000, coincident with a system-wide drought (we cannot assess piscivore density at Site 50 because access by airboat is not permitted). Thus, for the Shark River Slough portion of the Everglades, it appears that the time between drying events is short enough that both piscivores and their prey fish are primarily limited by drying frequency. There are areas north of the Shark River Slough (Water Conservation Area 3A), where drying is much less frequent (over the 25 years of this study, drying in 1989 and partially in 2001). These areas have a lower density of small fish than Shark River Slough and (prior to 2001) a higher density of piscivores (Chick et al. 2004). Interestingly, the density of least killifish, bluefin killifish, and mosquitofish, increased in these very long hydroperiod areas after 2001 when localized drying greatly diminished the density of piscivores (Trexler, unpublished data). In sum, Kushlan's predator-regulation hypothesis may hold for regions of the ecosystem experiencing very infrequent drying (Fig. 6b). Furthermore, this illustrates that disturbance limitation and predator regulation may be best viewed as part of a continuum of disturbance/stress effects along a single gradient (Fig. 6b).

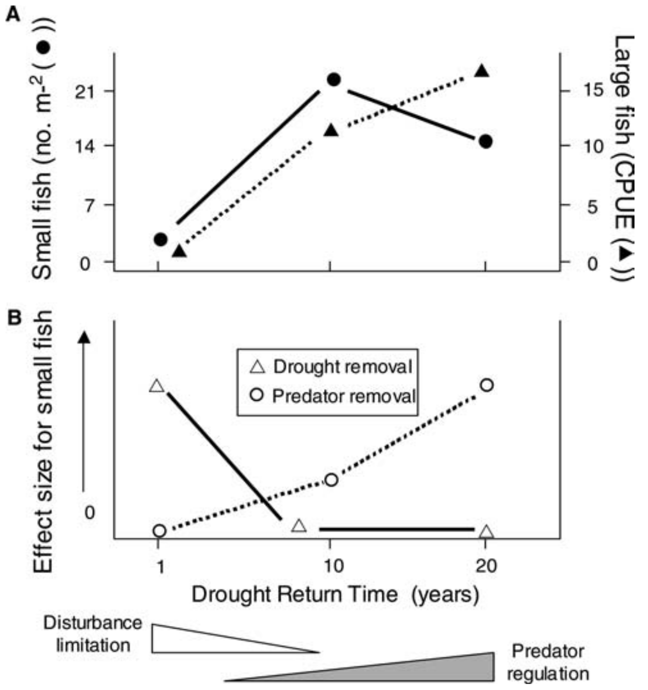

Fig. 6 **a** Observed patterns of fish density by size class versus time in years between drought events. Large fish have multiyear life cycles in this system, while all small fish have one or more generations per year. Data from Trexler et al. (2001) and Chick et al. (2004). **b** Conceptual model of hypothesized effect size for small fish from disturbance and predation in the Everglades system. Effect size is the predicted magnitude of change resulting from relaxation of predation rate or drought frequency (each while holding the other constant) at sites with the indicated drought return time. Wedges at the bottom of the figure indicate the relative importance of disturbance and predation at a given drought frequency. Note these overlap for an intermediate range of frequency

Colonization ability and survival in aquatic refuges play an important role in shaping fish communities in Florida wetlands (Jorden et al. 1998; Baber et al. 2002). Mosquitofish recovered their density rapidly following drought, consistent with their strong dispersal and colonization ability (e.g., Snodgrass et al. 1996). Similar to our study, Jorden et al. (1998) observed a short-lived density increase in flagfish in the post-dry-down marshes in north Florida. It is not clear whether flagfish density continues to decrease as the time-since-dry-down increases because environmental conditions become less suitable or because other fishes, perhaps piscivores, become more abundant. 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, marsh killifish absolute density did not decline as time following the drought increased, instead their relative abundance declined as the rest of the community increased. Thus, species-level patterns resulted from interspecific variation in survival through the drought in local aquatic refuges, long-distance dispersal ability from distant refuges, and population growth rate in the postdrought environment (Magoulick and Kobza 2003). Clearly, some prey species within a community could be regulated by their predators when experiencing a particular disturbance regime while others are not, depending on their life histories, those of their predators, and the extent of diet specialization by the predators.

Community dissimilarity and community convergence

Community dissimilarity analyses indicated that spatial variation and temporal variation coincide: our long-hydroperiod site became more like the short-hydroperiod one when the DSD overlapped, then diverged from it as the DSD extended beyond those observed at the short-hydroperiod site. At all three sites, community dissimilarity was positively correlated with the difference in DSD, indicating a temporal covariance in community structure, set less by an annual or seasonal clock than by a hydrological one.

Local-community dissimilarity is a function of regional species-pool size, spatial connectance, productivity, and disturbance frequency (Chase 2003). Our results are consistent with predictions for systems with small regional species pools, high rates of connectance, low productivity, and high disturbance. Local dissimilarity varied as a function of time since disturbance, and regional dissimilarity decreased as time since disturbance and frequency of disturbance converged. Though long time periods may be necessary to assert that communities have converged (Inouye and Tilman 1995; Samuels and Drake 1997), the consistency of temporal and spatial convergence we observed suggests a single or small number of local stable community states determined by recent disturbance history. The outcome of ecological restoration in such communities may be more predictable than those with dynamics dominated by priority effects and contingency of recolonization and recruitment (Young et al. 2001).

Disturbance in landscapes: environmental covariance

All four aspects of disturbance (frequency, intensity, scale, and sequence) contributed in explaining community dynamics in this study. Disturbance frequency (or return time) was manipulated, revealing that disturbance intensity covaried with frequency. The spatial scale of disturbances that were manipulated was large (water flow through 20 culverts scattered over approximately 15 kms of levee). Disturbance scale is intimately related to disturbance intensity because of the basin configuration of this and other aquatic systems (Benda et al. 2004); the lower the water table drops, the larger the area of the basin that is dried, and the longer that a location that does dry remains so. The sequence of years with different intensity of disturbance was not under our control, but clearly had an impact on the communities we studied. For example, the two-year drought in 1989–1990 left a persistent influence on aquatic communities at all three study areas for several years, though community change in the intervening wet season of 1989–1990 was not so marked. It appeared that two consecutive years of drought in areas seldom dried created a profound impact, while that period failed to yield marked effects on sites that dried routinely.

Covariance of disturbance frequency, intensity, and scale in a landscape means that some combinations of these factors are not observed in this ecosystem. An orthogonal analysis of these factors is only possible in a manipulative experiment that controls landscape; thus, our study conducted in the “natural” landscape was not completely successful in isolating frequency from intensity. However, the spatial scale needed for a controlled experiment of hydrological effects may not be practical for aquatic communities including relatively mobile species of fish (e.g., we have tracked radio-tagged gar moving 8 km per week in response to declining water depths). Our intervention approach capitalizing on a management action proved an informative compromise of manipulation scale and experimental design by incorporating multiple “control” sites bracketing the pre- and postmanipulation conditions.

This study revealed pervasive spatial and temporal covariance in components of disturbance imposed by the landscape of this and other aquatic systems. Spatial and temporal covariances are particularly difficult to interpret in sampling data (Ranta et al. 1999). An experimental approach is the only real solution to this analytical constraint. While pervasive environmental covariance mandates that some combinations of environmental factors are rare or absent in natural systems, anthropogenic activity that creates these combinations unintentionally are probably a major source of ecological “surprises” in environmental management (Hollings 1986). Thus, exploring them has merit for a predictive environmental science.

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