

Disturbance regime and limits on benefits of refuge use for fishes in a fluctuating hydroscape

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Refuge habitats increase survival rate and recovery time of populations experiencing environmental disturbance, but limits on the ability of refuges to buffer communities are poorly understood. We hypothesized that importance of refuges in preventing population declines and alteration in community structure has a non-linear relationship with severity of disturbance. In the Florida Everglades, alligator ponds are used as refuge habitat by fishes during seasonal drying of marsh habitats. Using an 11-year record of hydrological conditions and fish abundance in 10 marshes and 34 alligator ponds from two regions of the Everglades, we sought to characterize patterns of refuge use and temporal dynamics of fish abundance and community structure across changing intensity, duration, and frequency of drought disturbance. Abundance in alligator ponds was positively related to refuge size, distance from alternative refugia (e.g. canals), and abundance in surrounding marsh prior to hydrologic disturbance. Variables negatively related to abundance in alligator ponds included water level in surrounding marsh and abundance of disturbance-tolerant species. Refuge community structure did not differ between regions because the same subset of species in both regions used alligator ponds during droughts. When time between disturbances was short, fish abundance declined in marshes, and in the region with the most spatially extensive pattern of disturbance, community structure was altered in both marshes and alligator ponds because of an increased proportion of species more resistant to disturbance. These changes in community structure were associated with increases in both duration and frequency of hydrologic disturbance. Use of refuge habitat had a modal relationship with severity of disturbance regime. Spatial patterns of response suggest that decline in refuge use was because of decreased effectiveness of refuge habitat in reducing mortality and providing sufficient time for recovery for fish communities experiencing reduced time between disturbance events.

Understanding the role of refuge habitats in the response of mobile animals to disturbance is becoming increasingly important as climate projections forecast increases in disturbances such as drought (Bates et al. 2008). Disturbance can be defined as a temporally discrete removal of biomass, resulting in changes in the physical environment (Sousa 1984, White and Pickett 1985). Animal and plant communities have a variety of coping mechanisms that increase survival (resistance) and recovery (resilience) from potentially catastrophic physical disturbances, and many studies have detailed the complex outcomes of disturbance on communities of sessile organisms (Connell and Keough 1985). In contrast, less is known about the responses of mobile animals to disturbance. Refuge-seeking behavior is one coping mechanism used by mobile organisms, wherein animals use habitat patches that ameliorate physiological stress and reduce mortality caused by unfavorable conditions. While previous studies have documented the role of refuge patches in the dynamics of animal communities that experience physical disturbances (Robertson et al. 1995, Palmer et al. 1996), few have quantified the spatial-temporal dynamics of mobile animals and refuge use when there are large changes

in disturbance regime (Perry and Bond 2009). Sources of variability in refuge use are still not well understood and it is unknown if refuge-seeking behavior can buffer populations and communities from a disturbance regime that becomes increasingly severe.

Characteristics of disturbance regime, and composition of the community experiencing it, influence the linkage between refuge and disturbed habitats. Here, we seek to examine how the severity of a disturbance regime, measured as its impact on communities, is determined by the intensity, duration, and return time of physical events (White and Pickett 1985), and is perhaps modified by refuge use. Intensity (defined here as magnitude of physical event) and duration of a disturbance influence both the strength of the environmental stimulus promoting a response to seek shelter and the likelihood of surviving the disturbance. Return time of a disturbance influences the level of recovery of former abundance and composition in the disturbed habitat until the next stimulus to seek shelter. Intensity, duration and frequency of disturbance should influence spatial and temporal patterns of refuge use, as well as the relative role of refuges in population and community dynamics. Disturbances are

often heterogeneous across landscapes because of variation in habitat structure, topography, and the arrangement of habitat patches (Pickett and White 1985). A further source of variation in refuge use is the characteristics of the species composing the community in the disturbed habitat because species vary in their susceptibility and responses to disturbance (Woodin 1978, Davey et al. 2006). A closed equilibrium community is comprised solely of species with life histories yielding net zero replacement rates through strategies coping with the disturbance regime, but in a world of changing disturbance or spatially open communities, species with inadequate refuge use strategies may persist for some time on their way to local extinction. The role of refugia in the responses of communities to disturbance will depend in part on how refuge use is determined by the combined influences of disturbance characteristics, habitat features, species traits and landscape structure, and is important in shaping species pools at both the local and regional scales (Poff 1997, Keddy and Weiher 1999).

The Florida Everglades is an aquatic system that experiences periodic droughts as a result of seasonally and annually fluctuating rainfall and anthropogenic diversions of water. Currently, droughts are an understudied type of disturbance regime, even though they can drive spatial-temporal dynamics of communities (Lake 2003, Perry and Bond 2009). Natural heterogeneity in topography across the Everglades hydroscape has resulted in spatial variability in the frequency and intensity of droughts (Trexler et al. 2002, Ruetz et al. 2005). Human influences on the Everglades hydroscape, such as canals and compartmentalization of the Everglades into separate regions, have added additional spatial variability in patterns of drought disturbance. Topographic heterogeneity in the Everglades hydroscape is increased by trails and ponds formed by the movement and digging behavior of American alligators *Alligator mississippiensis*. Alligators act as ecosystem engineers by creating and maintaining natural depressions dispersed across the Everglades hydroscape and these alligator ponds act as refuge habitat for fishes during seasonal droughts (Kushlan 1974). Fishes in the Everglades also have access to artificial refuge habitat, such as impoundments and canals.

Characterizing fish response to drought in a large ecosystem like the Everglades is complicated by interspecific differences in strategies for coping with drought and in resistance and resilience to disturbance. For example, bowfin *Amia calva* and Florida gar *Lepisosteus platyrhincus* use their swim bladders for aerial respiration, and bowfin can also aestivate under the sediment of dried marshes (Loftus and Kushlan 1987). Fishes in the Everglades also vary in their dispersal abilities by size (Trexler et al. 2002) and species (Ruetz et al. 2005). Large fishes (total length ≥ 8 cm) are especially vulnerable to droughts because they become stranded and die at higher water levels than small species (Chick et al. 2004). Many of these large fish species are piscivores; therefore, the presence of refuge habitat that reduces predator mortality from droughts likely influences the role of predation in this ecosystem.

We quantified and compared fish population and community dynamics in marshes and alligator ponds that experienced disturbance regimes that varied spatially and temporally. Specifically, we were interested in: (1) quantifying

patterns of refuge use during hydrologic disturbance and (2) evaluating the role of refuge use in the dynamics of communities in the disturbed habitat. We determined which species from the marsh habitat populated alligator ponds during hydrologic disturbances by comparing community structure in refuge habitat before and during seasonal droughts. To investigate sources of variation in fish abundance among alligator ponds, we quantified the importance of disturbance intensity, fish abundance in donor habitat prior to disturbance, and proximity of deepwater habitats other than alligator ponds. We also examined how spatiotemporal patterns in disturbance influenced the use of alligator ponds as refuge and asked if alligator ponds are able to buffer fish communities from disturbance-induced changes.

Across a range of disturbances, we predicted that the use of refuge habitat increases as either a positive linear relationship with severity of disturbance regime, an asymptotic relationship with disturbance resulting from decreasing benefits of refuge use, or a modal relationship with disturbance resulting from a loss of resistance and resilience of the fish community as disturbance becomes more intense, more frequent, or of greater duration (Fig. 1). Under conditions that are relatively benign due to low intensity or frequency of disturbance, the use and importance of refuge habitat will be low. As disturbances become more frequent or intense, use of refuge habitats will increase and the importance of these habitats for buffering communities of mobile animals will grow (Fig. 1A). If refuges provide sufficient buffering from disturbance, then abundance and community structure outside them should not exhibit a long-term response to an increasingly severe disturbance regime. Use of refuge habitats may eventually plateau as refugia become saturated (Fig. 1B). However, as disturbance regime increases in severity, a threshold in refuge benefits may be reached due to insufficient recovery time, too strong a disturbance, or both. Past this threshold, the pool of surviving animals that uses the refuge patches is smaller than before, resulting in declining abundance (Fig. 1C). Quantifying these spatiotemporal dynamics not only details the influence of variable disturbance regime on refuge-seeking behavior but also clarifies the role of refuges in the response of animal communities to environmental disturbance.

Methods

Study area and sampling design

The Florida Everglades is a karstic, oligotrophic wetland that experiences strong seasonal variation in rainfall. Approximately 79% of average annual precipitation falls during the wet season (May–October; 110.5 cm), with an average of 29 cm of rain during the dry season (November–April; 40-Mile Bend Station; 1940–2006; Southeast Regional Climate Center). During seasonal droughts, water level declines throughout the Everglades with variation in topography influencing the amount of water retained in local marshes and sloughs. Historically, water from the Everglades flowed uninterrupted from its source in Lake Okeechobee south to Florida Bay. Currently, a series of canals and levees interrupts the southerly water flow and divides the Everglades

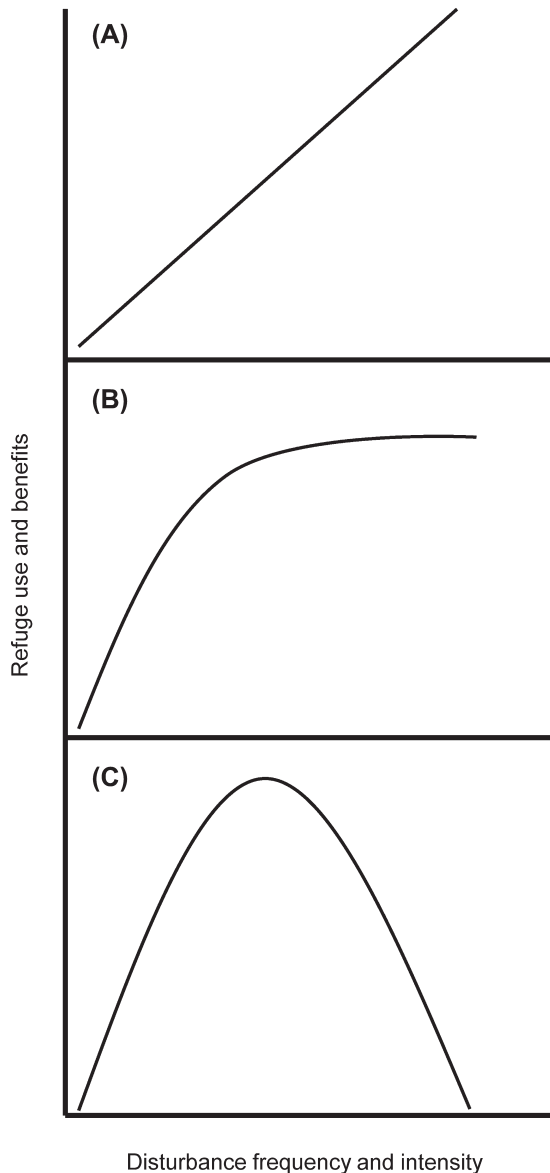


Figure 1. The relationship between disturbance frequency or intensity and either the use or benefits of refuge habitat is predicted to be (A) linear, (B) asymptotic, or (C) modal. Disturbance frequency and intensity increase from left to right on this graph. We hypothesize similar patterns with return time of disturbance or time passed since the most recent disturbance, but with x-axis values decreasing from left to right or the patterns being reversed.

landscape into regional compartments that vary in hydrology (Fig. 2). Among regional compartments, number of days in a year that marshes are inundated with water declines from north to south because of blockage of water flow out of Water Conservation Area 3A (WCA 3A) and into Shark River Slough (SRS), resulting in more frequent and extensive marsh drying in SRS than in WCA 3A (Fig. 2, 3). In addition to seasonal rainfall leading to intra-annual variation in water level, inter-annual variability arises from both natural variation in precipitation and changes in human-controlled patterns of water release. During the time period of this study (1997–2007), marked inter-annual change in hydrologic disturbance regime was measured in all regions (Fig. 3). Decline of water level below 10 cm was considered

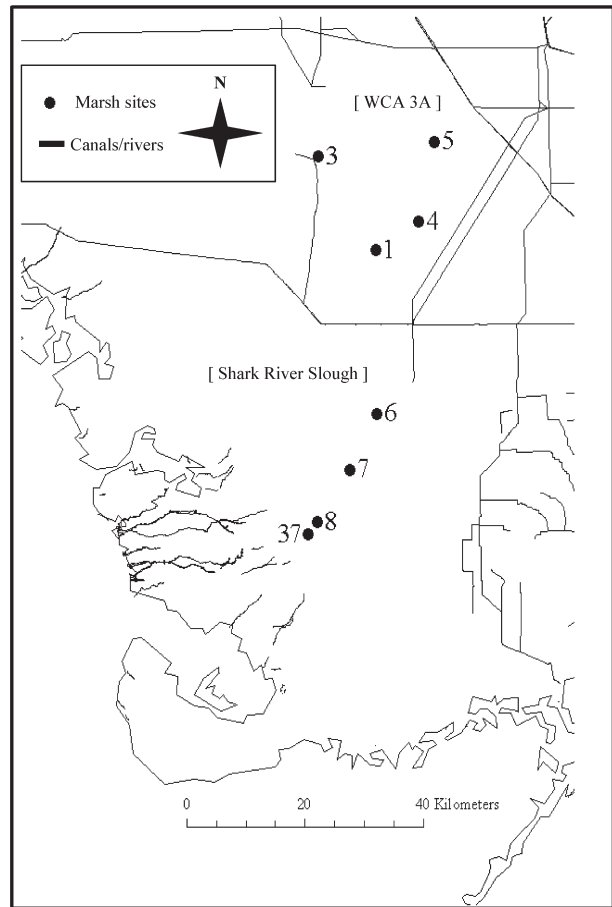


Figure 2. Map of marsh site locations in two regions (Shark River Slough and WCA 3A) of the Florida Everglades sampled for large fish ($SL \geq 8$ cm SL) abundance.

a hydrologic disturbance for fishes 8 cm standard length (SL) and larger because these fish are forced to disperse to avoid mortality (Chick et al. 2004). All regions experienced an increase in severity of hydrologic disturbance regime during the study. After 2000, SRS experienced both an increase in duration of and a decrease in recovery time between marsh dry-downs (Fig. 3). Duration and frequency of disturbance also exhibited a great deal of spatial variation within hydrologic regions (i.e. SRS and WCA 3A; Fig. 3). Dry-downs were initially less spatially extensive in WCA 3A, but increased in spatial extent and duration following 2000 (Fig. 3). These changes in disturbance patterns corresponded to a change in water management and the onset of a period of reduced rainfall (Trexler and Goss 2009).

We measured the catch per unit effort (CPUE) of large fish species ($SL \geq 8$ cm) in SRS and WCA 3A by airboat electrofishing in four marsh sites and 10 alligator ponds in each region (Fig. 2, Appendix 1). CPUE from airboat electrofishing has been shown to be an effective index of the density of large fish in shallow wetlands (Chick et al. 1999). We used pulsed DC current and standardized power at 1500 W at each site to increase the precision of abundance estimates (Burkhardt and Gutreuter 1995, Chick et al. 1999). Each marsh site was divided into three 1-ha plots containing three transects per plot, with each transect consisting of five min of electrofishing effort (Chick et al. 1999, 2004).

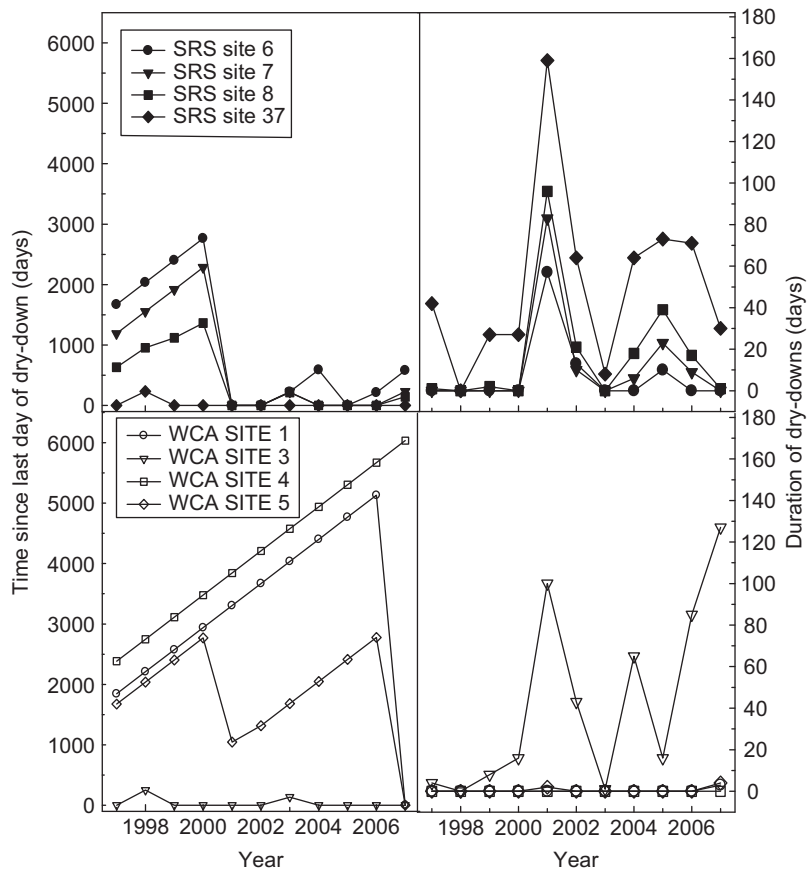


Figure 3. Number of days since last day of dry-down (water depth < 10 cm) and duration of marsh dry-downs (days) in Shark River Slough (SRS) and Water Conservation Area 3A (WCA 3A). Data points are annual averages for each site based on model estimates of daily depth for each location.

Alligator ponds (diameter = 3.7–73.2 m) were embedded within larger patches of marsh prairie, with each alligator pond associated with a marsh sampling location (Appendix 1). We sampled fish in alligator ponds by electrofishing for five min within each pond site. Each year, sampling events occurred twice in the dry season (February, April) and twice in the wet season (July, October). Standardized airboat electrofishing began in the marshes in 1997 and in alligator ponds in 1998. Low water barred our access to refuge sites in the dry season of some years, limiting our data on fish use of alligator ponds during low water conditions to 1998, 2002–2004 for SRS and 1998, 2001–2007 for WCA 3A. Analysis of trends in fish abundance in marsh habitat was based on data for the time period 1997–2007 for both regions.

Patterns of refuge use

To determine which fish species from the marshes use alligator ponds as refuge during the dry season, we averaged species CPUE by alligator pond site and season for each region and used analysis of similarity (ANOSIM) and similarity percentage breakdown analysis (SIMPER) to compare alligator pond species composition between high- and low-water conditions. We transformed CPUE data by taking the square root of each measurement, standardized abundances by converting CPUE to relative abundance, and then used

these standardized, transformed numbers to calculate a triangular Bray–Curtis similarity matrix (Clarke and Warwick 1994). We employed the square-root transformation because we were primarily interested in categorizing habitats by the dominant species present and this transformation weights common species over rare ones when similarities between samples are calculated. We used ANOSIM tests to determine if average rank similarities between sites within seasons were greater than average rank similarities between seasons. The significance of global R statistics from ANOSIM tests was assessed by comparing the global value to a null distribution of R generated by either 1000 permutations or as many permutations as possible given the sample size (Clarke and Warwick 1994). The value of R increases as replicates within a category, such as season, become more similar in community structure than replicates between categories. If fish communities in alligator ponds were found to be different between seasons, then we used a SIMPER analysis with square root-transformed data to determine which fish species were contributing the most to dissimilarity in community composition between the wet and dry season. To test for regional differences in community structure of alligator ponds, we used the above ANOSIM and SIMPER approach on regional means of species abundance for each year. Differences were considered significant when $p \leq 0.05$.

We used reduced maximum likelihood (REML) techniques to model fish CPUE in alligator ponds during April

when water levels were lowest during sampling. Models were constructed for the CPUE of all fish combined as well as for each of the four most common species (yellow bullhead *Ameiurus natalis*, warmouth *Lepomis gulosus*, Florida gar, lake chubsucker *Erimyzon sucetta*). We used Akaike's information criteria corrected for small-sample bias (AIC_c ; Anderson 2007) to quantify whether adding marsh water depth, distance to nearest non-alligator pond refuge, marsh fish CPUE the preceding wet season, CPUE of dry-down tolerant species in marshes the previous wet season, or any combination of these explanatory variables improved model performance from a base model consisting of only alligator pond size as an explanatory variable. Models with the most support have the lowest AIC_c values. Alligator pond size (measured as diameter) was used as a base model because of our expectation that number of animals should increase with size of habitat patch. We used water-depth estimates with a 30-day lag from marsh sites adjacent to sampled alligator ponds to capture possible environmental conditions leading up to fish sampling. Water depths for each marsh plot were daily estimates from regression models based on comparisons between depth measurements taken during fish sampling and measurements taken by continuous hydrological recording stations located near each plot ($R^2 > 0.90$). If close enough, large fish species may choose canals or headwater streams over alligator ponds as refuge from declining water levels. We used the measuring tool in Google Earth to determine the distance between each alligator pond and the closest alternative deepwater refuge. We defined dry-down tolerant species as those that could use aerial respiration to survive the drying out of their habitat. In the Florida Everglades these species included two native (Florida gar, bowfin) and one introduced (walking catfish *Clarias batrachus*) fish species. Higher numbers of dry-down tolerant species may be an indication of highly disturbed conditions. CPUE of dry-down tolerant species was not used as a variable when analyzing CPUE of either Florida gar, because this species is part of the dry-down tolerant group, or all fish combined. When more than one model contained equivalent information (i.e. $\leq 2 AIC_c$ units apart; Anderson 2007), we focused on the most parsimonious model. We also calculated evidence ratios for all models and coefficients of determination for the highest performing models in order to measure fit to the observed data (Anderson 2007). Evidence ratios illustrate the strength of empirical support for the best model and were calculated as the ratio of Akaike weights between the model with the lowest AIC_c score and each subsequent model (Anderson 2007). In general, the greater the evidence ratio, the weaker the relative support for a given model within a set of models, compared to the most supported model (i.e. lowest AIC_c). To facilitate comparison across sets of models, we used coefficient of determination (R^2) as an absolute measure of model fit. Due to increasing correlation between fish abundances as time between measurements decreased, we applied a first-order autoregressive covariance structure to all analyses (Littell et al. 1996). To normalize data, all variables were natural-log transformed ($N + 1$ for variables where zeros were possible).

To examine the shape of the relationship between disturbance and the use of alligator ponds as refuge during the dry season, we modeled total CPUE of fish in alligator ponds during the dry season as either a linear or

quadratic function of time since the last hydrologic disturbance (i.e. days since last day of marsh dry-down), using nested repeated-measures regression models. Support for each model was evaluated with AIC_c scores and model fit to the data assessed by R^2 . Models were based on CPUE for individual alligator ponds from each sampling date in the dry season, when alligator ponds are used as deep-water refuge from low-water conditions in the marshes. We estimated days since last day of dry-down (i.e. water depth ≤ 10 cm) for each marsh site adjacent to an alligator pond based on estimated daily water depth. Covariance structure and data transformation were handled as described for the REML analysis.

Spatio-temporal dynamics

Patterns of fish CPUE in marsh habitat were examined across a time period of changing disturbance regime. We used nested repeated-measures ANOVA to test for temporal trends in fish CPUE at two spatial scales. Tests were based on mean CPUE from each sampling date for the three plots at each marsh site. For within-region dynamics in fish CPUE, the subject of repeated-measures tests was plot nested within site. When testing for trends at the regional scale, plots were nested within site and region. The fixed effect in each ANOVA model was the spatial scale of interest (i.e. site or region), with date and days since last day of dry-down as random effects. When either date or days since last day of dry-down was significant, we tested for significant slopes for each region or site and examined predicted trends from significant slopes (covariates and slopes considered significant at $p \leq 0.05$). Predicted trends at the regional level were examined for all species combined and for eight common species.

We used ANOSIM and SIMPER to quantify potential differences between regions and among years in fish assemblages. Spatial comparisons were based on regional averages of species CPUE for each year. In examining temporal trends in marshes, we grouped regional means into data collected before (1997–2000) and after (2002–2007) change in disturbance regime (Fig. 3; Trexler and Goss 2009). We also tested for temporal differences in alligator pond communities within each region by comparing community structure in 1998 (i.e. before change in disturbance regime) to that found in each year following 2001 (i.e. after change in disturbance regime). When ANOSIM tests of differences between groups were significant ($p \leq 0.05$), we used SIMPER analysis to identify species contributing to among-group differences. Potential relationships between spatial and temporal differences in community structure and hydrological characteristics (regional means of days since last day of dry-down, duration of dry-downs, maximum water depth, and minimum water depth for each year) were tested by performing rank correlations between a triangular matrix of Bray–Curtis similarity values (community structure) and a triangular matrix of Euclidian distances (hydrological variables). The significance of each Spearman rank correlation was assessed by comparing the strength of correlation arising from collected data to 999 correlations generated by random permutation of sample data (Clarke and Warwick 1994).

Results

From 1997–2007, we collected 2980 fish from 20 species from marshes and 9319 individuals from 21 species from alligator ponds. Florida gar and lake chubsucker were the two most common species in the marshes and yellow bullhead, warmouth, and Florida gar were the most abundant species in the alligator ponds (Appendix 2).

Patterns of refuge use

Fish CPUE in alligator ponds greatly increased from the wet season (SRS: 3 ± 0.5 fish/5 min; WCA 3A: 2 ± 0.2 fish/5 min) to the dry season (SRS: 73 ± 19 fish/5 min; WCA3A: 27 ± 9 fish/5 min). In alligator ponds from both regions, increased CPUE between seasons also resulted in significant changes in community structure (Global permutation test; SRS: $R = 0.752$, $p = 0.001$; WCA 3A: $R = 0.366$, $p = 0.001$; 999 permutations), with increased CPUE of yellow bullhead and warmouth during low water levels accounting for 40–51% of the dissimilarity in community composition (Fig. 4). Increases in Florida gar and lake chubsucker during the dry season were also consistent top contributors, adding an additional 10–13% each to community dissimilarity between seasons. Various centrarchid species were present in alligator ponds throughout the year, with only modest increases in CPUE during the dry season (Fig. 4). These species-specific, seasonal patterns of refuge use were similar in SRS and WCA 3A (Fig. 4), and as a result, alligator pond community structure did not differ between the two regions (Global permutation test; $R = 0.086$, $p = 0.07$, 999 permutations).

CPUE of fish in alligator ponds during seasonal droughts was related to hydrological conditions and fish CPUE in the

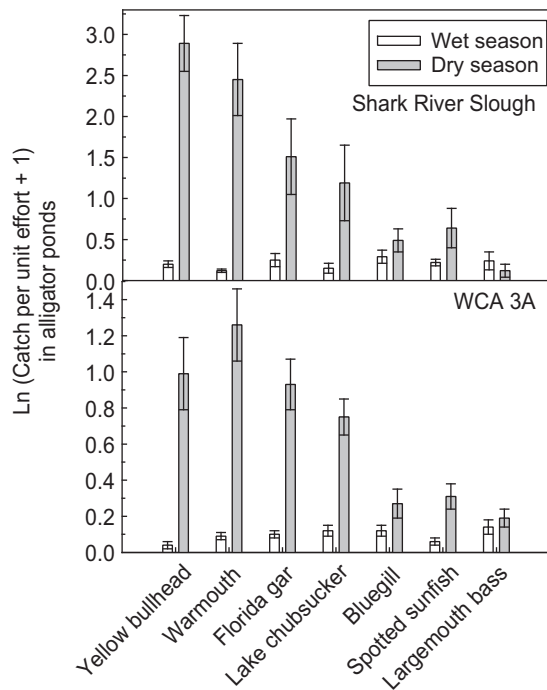


Figure 4. Seasonal abundance within two regions of the Florida Everglades of seven species of fish commonly found in alligator ponds. Bars are natural logarithm-transformed means \pm 1 SE.

surrounding marsh, as well as position of alligator ponds within the overall hydroscape. For the two most common species, yellow bullhead and warmouth, the most informative model of CPUE in alligator ponds was the global model that included pond area, marsh water depth, distance to alternative refuge habitat, CPUE in the previous season, and marsh CPUE of dry-down tolerant species (yellow bullhead global model $R^2 = 0.54$; warmouth global model $R^2 = 0.42$). For yellow bullhead, preference for the global model was also supported by the evidence ratio between the global model and the model with the next lowest AIC_c score ($\Delta_i = 7$; evidence ratio = 33). For warmouth, there was some support for both the global model and, arguably, a slightly simpler model of warmouth abundance (pond area + marsh depth + distance to nearest refuge + CPUE dry-down tolerant species; $\Delta_i = 4$; evidence ratio = 7). Evidence ratios for all other warmouth models were ≥ 55 . The global model also was among a set of four models with equal support ($\Delta_i \leq 2$) for lake chubsucker CPUE, but the most parsimonious model consisted of pond area, distance to alternative refuge, and CPUE of dry-down tolerant species. All four models with equal AIC_c support yielded evidence ratios less than 4, in contrast to subsequent models that had evidence ratios ≥ 20 . The reduced global model relating CPUE in alligator ponds during the dry season to pond area, marsh depth, distance to alternative refuge habitat, and CPUE the previous wet season was the most informative one for both Florida gar (global model $R^2 = 0.35$) and all species combined (global model $R^2 = 0.46$). Evidence ratios for other Florida gar models were ≥ 33 and for all species combined were ≥ 148 ; therefore, models with the lowest AIC_c had strong support compared to alternative models. Fish CPUE in alligator ponds decreased with water depth in adjacent marsh habitat and increased with pond area and distance from alternative deepwater habitat (Table 1). In the dry season, CPUE in alligator ponds of all species combined was negatively related to total fish CPUE in marshes the previous wet season; however, when considering each species individually, CPUE in alligator ponds was positively related to CPUE in marshes the previous season. CPUE of lake chubsucker, warmouth and yellow bullhead declined with increasing CPUE of dry-down tolerant species from the previous wet season (Table 1). Increasing CPUE of dry-down tolerant species, such as Florida gar, in marsh habitat, while CPUE of other fishes declined, was likely the cause of the negative relationship between marsh and alligator pond CPUE of all species combined. There was more support for a quadratic than a linear relationship between disturbance frequency and fish use of alligator ponds as refuge (linear $AIC_c = 713$, $R^2 = 0.29$; quadratic $AIC_c = 693$, $R^2 = 0.33$; Fig. 5).

Spatio-temporal dynamics

From 1997–2007, total CPUE declined at all marsh sites within the SRS region ($p \leq 0.003$), resulting in an overall decline at the regional scale ($p < 0.001$; Fig. 6A). Declines in CPUE were accompanied by a shift in community structure following the increased severity of hydrologic disturbance (Global permutation test; $R = 0.38$, $p = 0.01$, 210 permutations). CPUE declined for common species, such as lake chubsucker, yellow bullhead, bowfin, largemouth

Table 1. Parameter estimates from mixed-model analyses of sources of variation in refuge use by four common fishes and all species combined.

Variable	Yellow bullhead		Warmouth		Florida gar		Lake chubsucker		All species	
	Estimate	p	Estimate	p	Estimate	p	Estimate	p	Estimate	p
Pond area	0.802	0.008	0.651	0.008	0.525	0.140	0.553	0.020	0.970	0.004
Refuge distance	0.610	0.090	0.072	0.800	0.119	0.780	0.036	0.890	0.090	0.810
Marsh depth	-2.187	<0.001	-1.947	<0.001	-1.458	<0.001	-	-	-1.07	0.001
Marsh CPUE	9.619	0.080	1.637	0.430	0.870	0.260	-	-	-0.335	0.570
Air breathing spp.	-1.963	0.020	-3.577	<0.001	-	-	-3.600	<0.001	-	-

bass *Micropterus salmoides*, warmouth and spotted sunfish *Lepomis punctatus* ($p \leq 0.05$), with no significant change in Florida gar CPUE ($p = 0.08$). Change in community structure of SRS marshes was correlated with duration of marsh dry-downs ($\rho = 0.33$, $p = 0.03$, 999 permutations). Alligator ponds in SRS also experienced a significant change in community structure after increased frequency of hydrologic disturbance (1998 vs each year following 2001; $R = 0.35$ – 0.72 , $p \leq 0.002$, 999 permutations). Following change in the disturbance regime in SRS, CPUE in alligator ponds increased for Florida gar, warmouth and yellow bullhead, and decreased for lake chubsucker, largemouth bass and bluegill *Lepomis macrochirus*. There were also signs of increased CPUE of exotic species, such as blue tilapia *Oreochromis aureus*, Mayan cichlid *Cichlasoma urophthalmus* and walking catfish. Lake chubsucker and warmouth were often the most informative species distinguishing assemblage structure in alligator ponds in SRS before and after the increase in disturbance severity (Table 2).

Within the WCA 3A region, temporal trends in CPUE varied by site (site \times time: $p = 0.001$), with decline over time only occurring at site 3 (site 3: $p < 0.001$; all other sites: $p \geq 0.11$), the site with the most frequent and severe dry-downs in WCA 3A (Fig. 3). This site-specific decline translated into an overall negative trend in total CPUE at the regional level ($p = 0.02$; Fig. 6B), with a significant shift in community structure (Global permutation test; $R = 0.29$, $p = 0.05$, 210 permutations). CPUE declined for fewer species in WCA 3A than in SRS, with significant declines

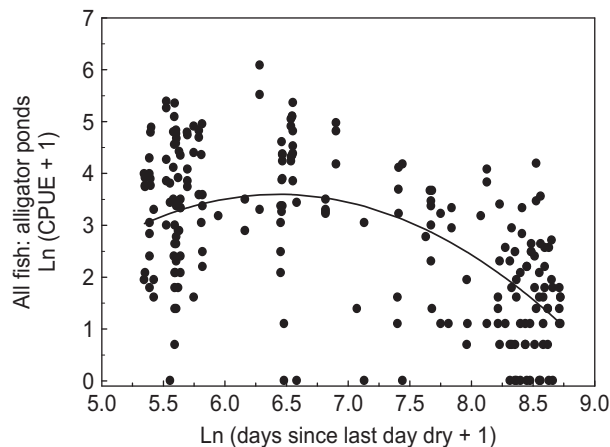


Figure 5. Quadratic relationship between fish abundance in alligator ponds during the dry season and days since last day of marsh dry-down. The solid line superimposed on the scatter plot is the predicted relationship between days since last dry-down and total abundance in alligator ponds.

in WCA 3A only measured for lake chubsucker, largemouth bass, bowfin, and bluegill ($p \leq 0.009$). Temporal change in community structure of WCA 3A marshes was related to days since last dry-down ($\rho = 0.46$, $p = 0.002$; 999 permutations). Community structure within alligator ponds did not change following increased severity of disturbance regime in WCA 3A (1998 vs each year following 2001; $R = -0.08$ – -0.1 , $p \geq 0.21$, 36–792 permutations).

Total CPUE of fish in marsh habitat differed between regions ($p = 0.005$), with greater CPUE in WCA 3A than SRS (Fig. 6). Regional differences in CPUE translated into a difference in marsh community structure (Global permutation test; $R = 0.54$, $p = 0.001$, 999 permutations), with lake chubsucker, warmouth, Florida gar, redfin pickerel *Esox americanus*, bowfin and largemouth bass contributing over 50% of the total dissimilarity between regional marsh communities. In general, CPUE of nonnative cichlids

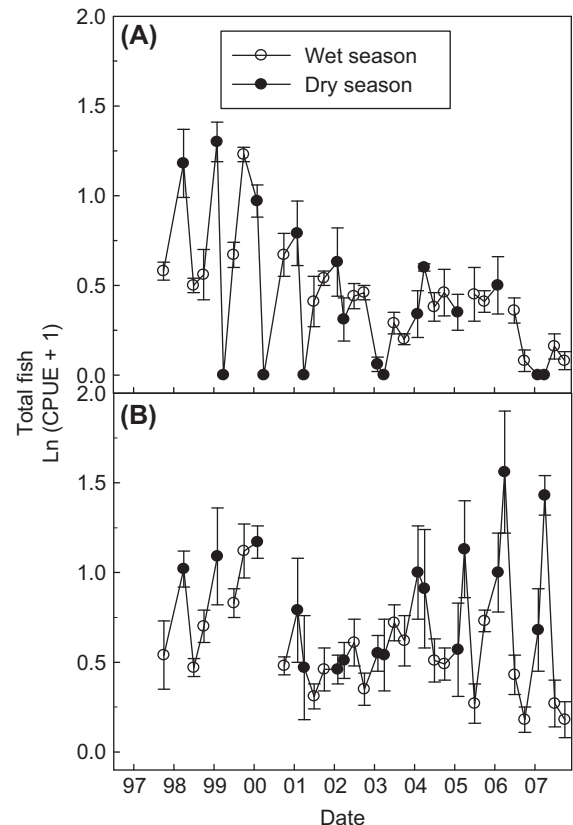


Figure 6. Total catch per unit effort (CPUE) of all large fishes in marshes of (A) Shark River Slough and (B) Water Conservation Area 3A. Data points are natural logarithm-transformed means \pm 1 SE.

Table 2. SIMPER analyses of species contributing to differences in community structure in Shark River Slough alligator ponds during the dry season in 1998 from community structure in alligator ponds in dry seasons following change in disturbance regime. Only fish species cumulatively contributing 90% to dissimilarity are presented. Mean regional catch per unit effort (CPUE; N/5 min \pm 1 SE) in alligator ponds is presented for each species. The consistency of an individual species' contribution to dissimilarity is presented as the ratio between a given species' average dissimilarity value and the standard deviation of that value (Diss/Sdev), with larger ratios indicating greater consistency.

Species	1998		2002		2003		2004	
	CPUE (SE)	Diss/Sdev	CPUE (SE)	Diss/Sdev	CPUE (SE)	Diss/Sdev	CPUE (SE)	
Florida gar	0.2 (0.1)	1.2	16.5 (7.3)	1	18.7 (10.7)	1.6	10.3 (2.4)	
Yellow bullhead	8.8 (1.7)	1.4	46.0 (11.7)	1.2	25.5 (11.3)	1.3	45.0 (12.4)	
Lake chubsucker	7.6 (2.3)	1.9	0.08 (0.1)	1.4	1.9 (0.6)	1.4	9.8 (2.8)	
Warmouth	6.1 (0.9)	1.6	23.3 (6.8)	1.7	8.8 (4)	2.5	40.9 (5.9)	
Bluegill	1.8 (0.6)	1	0.7 (0.4)	1.1	0.3 (0.2)	1.3	1.3 (0.5)	
Redear sunfish	1.1 (0.6)	0.8	0.6 (0.4)	0.9	0.3 (0.2)	1.6	3.1 (1)	
Spotted sunfish	2.1 (0.5)	1.5	0.2 (0.1)	1.3	0.6 (0.3)	1.4	2.6 (0.7)	
Largemouth bass	0.6 (0.2)	0.9	0.0	0.9	0.0	0.9	0.2 (0.1)	
Walking catfish	0.2 (0.1)	–	–	–	–	0.9	0.6 (0.2)	
Mayan cichlid	0.0	–	–	0.7	0.7 (0.4)	–	–	
Blue tilapia	0.1 (0.1)	–	–	0.6	0.9 (0.6)	–	–	

(Mayan cichlids, blue tilapia, spotted tilapia) was higher and CPUE of native piscivores (Florida gar, redbfin pickerel, bowfin, largemouth bass) was lower in SRS than WCA 3A (Table 3). Hydrological features associated with regional differences in marsh community structure included maximum depth ($p = 0.16$, $p = 0.04$, 999 permutations) and days since last day of dry-down ($p = 0.38$, $p = 0.001$, 999 permutations).

Discussion

Variable patterns of disturbance among years and across the hydroscape of the Florida Everglades had a strong effect on patterns of refuge use and resulting trends in abundance and community structure. The formation and spatial distribution of habitat patches often result from ecosystem engineering by local members of a community, with some of these animal-formed patches serving as a source of colonists (Schlosser

1995) and refuge from the effects of disturbance (Woodin 1978). The mosaic of patches resulting from the habitat-forming actions of animals can be crucial to the community structure of other organisms in the system (Schlosser and Kallemeyn 2000). Trails and ponds formed by alligators are considered critical to the persistence of fishes in the Everglades because they allow for dispersal away from hydrologic disturbance and into spatial refuges. Nonetheless, seasonal droughts can be of sufficient duration to cause mortality within this refuge habitat (Kushlan 1974); therefore, components of the disturbance regime, such as strength, duration and frequency, can influence relative benefits of refuge habitat for animals living in disturbed environments. We found that patterns of refuge use were an outcome of the interplay between disturbance, species identity, patch size, position in the landscape and pool of potential occupants.

The role of refuge use in population and community dynamics varied as disturbance regime increased in severity. As time between hydrologic disturbances decreased,

Table 3. SIMPER analyses of regional community structure distinguishing marshes in Shark River Slough (SRS) from marshes in Water Conservation Area 3A (WCA 3A) and mean regional catch per unit effort (CPUE; N/5 min \pm 1 SE) for each species. Only those species cumulatively contributing up to 90% of the difference in community structure are presented. The consistency of an individual species' contribution to dissimilarity is presented as the ratio between a given species' average dissimilarity value and the standard deviation of that value (Diss/Sdev), with higher ratios indicating greater consistency.

Species	Diss/Sdev	% contribution	Cumulative %	CPUE	
				SRS	WCA 3A
Lake chubsucker	1.54	12.36	12.36	0.34 (0.13)	0.29 (0.05)
Warmouth	1.13	9.61	21.97	0.05 (0.01)	0.19 (0.06)
Florida gar	1.36	9.05	31.02	0.16 (0.03)	0.33 (0.05)
Redfin pickerel	1.65	8.49	39.51	0.01 (0.01)	0.08 (0.02)
Bowfin	1.40	6.91	46.42	0.05 (0.01)	0.13 (0.02)
Largemouth bass	1.31	6.14	52.56	0.04 (0.01)	0.11 (0.02)
Mayan cichlid	1.66	6.06	58.62	0.08 (0.01)	0.02 (0.01)
Spotted tilapia	1.21	5.65	64.27	0.05 (0.02)	0.01 (0.01)
Yellow bullhead	1.45	5.48	69.75	0.06 (0.02)	0.03 (0.01)
Blue tilapia	1.31	4.85	74.60	0.02 (0.01)	<0.01 (<0.01)
Spotted sunfish	1.34	4.84	79.44	0.09 (0.02)	0.09 (0.02)
Bluegill	1.21	4.45	83.89	0.01 (<0.01)	0.03 (0.01)
Redear sunfish	1.28	4.07	87.96	0.01 (0.003)	0.02 (0.01)
Walking catfish	1.19	3.40	91.36	0.01 (0.01)	0.01 (0.01)

importance of alligator ponds as refuge initially increased, until a threshold in disturbance frequency was passed, and abundance in refuge patches declined. This pattern matched the prediction of a modal relationship between refuge importance and disturbance severity (Fig. 1C). Spatio-temporal patterns of community response to disturbance across the Everglades landscape suggests that declines in refuge use at high frequency of disturbance are an outcome of declines in the resistance and resilience of component species.

Patterns of refuge use

Net immigration of fishes into alligator ponds during the dry season, followed by net emigration back into marshes, was a predictable pattern of temporal variation in fish abundance in refuge habitat. Natural systems have many examples of predictable temporal patterns of animal movement between habitats to escape competitors, predators, or stressful physical conditions (Cox 1985, Wiens 1985). These patterns of movement are likely to have important food web and ecosystem consequences because they represent predictable fluxes of biomass and nutrients between different habitats. When these movements concentrate animals into smaller patches of habitat than their original location, this between-habitat exchange can result in locally high concentrations of nutrients, as well as increased biotic interactions, such as competition and predation (Magoulick and Kobza 2003, Matthews and Marsh-Matthews 2003). Seasonal pulses of fish from marshes into alligator ponds linked these two habitats, and the strength of this linkage increased with harshness of disturbance regime, especially frequency of disturbance.

The importance of alligator ponds as refuge depended on the severity of hydrologic disturbance experienced by fishes found within the adjacent marshes, with use of refuge habitat highest where drops in water level were frequent and intense. Disturbance regime characteristics, such as frequency and intensity of disturbance, often vary spatially because of local community composition and topographical gradients (Connell and Keough 1985, Runkle 1985), resulting in patchy disturbance effects across landscapes (Pickett and White 1985). Though characterized by low relief, spatial variation in elevation in the Everglades is sufficient to cause differences in hydroperiod among marshes found within the same region (Ruetz et al. 2005). The construction of levees and canals by humans has added additional spatial variability in disturbance regime. A levee impounds water in WCA 3A and water control structures regulate discharge from WCA 3A into SRS, resulting in generally higher water levels in WCA 3A during the dry season than in SRS (Chick et al. 2004).

Fish abundance in alligator ponds was influenced by position of refuge patches within the Everglades hydroscape. The spatial distribution of refuge patches in terms of distance between refuges and disturbed habitat has been found to influence both propensity to use refuge habitat and patterns of recolonization following disturbance in intermittent streams (Davey and Kelly 2007). A similar effect was measured in the Everglades, except that in this case, it was the position of alligator ponds relative to other deepwater habitats (mainly canals), with use of alligator ponds increasing with distance from alternative refuges. Canals are often used as refuge

habitat by fishes living in habitats characterized by seasonal fluctuations in water level (Cowley et al. 2007). Canals may provide superior refuge conditions to those experienced by fishes in alligator ponds because of the greater depth and larger area of canals than alligator ponds. The addition of canals may have increased the abundance of large fish species in the Everglades over historical levels by reducing mortality of these species during the dry season, as well as altering the strategies of large fish species for coping with seasonal droughts by providing another, potentially more attractive, type of refuge habitat (Rehage and Trexler 2006). The construction of canals and fluctuation in numbers of alligators also may have changed the spatial distribution of alligator ponds across the hydroscape by concentrating alligators in canals and sloughs, reducing numbers of alligator-maintained ponds in peripheral marshes of the Everglades (Mazzotti and Brandt 1994). This alteration of the distribution of alligator ponds could have consequences for fish community structure following droughts because the spatial relationship of source and sink habitat patches can influence productivity and composition of communities (Schlosser 1995).

Size of each refuge patch and the pool of potential occupants also influenced fish use of alligator ponds. Increase in fish abundance with patch size was likely due to amount of space available in each alligator pond. Another potential factor influencing the fish abundance–pond size relationship is that dispersing animals are more likely to encounter large patches than small ones (e.g. target effect; Lomolino 1990). Patterns of patch occupancy are subject to conditions in neighboring habitats (Schooley and Branch 2007). Alligator ponds are small habitat patches embedded within much larger habitat patches of marsh, and as such, fish abundance in these refuge patches partly reflects fish numbers in the surrounding habitat. This pattern of linked population dynamics between two habitat types was demonstrated by the increase in fish abundance in alligator ponds with increasing abundance in marshes.

Response to disturbance varies across organisms that differ in behavior and life history (Connell and Keough 1985, Davey et al. 2006). Spatial differences in marsh community structure were not found in alligator pond communities because the same subset of species from each region used alligator ponds. In both regions of the Everglades, alligator ponds mainly contained low numbers of centrarchid species, Florida gar, lake chubsucker and yellow bullhead in the wet season and high numbers of Florida gar, lake chubsucker, warmouth and yellow bullhead in the dry season. Bowfin and redbfin pickerel were two species that were relatively common in marsh habitat but rarely found in alligator ponds, even during low-water conditions in marshes. The bowfin is capable of aestivating during marsh dry-downs and is also known to be highly abundant in canals (Loftus and Kushlan 1987); therefore, bowfin may only rarely choose to use alligator ponds as refuge habitat. Warmouth, yellow bullhead and Florida gar, three of the four species responsible for the increase in fish abundance in alligator ponds during the dry seasons, are tolerant of the low oxygen conditions that often develop in crowded alligator ponds (Kushlan 1974, Loftus and Kushlan 1987). That only four species of fish were primarily responsible for the increase in fish abundance in alligator ponds during the dry season may partly reflect that these are among the most abundant species in

the surrounding marsh (Chick et al. 1999, 2004). Alternatively, aquatic animals are known to vary in their strategies for coping with drought conditions (Davey et al. 2006), and some individuals and species may actively avoid using alligator ponds as dry season refuge (e.g. bowfin). Whether or not mobile animals become trapped in refuge patches during droughts or actively select these habitats continues to be an open question in the study of refuge use (Trexler et al. 2002, Magoulick and Kobza 2003). Increasing severity of hydrologic disturbance and ongoing alterations to the Everglades landscape make it important to know which fish species use alligator ponds as refuge in order to forecast the likely consequences of these temporal changes for fish communities.

Spatio-temporal dynamics

In some cases, refuge habitat may sufficiently buffer enough individuals from a disturbance that following recolonization there is little or no loss of community structure (Robertson et al. 1995). By providing a relatively benign environment, refuge habitats may promote stability (e.g. similar relative abundances over time) and persistence (e.g. similar patterns of presence/absence over time) of communities that experience severe disturbances. Time elapsed until the recovery of former community structure will depend on the dispersal abilities and life history characteristics of the organisms involved. Communities of animals capable of rapid reproductive rates and dispersal over large distances should be able to quickly recover their former productivity and community structure. The majority of fish species in the Florida Everglades are small animals (<8 cm SL) that can produce multiple generations per year, but nonetheless most of these species require 3–5 years to recover pre-disturbance numbers and exhibit declines in abundance when dry-downs occur less than three years apart (Trexler et al. 2005). The large dispersal ability and relatively low reproductive potential of the large fish species in this study would mean that, following disturbance, these species would be capable of swiftly reoccupying much of their former distribution, but need a relatively long time to recover their former abundance if there was high mortality of individuals during the dry season.

Despite the availability of alligator ponds as refuge during low-water conditions, we noted a limit as to how long and frequent marsh dry-downs could be in order for the fish community to be buffered from disturbance-induced changes. In SRS, the region experiencing the greatest increase in disturbance severity, large fish species declined in abundance throughout all of the monitoring sites, resulting in region-wide decline in abundance and shift in community structure in both marsh and refuge habitat. The relationship in SRS between change in marsh community structure and increase in duration of dry-down events suggests that, in this region of the Everglades, fish mortality has increased during the dry season. Prolonged marsh dry-downs confine fishes within alligator ponds for long periods of time, with prolonged confinement increasing the possibility of mortality of more sensitive species from deteriorating conditions within the refuge (Kushlan 1974, Magoulick and Kobza 2003). In WCA 3A, the region experiencing less hydrologic disturbance, increased disturbance severity and its effects on fish abundance were more localized to sites characterized by more frequent and

severe dry-downs. Some fish species, such as lake chubsucker, bowfin and largemouth bass, appeared to be more susceptible to disturbance because they declined in both regions. Other species, such as warmouth and yellow bullhead, were more resilient in that they declined only in SRS, a region where the increase in disturbance was more spatially extensive than in WCA 3A. Florida gar, a common piscivore with the ability to breathe air, was the only species to not decline in either region. Though the bowfin also has the ability to breathe air, this species appeared to be vulnerable to change in disturbance regime. As bowfin were not a common species that used alligator ponds during the dry season, its strategy for coping with marsh dry-downs may not buffer its populations to the same extent as species such as warmouth and yellow bullhead that commonly use alligator ponds. The interplay between inter-specific differences in response to disturbance and spatial variation in severity of disturbance regime, particularly in frequency of disturbance, ultimately led to regional differences in community structure.

Our findings have important implications for animal populations and communities that experience disturbance regimes that are increasing in frequency and intensity. Refuge use will be influenced by refuge position within the landscape, characteristics of the disturbance regime and the abundance and composition of the species pool. Other studies of disturbance in aquatic systems also have found that use of refuge patches with disturbance intensity, species identity, and patch characteristics such as physical traits of patch and patch position in landscape (Palmer et al. 1996, Davey et al. 2006, Davey and Kelly 2007). Based on our study, we predict that benefits of refuge use will decline after a threshold of disturbance frequency is passed. Persistent disruption of community structure is likely when frequency of disturbance is high relative to populations growth rates (Huston 1994). As we found in the Everglades, increasing frequency of disturbance also can be associated with an increase in intensity of disturbance, resulting in a shift of community structure towards increased relative abundance of disturbance-resistant species (Benedetti-Cecchi et al. 2006). Species vary in their inclination to use specific refuge types, their ability to persist in refuges during disturbance conditions, and the time scale and likelihood to recover their former abundance following disturbances. In systems where organisms have more restricted dispersal capabilities than the fish in our study, disruption of community structure may occur at relatively small increases in disturbance frequency (Lundquist et al. 2010). Anthropogenic changes to natural landscapes may both provide and reduce habitats that can serve as refuge during extreme environmental conditions. Consideration of the consequences of habitat alteration for communities that experience harsh disturbance regimes is critical for successful ecosystem management and restoration. Understanding the role of refuges in the responses of ecological communities to disturbance is needed to predict the temporal dynamics of communities of mobile animals responding to changes in disturbance regime, especially the more frequent and severe disturbances predicted to occur from climate change.

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Appendix 1. Location, diameter and nearest distance to other deep-water habitats for alligator ponds sampled for large fishes. Each location includes a region of the Florida Everglades and an adjacent marsh site. Other deep-water habitats included canals and headwater streams.

Region	Marsh	Alligator pond	Pond diameter (m)	Distance to canal or stream (km)
Shark River Slough	8	S1	73.2	2.3
Shark River Slough	8	S2	25.6	3.8
Shark River Slough	8	S3	36.6	5.7
Shark River Slough	8	S4	22	4.2
Shark River Slough	7	S5	14.6	8.2
Shark River Slough	7	S6	29.3	10.5
Shark River Slough	7	S7	22	9.6
Shark River Slough	6	S8	18.3	4.8
Shark River Slough	6	S9	22	4.8
Shark River Slough	6	S10	9.15	7.8
Shark River Slough	6	S11	16.5	7.4
Shark River Slough	6	S12	12.8	7.4
Shark River Slough	37	–	–	–
WCA 3A	1	W1	11	10.1
WCA 3A	1	W2	–	9
WCA 3A	1	W3	11	5.4
WCA 3A	4	W4	11	8.1
WCA 3A	4	W5	14.6	6.8
WCA 3A	4	W6	7.32	7.1
WCA 3A	3	W7	58.6	1.7
WCA 3A	3	W8	73.2	3.1
WCA 3A	3	W9	12.8	4.8
WCA 3A	5	W10	36.6	11.3
WCA 3A	5	W11	7.32	10.5
WCA 3A	5	W12	9.15	–

Appendix 2. Percentage of catch of fish collected by airboat electrofishing in marshes and alligator ponds in two regions (SRS = Shark River Slough, WCA 3A = Water Conservation Area 3A) of the Florida Everglades based on the total number of individuals collected for each habitat type in each region. Each year (marshes: 1997–2007; alligator ponds: 1998–2007), an attempt was made to sample twice each in the wet and dry seasons. Non-native species are marked with an asterisk.

Species	Common name	% of catch			
		Marsh		Alligator Pond	
		SRS	WCA 3A	SRS	WCA 3A
<i>Lepisosteus platyrhincus</i>	Florida gar	16.2	25	15	20.1
<i>Amia calva</i>	Bowfin	5.7	9.7	0.2	1.6
<i>Esox americanus</i>	Redfin pickerel	1.1	5.4	0.1	0.4
<i>Esox niger</i>	Chain pickerel	0	0.9	0	0.1
<i>Notemigonus crysoleucas</i>	Golden shiner	0	0	<0.1	0.3
<i>Aphrododerus sayanus</i>	Pirate perch	0	0	0	<0.1
<i>Erimyzon sucetta</i>	Lake chubsucker	32.1	19.1	7.3	10.5
<i>Ameiurus natalis</i>	Yellow bullhead	6.6	2.3	35.3	22.5
<i>Ameiurus nebulosus</i>	Brown bullhead	0	0.7	0.2	1.6
<i>Clarias batrachus</i>	Walking catfish*	1.4	1.2	0.3	0.3
<i>Hoplosternum littorale</i>	Brown hoplo*	1.1	0.1	0.1	0.5
<i>Fundulus seminolis</i>	Seminole killifish	0.3	0	0	0
<i>Belonesox belizanus</i>	Pike killifish*	0	0	0.1	0.1
<i>Centropomus undecimalis</i>	Snook	0.2	0	0	0
<i>Lepomis macrochirus</i>	Bluegill	1.3	2.4	3.6	4.4
<i>Lepomis microlophus</i>	Redear sunfish	0.5	1.5	2.1	2.1
<i>Lepomis punctatus</i>	Spotted sunfish	8.6	6.2	3.6	3.3
<i>Lepomis gulosus</i>	Warmouth	4.9	15.6	29.4	27.8
<i>Micropterus salmoides</i>	Largemouth bass	4.5	7.4	1.4	3.9
<i>Cichlasoma bimaculatum</i>	Black acara*	0	0.1	<0.1	<0.1
<i>Cichlasoma urophthalmus</i>	Mayan cichlid*	7.8	1.5	0.7	0.3
<i>Oreochromis aureus</i>	Blue tilapia*	2.6	0.1	0.4	0.1
<i>Tilapia mariae</i>	Spotted tilapia*	5.1	0.7	0.3	0.2
	total individuals	1114	1769	6497	2822
	species richness	17	18	19	21