

Population dynamics of wetland fishes: spatio-temporal patterns synchronized by hydrological disturbance?

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Summary

1. Drought is a natural disturbance that can cause widespread mortality of aquatic organisms in wetlands. We hypothesized that seasonal drying of marsh surfaces (i.e. hydrological disturbance) shapes spatio-temporal patterns of fish populations.
2. We tested whether population dynamics of fishes were synchronized by hydrological disturbance (Moran effect) or distance separating study sites (dispersal). Spatio-temporal patterns were examined in local populations of five abundant species at 17 sites (sampled five times per year from 1996 to 2001) in a large oligotrophic wetland.
3. Fish densities differed significantly across spatio-temporal scales for all species. For all species except eastern mosquitofish (*Gambusia holbrooki*), a significant portion of spatio-temporal variation in density was attributed to drying events (used as a covariate).
4. We observed three patterns of response to hydrological disturbance. Densities of bluefin killifish (*Lucania goodei*), least killifish (*Heterandria formosa*), and golden topminnow (*Fundulus chrysotus*) were usually lowest after a dry down and recovered slowly. Eastern mosquitofish showed no distinct response to marsh drying (i.e. they recovered quickly). Flagfish (*Jordanella floridae*) density was often highest after a dry down and then declined. Population growth after a dry down was often asymptotic for bluefin killifish and golden topminnow, with greatest asymptotic density and longest time to recovery at sites that dried infrequently.
5. Fish population dynamics were synchronized by hydrological disturbance (independent of distance) and distance separating study sites (independent of hydrological disturbance). Our ability to separate the relative importance of the Moran effect from dispersal was strengthened by a weak association between hydrological synchrony and distance among study sites. Dispersal was the primary mechanism for synchronous population dynamics of flagfish, whereas hydrological disturbance was the primary mechanism for synchronous population dynamics of the other species examined.
6. Species varied in the relative role of the Moran effect and dispersal in homogenizing their population dynamics, probably as a function of life history and ability to exploit dry-season refugia.

Key-words: dispersal, drought, Florida Everglades, Moran effect, spatial synchrony.

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Introduction

A central goal of population ecology is to understand spatio-temporal patterns of population fluctuations. Synchronous dynamics of animal populations over large spatial scales is emerging as a common phenomenon

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(Ranta *et al.* 1995; Cattadori, Merler & Hudson 2000; Post & Forchhammer 2002; Cattaneo, Hugueny & Lamouroux 2003). Identifying mechanisms that cause spatial synchrony has proved both difficult and central to understanding population regulation. Synchronous population dynamics are generally attributed to the Moran effect, dispersal or nomadic predators (Koenig 1999; Ripa 2000). The role of each factor in synchronizing population dynamics is not mutually exclusive. The Moran effect occurs when population dynamics are synchronized by a common environmental factor (Hudson & Cattadori 1999; Ripa 2000). Dispersal between neighbouring populations can cause populations to be synchronized (Schwartz *et al.* 2002), and nomadic predators that are attracted to areas of high prey density may synchronize prey population dynamics (Ydenberg 1987).

Disentangling the contribution of the Moran effect and dispersal on synchronous population dynamics is difficult (Ranta, Kaitala & Lindström 1999; Cattadori *et al.* 2000; Ripa 2000). Environmental fluctuations are often correlated with distance between sites (Koenig 1999, 2002). Therefore, the underlying mechanism of a decline in population synchrony with increasing distance between sites may be a Moran effect or dispersal because frequency of dispersal usually decreases as greater distances separate sites (Ranta, Kaitala & Lundberg 1998; Koenig 1999). An approach to distinguishing the Moran effect from dispersal is to examine synchrony in populations, synchrony in environmental factors and relationships between population and environmental synchrony (Koenig 1999; Ranta *et al.* 1999; Cattaneo *et al.* 2003).

Wetlands are well suited to study the effects of disturbance on spatio-temporal patterns of animal populations. Disturbance (e.g. flood and fire regimes) is a defining feature of many wetlands, including the oligotrophic wetlands of the Florida Everglades, United States (Loftus & Kushlan 1987; Turner *et al.* 1999; Lockwood, Ross & Sah 2003). Water in the Everglades is derived from seasonal rainfall and overland sheet flow. Most annual rainfall (~85%) occurs during the wet season (May–October), but the duration and intensity of annual rainfall is variable (Loftus & Kushlan 1987; Loftus & Eklund 1994). Water-level fluctuations can cause high mortality among fishes that become stranded in drying wetlands (Kushlan 1974a; Kobza *et al.* 2004). Thus, hydrological disturbance can have system-wide impacts on the abundance and structure of fish communities in the Everglades (Kushlan 1976, 1980; Loftus & Eklund 1994; Trexler *et al.* 2002; Trexler, Loftus & Chick 2003; Kobza *et al.* 2004). However, effects of hydrological disturbance are mediated by the ability of fishes to colonize and exploit dry-season refugia (Kushlan 1974b; Trexler *et al.* 2002; McElroy *et al.* 2003).

In this study, we examined spatio-temporal patterns in local populations of five abundant fishes and assessed the role of hydrological disturbance (i.e. drying of marsh surfaces) on population dynamics in the Florida Ever-

glades. We studied several species to determine whether spatio-temporal patterns were homogeneous. We expected to find synchronous fish population dynamics in the Everglades because monthly fish densities at two sites separated by 10 km tracked closely from 1977 to 1985 (Loftus & Eklund 1994). Our objectives were to: (1) identify spatio-temporal patterns in fish density, (2) assess the role of hydrological disturbance in shaping spatio-temporal patterns and (3) examine the relative importance of hydrological disturbance and dispersal on spatial synchrony of fish populations.

Materials and methods

STUDY AREA AND SAMPLING DESIGN

Levees and canals subdivide the Everglades drainage into several water-management units (Light & Dineen 1994). Fishes were sampled at 17 sites throughout three water-management units (Fig. 1): Water Conservation Area 3 A (WCA-3 A), Shark River Slough (SRS) and Taylor Slough (TS). Each study site was sampled five times per year from 1996 to 2001. Sampling events were conducted during the dry season (February and April), wet season (July and October) and transition (December). Sites were limited to wet-prairie sloughs dominated by spikerush (*Eleocharis* spp.) in the central and southern Everglades (Busch, Loftus & Bass 1998). In this region, the Everglades is a habitat mosaic with wet-prairie

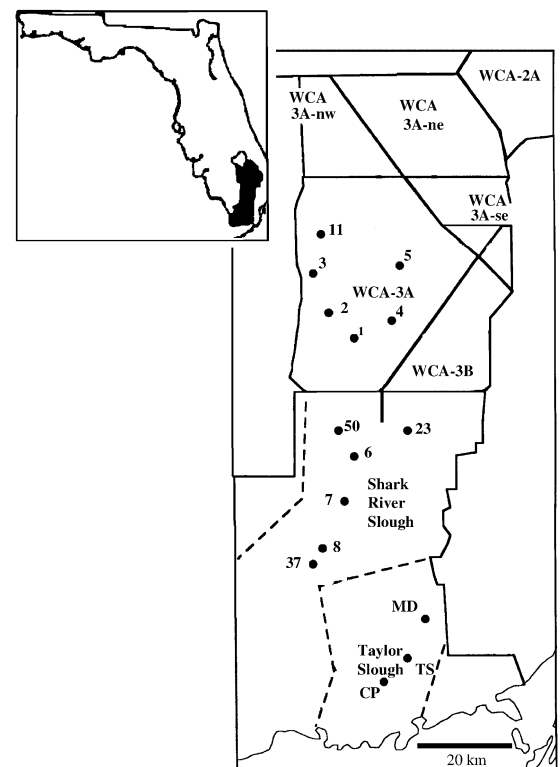


Fig. 1. Map of study sites in the Everglades, Florida, USA. Sites MD and TS are each bordered by two short-hydroperiod plots not visible at this scale. Short-hydroperiod plots at sites MD and TS were treated as separate sites (i.e. MDsh and TSsh) to yield five sites in Taylor Slough.

Table 1. Hydroperiod (days per year water depth was > 5 cm) and hydrological classification for each study site. Hydroperiod was estimated based on predicted daily depth at each plot from 1996 to 2001. Sites were classified into two groups (long or short hydroperiod) based on the number of days water depth at a site was predicted to be ≤ 5 cm from 1996 to 2001

Site	Hydroperiod (days)		Hydrological classification
	Mean	Range	
Shark River Slough			
6	358	312–366	Long
7	356	301–366	Long
8	352	275–366	Short
23	354	271–366	Long
37	344	245–366	Short
50	328	221–365	Short
Taylor Slough			
CP	354	301–366	Long
MD	359	335–366	Long
MDsh	297	174–364	Short
TS	353	311–366	Short
TSsh	346	295–366	Short
Water Conservation Area 3 A			
1	365	365–366	Long
2	361	327–366	Long
3	347	267–366	Short
4	365	365–366	Long
5	365	362–366	Long
11	327	279–366	Short

sloughs subdivided by ridges dominated by dense stands of sawgrass (*Cladium jamaicense* Crantz). Wet-prairie habitats are 10–20 cm lower than adjacent sawgrass ridges and retain water longer (Jordan, Jelks & Kitchens 1997; Ross *et al.* 2003). Fish densities are typically higher in wet-prairie sloughs than adjacent sawgrass habitats (Jordan 1996; Trexler *et al.* 2002).

A nested study design was used to sample fishes at three spatial scales: water-management units, sites and plots. Sites were chosen haphazardly to cover the spatial area of a water-management unit. Sites within each water-management unit represented a range of hydroperiod (days per year water depth > 5 cm). WCA-3 A had more long-hydroperiod sites and TS had more short-hydroperiod sites (Table 1), indicative of the landscape and water-management actions. Three plots (100 m²) per site were sampled, except at two short-hydroperiod sites in TS that had two plots per site (Fig. 1). Distances among plots at a site (0.5–2 km) were less than among sites within water-management units (SRS: 3–13 km, TS: 0.3–7 km, WCA-3 A: 8–13 km). Maximum distance between sites was 93 km (Fig. 1). For logistical reasons, seven samples were collected at each plot in SRS and TS, and five samples were collected at each plot in WCA-3 A. Locations of samples within a plot were randomly chosen for each sampling event. Each plot had 1200–10 000 possible sampling locations, minimizing the chance of re-sampling an area during subsequent visits. Impacts of

repeated visitation to these plots appeared negligible when compared to adjacent areas that had not been sampled previously (Wolski *et al.* 2004).

A 1-m² throw trap (2-mm mesh) was used to collect fishes (Jordan, Coyne & Trexler 1997). Once a trap was deployed, water depth was measured and a bar seine (2-mm mesh) was passed through the trap until three consecutive passes were completed without collecting a fish. Two dip nets (1-mm and 5-mm mesh, respectively) were then used to capture any remaining individuals by alternating dips between nets until five consecutive sweeps from each net were completed without collecting a fish. Fishes were euthanized by immersion in a solution of MS-222, preserved in 10% formalin and identified in the laboratory.

DATA ANALYSIS

Analyses were limited to abundant fish species to avoid taxa with a preponderance of samples with zero specimens. The most abundant species were the least killifish (*Heterandria formosa* Agassiz), eastern mosquitofish (*Gambusia holbrooki* Girard), bluefin killifish (*Lucania goodei* Jordan), flagfish (*Jordanella floridae* Goode & Bean) and golden topminnow (*Fundulus chrysotus* Günther). These small-bodied fishes are dominant taxa in the Everglades in terms of numbers and standing crop (Loftus & Kushlan 1987; Turner *et al.* 1999).

To examine patterns of fish density related to hydrological disturbance, time since a dry down was estimated for each sampling event. Linear regression was used to estimate relationships between mean water depth at a plot and water level for the same day at a nearby, long-term hydrological recorder ($R^2 = 0.788–0.993$). Corresponding regression equations were used to predict daily water depth at a plot. A dry down was defined as an event when daily water depth was ≤ 5 cm. At this depth, fishes are trapped in a slurry of sediment and organic material.

A mixed linear model (based on restricted maximum likelihood) was used to test for differences in fish density among spatio-temporal scales (Littell *et al.* 1996). Covariance structure was modelled as a first-order autoregressive process (Littell *et al.* 1996), which fitted the data well. Plot (nested within site and water-management unit) was the random subject factor, and we partitioned variance in the fixed effects by water-management unit, site (nested within water-management unit), year, sampling period (nested within year) and the corresponding interactions. Additionally, time since a dry down was used as a covariate in the mixed linear model to determine whether hydrological disturbance affected spatio-temporal patterns. Fish density was transformed using $\ln(x + 1)$ to reduce over-dispersion of plot means.

To assess more effectively temporal variation and the role of hydrological disturbance on patterns of fish density, linear and polynomial regression was used to model the relationship between fish density and time

since a dry down for each site (Trexler *et al.* 2003). Plots were treated as replicates of a site. If slope coefficients were significant for linear and quadratic regression models, then results were reported for the linear model unless R^2 for the quadratic model was 0.05 greater than R^2 for the linear model.

Regression models (fish density vs. time since a dry down) were used to calculate maximum fish density following a dry down (N_{\max}) and time to reach N_{\max} (d_{\max}) at each study site. Modelling N_{\max} and d_{\max} was most meaningful when the increase in fish density following a dry down was asymptotic and well described by a quadratic model. In these cases, N_{\max} was a measure of asymptotic density and d_{\max} was a measure of time needed to reach asymptotic density after a dry down. Sites 1 and 4 did not experience a dry down during our study (Table 1) and were excluded from this analysis. If the best regression model was linear, then d_{\max} was the maximum time a plot went without drying. For the quadratic regression model [$\ln(\text{density} + 1) = \beta_0 + \beta_1 d + \beta_2 d^2$, where β_0 was the intercept, β_1 and β_2 were slope coefficients, and d was time since a dry down], $d_{\max} = -\beta_1 / (2\beta_2)$. However, if β_1 was negative in the quadratic model, then $d_{\max} = 0$ or d_{\max} was the maximum time a plot went without drying (based on the estimate of d_{\max} that maximized N_{\max}). N_{\max} was calculated from the regression model based on the estimate of d_{\max} . If regression coefficients were not significant ($P > 0.05$), then d_{\max} could not be estimated and N_{\max} was mean fish density for a site.

Spatial synchrony was estimated for each species to assess the similarity of population dynamics among sites (Ranta *et al.* 1995; Koenig 1999). Population synchrony was estimated by calculating correlation coefficients based on fish densities (measured for each sampling event) between all pairs of sites. Similarly, hydrological synchrony was estimated by calculating correlation coefficients based on time since a dry down (calculated for each sampling event) between all pairs of sites. For population and hydrological synchrony, high positive values signified synchronous dynamics and negative values signified that the series fluctuated in opposite phase (Ranta *et al.* 1998). Partial correlations were calculated to quantify the association between population synchrony and distance separating a pair of sites when hydrological synchrony was held constant and between population synchrony and hydrological synchrony when distance was held constant over all sites. Partial correlation coefficients were used to account for the potential association between hydrological synchrony and distance. Mantel tests were used to estimate the significance of partial correlation coefficients (Koenig 1999) by calculating 100 000 random permutations of rows and columns of the population synchrony matrix (Resample Stats, version 5.0). Additionally, sites were classified based on local hydrology as long or short hydroperiod (Table 1). The association between population synchrony and distance was compared among short-hydroperiod sites, among long-hydroperiod sites

and between long- and short-hydroperiod sites. This examined whether the importance of dispersal on population synchrony varied according to the hydrological classification of sites.

Results

The density of each fish species varied across spatial and temporal scales (without covariate, Table 2). However, significant interactions between spatial and temporal scales made interpreting patterns difficult (Fig. 2). All spatial scales, temporal scales and interactions continued to be significant for least killifish and flagfish when hydrological disturbance was included as a covariate (Table 2). Some main effects were no longer significant for bluefin killifish (water-management unit, site), eastern mosquitofish (water-management unit, site, year) and golden topminnows (water-management unit, year), even though most interactions between spatial and temporal scales remained significant (Table 2). The interaction between hydrological disturbance and site was significant for all species except eastern mosquitofish. The variance attributed uniquely to spatio-temporal scales decreased markedly for all species when hydrological disturbance was used as a covariate (Table 2). Thus, a statistically significant portion of the variation in fish density among spatio-temporal scales was attributed to hydrological disturbance.

A significant portion of temporal variation in fish density was often related to time since a dry down, although relationships varied among species and sites (Table 3). Densities of least killifish and bluefin killifish were typically lowest following a dry down (Fig. 3). The response of golden topminnows was usually similar to, but weaker than, least killifish and bluefin killifish (Table 3). The effect of dry downs on population dynamics of flagfish and eastern mosquitofish was weaker than the other species. Eastern mosquitofish showed no consistent pattern to dry downs (Table 3). Densities of flagfish were often highest after a dry down and gradually declined thereafter (Fig. 3). However, flagfish density increased after reaching a minimum at three sites. Across water-management units, responses of bluefin killifish, least killifish and golden topminnows to a dry down were usually weakest (more non-significant models and low R^2) in WCA-3 A (Table 3), which had the most long-hydroperiod sites (Table 1).

The effect of local hydrology on N_{\max} and d_{\max} was stronger for bluefin killifish and golden topminnows than the other species. The association between N_{\max} and hydroperiod was significant for golden topminnows ($r = 0.641$, $P = 0.010$, $n = 15$), whereas the association was not significant for least killifish ($r = 0.271$, $P = 0.329$, $n = 15$), eastern mosquitofish ($r = 0.278$, $P = 0.316$, $n = 15$), bluefin killifish ($r = 0.514$, $P = 0.050$, $n = 15$) and flagfish ($r = 0.251$, $P = 0.367$, $n = 15$; Fig. 4). When the analysis was restricted to sites with a significant relationship between fish density and time since a dry down (see Table 3), the association between

Table 2. A mixed linear model was used to test for differences in fish density [$\ln(\text{density} + 1)$] across water-management units (region), sampling sites nested within water-management units [site (region)], years, sampling periods nested within years [period (year)], and the corresponding interactions. The five sampling periods within years describe general seasonal patterns at sites. Time since a dry down (d) was the covariate [$\ln(d + 1)$]

Effect	d.f.	Least killifish		Eastern mosquitofish		Bluefin killifish		Golden topminnow		Flagfish	
		<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Without covariate											
Region	2, 32	516.75	< 0.001	232.86	< 0.001	39.57	< 0.001	3.67	0.037	68.43	< 0.001
Site (region)	14, 32	81.22	< 0.001	69.20	< 0.001	62.39	< 0.001	23.88	< 0.001	45.63	< 0.001
Year	5, 160	37.19	< 0.001	5.27	< 0.001	93.39	< 0.001	18.30	< 0.001	19.16	< 0.001
Period (year)	24, 666	16.80	< 0.001	12.20	< 0.001	31.47	< 0.001	16.65	< 0.001	24.82	< 0.001
Region × year	10, 160	21.34	< 0.001	4.32	< 0.001	18.35	< 0.001	7.91	< 0.001	7.81	< 0.001
Region × period (year)	47, 666	10.54	< 0.001	5.06	< 0.001	9.57	< 0.001	4.50	< 0.001	11.02	< 0.001
Site × year (region)	70, 160	5.56	< 0.001	4.11	< 0.001	4.76	< 0.001	3.75	< 0.001	6.03	< 0.001
Site × period (region × year)	285, 666	3.18	< 0.001	2.75	< 0.001	2.91	< 0.001	1.99	< 0.001	2.96	< 0.001
With covariate											
Region	2, 32	4.33	0.022	0.59	0.561	0.92	0.409	0.12	0.889	5.51	0.009
Site (region)	14, 32	2.05	0.046	1.72	0.100	1.64	0.121	3.87	0.001	3.11	0.004
Year	5, 160	6.96	< 0.001	1.73	0.131	4.10	0.002	1.00	0.421	4.70	0.001
Period (year)	24, 667	4.59	< 0.001	2.99	< 0.001	7.57	< 0.001	7.45	< 0.001	15.30	< 0.001
Region × year	10, 160	3.74	< 0.001	1.01	0.437	1.99	0.038	3.59	< 0.001	3.34	0.001
Region × period (year)	47, 667	5.76	< 0.001	2.27	< 0.001	5.81	< 0.001	3.14	< 0.001	7.23	< 0.001
Site × year (region)	70, 160	3.98	< 0.001	3.26	< 0.001	3.23	< 0.001	3.06	< 0.001	4.57	< 0.001
Site × period (region × year)	285, 667	2.88	< 0.001	2.57	< 0.001	2.72	< 0.001	2.14	< 0.001	2.82	< 0.001
ld	1, 809	5.41	0.020	< 0.01	0.951	2.75	0.098	< 0.01	0.987	< 0.01	0.970
ld × site (region)	16, 809	1.85	0.022	1.56	0.073	2.46	0.001	3.31	< 0.001	2.59	0.001

N_{\max} and hydroperiod was significant for bluefin killifish ($r = 0.624$, $P = 0.023$, $n = 13$) and golden topminnows ($r = 0.789$, $P = 0.007$, $n = 10$), but not significant for the other species ($P > 0.325$; Fig. 4). The association between d_{\max} and hydroperiod was significant for bluefin killifish ($r = 0.838$, $P < 0.001$, $n = 13$). Although not significant, a positive association was also apparent

for least killifish ($r = 0.488$, $P = 0.091$, $n = 13$) and golden topminnows ($r = 0.607$, $P = 0.063$, $n = 10$; Fig. 4). The association between d_{\max} and hydroperiod was significant for neither flagfish ($r = 0.099$, $P = 0.801$, $n = 9$) nor eastern mosquitofish ($r = 0.202$, $P = 0.744$, $n = 5$).

Fish population dynamics were more similar among sites in close proximity independent of hydrological

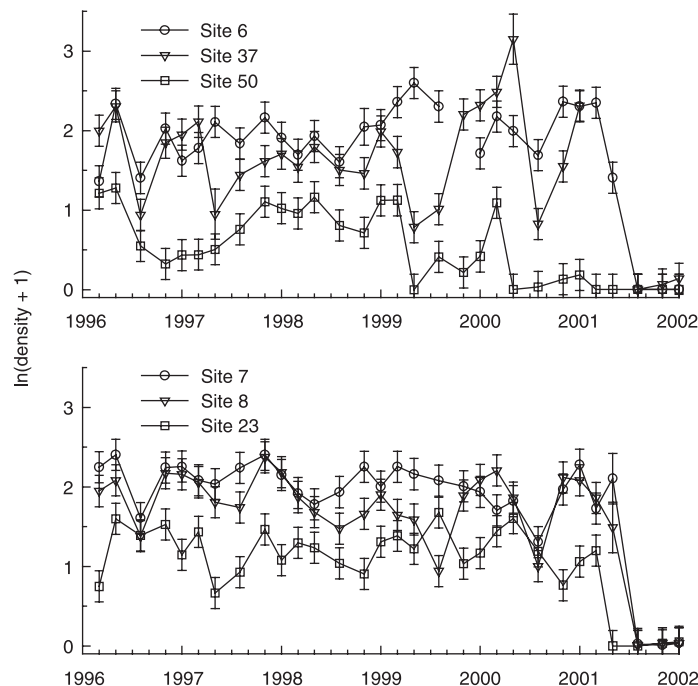


Fig. 2. Marked spatio-temporal variation in the density (no. m^{-3}) of bluefin killifish in Shark River Slough. Error bars represent ± 1 SE. Least-squares means and standard errors were estimated based on the mixed linear model.

Table 3. Regression models of fish density vs. time since a dry down for each species-site combination. The response variable is $\ln(\text{density} + 1)$, the explanatory variable is d (time since a dry down), and β_1 and β_2 are slope coefficients (the intercept is not shown). Only models with slope coefficients significantly different from zero were reported ($P \leq 0.05$). NS indicates that slope coefficients were not significant

Site	Least killifish		Eastern mosquitofish		Bluefin killifish		Golden topminnow		Flagfish	
	Model	R^2	Model	R^2	Model	R^2	Model	R^2	Model	R^2
Shark River Slough										
6	$\beta_1 d$	0.477	NS	–	$\beta_1 d - \beta_2 d^2$	0.701	$\beta_1 d$	0.083	$-\beta_1 d + \beta_2 d^2$	0.178
7	$\beta_1 d - \beta_2 d^2$	0.574	NS	–	$\beta_1 d - \beta_2 d^2$	0.757	$\beta_1 d - \beta_2 d^2$	0.186	$-\beta_1 d + \beta_2 d^2$	0.343
8	$\beta_1 d - \beta_2 d^2$	0.559	$\beta_1 d - \beta_2 d^2$	0.086	$\beta_1 d - \beta_2 d^2$	0.566	$\beta_1 d - \beta_2 d^2$	0.159	NS	–
23	$\beta_1 d$	0.375	NS	–	$\beta_1 d - \beta_2 d^2$	0.502	$\beta_1 d$	0.169	$\beta_1 d - \beta_2 d^2$	0.122
37	$\beta_1 d$	0.134	NS	–	$\beta_1 d - \beta_2 d^2$	0.176	NS	–	NS	–
50	$\beta_1 d - \beta_2 d^2$	0.354	$\beta_1 d - \beta_2 d^2$	0.282	$\beta_1 d - \beta_2 d^2$	0.416	$\beta_1 d - \beta_2 d^2$	0.202	NS	–
Taylor Slough										
CP	$-\beta_1 d + \beta_2 d^2$	0.292	NS	–	$\beta_1 d - \beta_2 d^2$	0.677	$\beta_1 d$	0.057	$-\beta_1 d + \beta_2 d^2$	0.117
MD	$\beta_1 d - \beta_2 d^2$	0.771	$\beta_1 d$	0.160	$\beta_1 d - \beta_2 d^2$	0.719	$\beta_1 d - \beta_2 d^2$	0.521	NS	–
MDsh	$\beta_1 d$	0.156	NS	–	$\beta_1 d$	0.241	NS	–	$-\beta_1 d$	0.199
TS	$\beta_1 d$	0.589	$\beta_1 d - \beta_2 d^2$	0.165	$\beta_1 d - \beta_2 d^2$	0.562	$\beta_1 d$	0.185	NS	–
TSsh	$\beta_1 d$	0.330	NS	–	$\beta_1 d$	0.461	$\beta_1 d$	0.182	$-\beta_1 d + \beta_2 d^2$	0.393
Water Conservation Area 3 A										
1	$\beta_1 d$	0.231	$-\beta_1 d + \beta_2 d^2$	0.488	$-\beta_1 d + \beta_2 d^2$	0.234	NS	–	$-\beta_1 d + \beta_2 d^2$	0.500
2	NS	–	$-\beta_1 d + \beta_2 d^2$	0.104	NS	–	NS	–	$-\beta_1 d + \beta_2 d^2$	0.874
3	$-\beta_1 d + \beta_2 d^2$	0.320	NS	–	$\beta_1 d$	0.291	$-\beta_1 d + \beta_2 d^2$	0.236	$-\beta_1 d$	0.066
4	$\beta_1 d$	0.131	$-\beta_1 d + \beta_2 d^2$	0.236	NS	–	$\beta_1 d$	0.368	$-\beta_1 d + \beta_2 d^2$	0.280
5	NS	–	NS	–	NS	–	NS	–	$-\beta_1 d + \beta_2 d^2$	0.726
11	$\beta_1 d$	0.140	NS	–	$\beta_1 d - \beta_2 d^2$	0.430	NS	–	NS	–

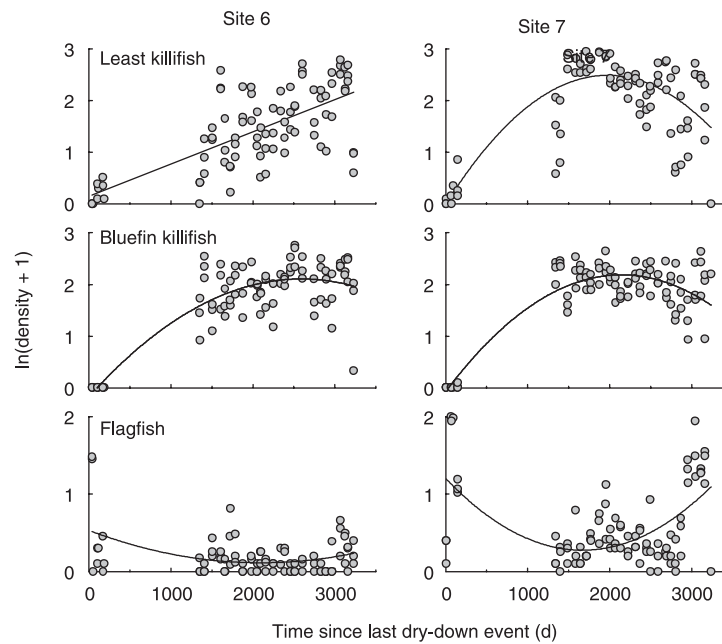


Fig. 3. Relationship between fish density (no. m^{-2}) and time since a dry down at two representative sites in Shark River Slough. Solid lines represent the fit of regression models (Table 3). The scale of the y-axis for flagfish differs from the other species.

disturbance, and population dynamics were more alike among sites with similar regimes of hydrological disturbance independent of distance (Fig. 5). Although significant, the association between hydrological synchrony and distance was weak ($r = -0.192$, $P = 0.013$, $n = 136$). Population synchrony was stronger (based on higher partial correlation coefficients) among sites with similar regimes of hydrological disturbance than among sites in close proximity for bluefin killifish, eastern

mosquitofish, golden topminnows and least killifish; however, population synchrony was stronger among sites in close proximity for flagfish (Fig. 5). Median population synchrony was greatest for bluefin killifish and golden topminnows and lowest for eastern mosquitofish and flagfish (Fig. 5). Most estimates of population synchrony were positive, comprising from 71% of observations for least killifish to 86% for bluefin killifish.

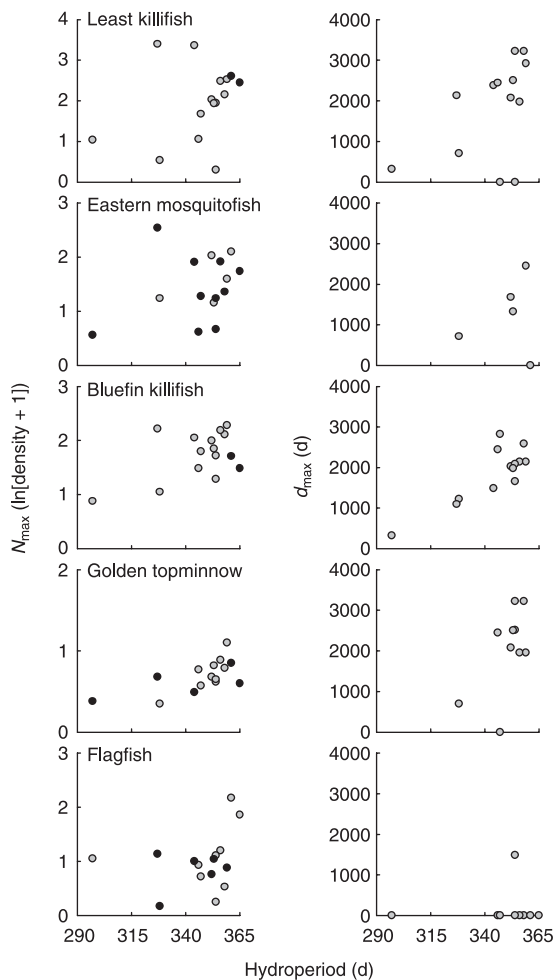


Fig. 4. Relationships among maximum fish density after a dry down (N_{\max}), time to reach N_{\max} (d_{\max}) and hydroperiod (days per year water depth was > 5 cm). N_{\max} and d_{\max} were estimated from site-specific regression models for each species (Table 3). Solid circles represent sites where the relationship between fish density and time since a dry down was not significant. The scale of the y-axis for N_{\max} differs among species.

For all species, the effect of distance on synchronous population dynamics depended on the hydroperiod of the sites compared. Distance was important for synchronizing fish population dynamics (independent of hydrological synchrony) for comparisons among long-hydroperiod sites and between long- and short-hydroperiod sites (Table 4). The association between hydrological synchrony and distance was significant only among long-hydroperiod sites, and the range in distances between sites was similar among the three groups (Table 4).

Discussion

MARSH DRYING AND POPULATION DYNAMICS

Three patterns of response to drought emerged for Everglades fishes. The density of bluefin killifish, least

killifish and golden topminnows was lowest after a dry down and recovered slowly, at times requiring several years to reach an asymptotic density. Density of eastern mosquitofish displayed weak or no relationship to time since a dry down and generally recovered quickly to their pre-dry-down level following a drought. Flagfish density peaked soon after a dry down and then declined. Thus, eastern mosquitofish and flagfish rapidly re-colonized marshes after a dry down, probably from dispersal (at least initially) given the rapid response (see also Jordan, Babbitt & McIvor 1998; Baber *et al.* 2002). Moreover, eastern mosquitofish and flagfish are better adapted than bluefin killifish, golden topminnows and least killifish for surviving poor water quality conditions that can occur during severe droughts (Kushlan 1974a).

N_{\max} and d_{\max} were associated more strongly with hydroperiod for species that responded negatively to dry downs. For local populations, fish density tended to be highest and recovery slowest at sites that infrequently experienced dry downs. We suspected that populations recovered more rapidly at sites that frequently experienced dry downs because N_{\max} tended to be less at short-hydroperiod sites (Fig. 4). Frequent dry downs appeared to limit the density of bluefin killifish and golden topminnows. In contrast, N_{\max} and d_{\max} were not strongly associated with hydroperiod for least killifish, eastern mosquitofish and flagfish, which may indicate that local population dynamics were not strongly limited by dry downs. This finding was unexpected for least killifish because their response to drought was more similar to bluefin killifish and golden topminnows than to flagfish or eastern mosquitofish.

A MORAN EFFECT IN THE EVERGLADES?

Fish population fluctuations were synchronous over the Everglades landscape. Species that exhibited the highest degree of synchrony (i.e. bluefin killifish, golden topminnow and least killifish) were those where populations declined dramatically following a drying event. Synchronous fish population dynamics appeared to be caused at least partly by a Moran effect from hydrological disturbance. However, after controlling for the effect of hydrological disturbance, population synchrony declined with distance separating study sites, probably resulting from dispersal. A decline in population synchrony with increasing distance is a common pattern for many animals (Ranta *et al.* 1995), and consistent with the hypothesis that frequency of dispersal decreases as greater distances separate populations (Ranta *et al.* 1998; Koenig 1999). We suspect that dispersal was the most parsimonious explanation for the role of distance on synchronous fish population dynamics in the Everglades because dispersal is required for fishes to re-colonize marshes after a dry down (although the spatial scale of dispersal will probably vary among species). Nevertheless, we cannot exclude the possibility that other factors (e.g. presence of nomadic predators) caused

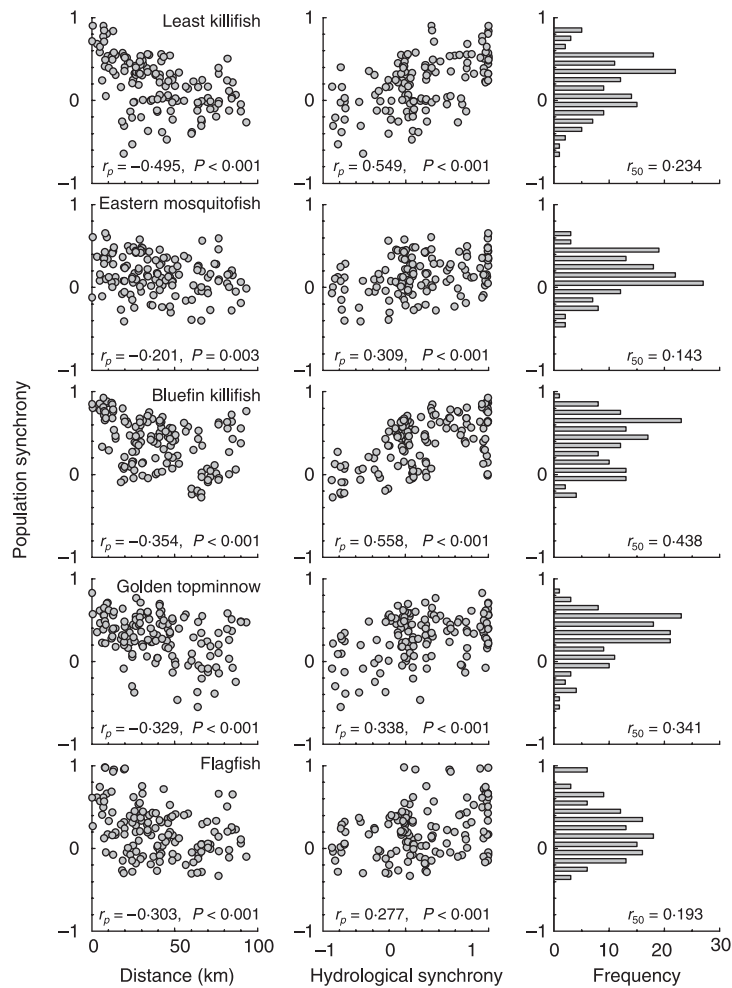


Fig. 5. Population synchrony related to distance separating study sites and hydrological synchrony. Relationships were quantified using partial correlation coefficients (r_p); P -values were calculated using Mantel tests. Population and hydrological synchrony are the correlations based on fish density and time since a dry down, respectively, for each pair of sites across all sampling events. Histograms display the distribution of population synchrony among all pairs of sites, with median values of population synchrony (r_{50}).

Table 4. Relationships between population synchrony and distance among short-hydroperiod sites (short), among long-hydroperiod sites (long), and between long- and short-hydroperiod sites (Table 1). Partial correlation coefficients are reported for each comparison with significant values given in bold type ($P \leq 0.05$). P -values were calculated using Mantel tests (given parenthetically)

Species	Short vs. short ($n = 28$) ^a	Long vs. long ($n = 36$) ^b	Long vs. short ($n = 72$) ^c
Least killifish	-0.657 (< 0.001)	-0.321 (0.030)	-0.516 (< 0.001)
Eastern mosquitofish	-0.256 (0.100)	-0.230 (0.089)	-0.171 (0.077)
Bluefin killifish	-0.376 (0.027)	-0.560 (< 0.001)	-0.452 (< 0.001)
Golden topminnow	-0.235 (0.122)	-0.602 (< 0.001)	-0.332 (0.003)
Flagfish	-0.238 (0.116)	-0.414 (0.006)	-0.353 (0.001)

^aCorrelation between distance and hydrological synchrony was not significant ($r = 0.074$, $P = 0.647$). Distance between sites: 0.3–90 km. ^bCorrelation between distance and hydrological synchrony was significant ($r = -0.628$, $P < 0.001$). Distance between sites: 8–87 km. ^cCorrelation between distance and hydrological synchrony was not significant ($r = -0.082$, $P = 0.250$). Distance between sites: 0.6–93 km.

population synchrony to decline with distance (Ydenberg 1987; Koenig 1999).

Disentangling the underlying mechanisms of spatial synchrony is difficult (Ranta *et al.* 1999; Cattadori *et al.* 2000; Ripa 2000; Koenig 2002; Post & Forchhammer 2002). Our ability to separate effects of dispersal and

hydrological disturbance was strengthened by statistically controlling the effect of each factor (i.e. distance or hydrological synchrony) with partial correlation coefficients. A weak association between distance and hydrological synchrony among sites further strengthened our ability to separate the effects of dispersal and

hydrological disturbance. Synchronous environmental fluctuations decline typically with increasing distances among areas (Koenig 2002). The surprisingly weak association between distance and hydrological synchrony in the Everglades probably resulted from the flat topography of the landscape and regional management of hydrology (Loftus & Eklund 1994; Ross *et al.* 2003).

The Moran effect and dispersal were important factors driving spatio-temporal patterns of Everglades fish populations. The Moran effect appeared to be a stronger mechanism than dispersal on the population dynamics of bluefin killifish, least killifish, golden topminnows and eastern mosquitofish. This suggested that site re-colonization by these species is primarily from *in situ* reproduction by individuals that survive a dry down in nearby deep-water habitats (at a spatial scale less than separating our study sites). We suspected that deep-water habitats are available at most, if not all, study sites, although the spatial distribution and quality (e.g. surface area and depth) of these habitats almost certainly varied across the landscape (Campbell & Mazzotti 2001; Kobza *et al.* 2004; Palmer & Mazzotti 2004). While bluefin killifish, least killifish and golden topminnows declined dramatically during droughts and recovered slowly afterwards, eastern mosquitofish did not. Thus, we believe the mechanism for recovery by eastern mosquitofish differed from bluefin killifish, least killifish and golden topminnows.

The Moran effect has been observed among a diversity of animals (Cattadori *et al.* 2000; Post & Forchhammer 2002; Cattaneo *et al.* 2003). For instance, population synchrony of young brown trout (*Salmo trutta*) in streams was associated with hydrological synchrony (based on high flows during the emergence period) but not connectivity or stream distance, suggesting the Moran effect was the primary mechanism (Cattaneo *et al.* 2003). The importance of the Moran effect for brown trout in streams (Cattaneo *et al.* 2003) was generally consistent with our observations for wetland fishes, although both the Moran effect and dispersal appeared to be important mechanisms in the Everglades. The Moran effect, together with dispersal-linked populations, often organize groups that fluctuate in step but out of phase with other groups (Ranta *et al.* 1999), which could be partly responsible for the negative values of population synchrony we observed between some sites (Fig. 5).

Dispersal appeared stronger than the Moran effect in synchronizing the population dynamics of flagfish. Population synchrony was more strongly related to distance than hydrological disturbance for flagfish, suggesting that site re-colonization results primarily from dispersal rather than *in situ* reproduction. We also expected dispersal to have a dominant role on population dynamics of eastern mosquitofish given their dispersal and colonization abilities in other ecosystems (Brown 1985, 1987). An alternative explanation for the weak association between population synchrony

and distance for eastern mosquitofish is that they re-populated sites more rapidly after a dry down than the time separating our sampling events (2–3 months). Thus, we may have failed to track the re-colonization process of this species in many instances, except to note that it occurred.

Population dynamics of Everglades fishes were generally consistent with a source–sink population model (Pulliam 1988). Over all species, population dynamics were synchronized more frequently by distance for comparisons among long-hydroperiod sites and between long- and short-hydroperiod sites (Table 4), suggesting that dispersers originate from long-hydroperiod marshes. Thus, long-hydroperiod marshes may function as source habitats during droughts, whereas short-hydroperiod marshes may function as sink habitats (Trexler *et al.* 2002). However, these generalizations were not equally applicable to all species. A source–sink population model appeared most appropriate for flagfish and golden topminnows.

In conclusion, we suggest that hydrological disturbance is an important factor shaping spatio-temporal patterns of local fish populations across the Everglades landscape and wetlands in general. The relative importance of hydrological disturbance and dispersal on synchronous fish population dynamics appear to vary among species, probably related to a species life history and ability to exploit dry-season refugia, although both factors appear to be important. We predict that dispersers are more likely to originate from long-hydroperiod marshes and short-hydroperiod marshes are more likely to function as sinks. Nevertheless, our results do not exclude the importance of other factors on fish population dynamics. Population dynamics at areas that experience frequent dry downs are more likely to be dominated by hydrological disturbance, whereas population control may be more complex at long-hydroperiod marshes (Snodgrass *et al.* 1996; Chick, Ruetz & Trexler 2004). We expect that both nutrient concentrations (Turner *et al.* 1999; Trexler *et al.* 2002) and predation (Loftus & Eklund 1994; Taylor, Trexler & Loftus 2001; Gawlick 2002; Kobza *et al.* 2004) also shape patterns of fish density in the Everglades, although hydrological disturbance appears to have the strongest effect on most fish species over much of the landscape. This study underscores the important role of environmental fluctuations on animal population dynamics and emphasizes the need to consider populations at multiple spatio-temporal scales and non-equilibrium states.

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