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Impact of hydropattern disturbance on crayfish population dynamics in the seasonal wetlands of Everglades National Park, USA

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ABSTRACT

1. The natural hydropattern in the seasonally-flooded marl prairie wetlands of Everglades National Park has been severely disrupted by human water control activities, seriously impacting higher trophic organisms, e.g. wading birds, that depend on these wetlands. Less is known about the impacts on key aquatic fauna, such as crayfish *Procambarus alleni*, or how these populations might respond to proposed habitat restoration strategies.
2. Under severe environmental stress, populations of burrowing crayfish are predicted to have skewed size structure, low reproductive success, low survival, and widespread dispersal. As predicted for populations in stressed habitats, crayfish density was low, small dispersing adults were dominant, juvenile abundance was low, and survival was low in habitats where the hydroperiod (duration of flooding) was short and groundwater level was lowest.
3. Crayfish dispersed during flooding, but during the drydown, they burrowed rather than sought deeper water. This dispersal strategy may be adaptive for surviving in seasonal wetlands, but this had severe consequences on survival in disturbed habitats with shortened hydroperiods. Survival in burrows during the dry season was high in the longer-hydroperiod habitats but was zero in the short-hydroperiod habitat where the groundwater level fell more than 1 m.
4. Long-hydroperiod marl prairie may function as sources, whereas short-hydroperiod habitats act as population sinks. Our study suggests that the threshold conditions for preventing mass mortality of crayfish in these wetlands are hydroperiods > 7 months and groundwater levels < 0.5 m below the surface during the dry season.
5. Historical (pre-drainage) hydroperiods appear to be restricted to the longest hydroperiod areas of the marl prairie. This indicates that much of the marl prairie wetlands now function as population sinks for crayfish and other invertebrates. The historical hydropatterns need to be re-established throughout the marl prairie wetlands to achieve the restoration goal of increasing productivity in the aquatic faunal community.

KEY WORDS: crayfish; Everglades; hydroperiod; wetland restoration

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INTRODUCTION

Increasing the population sizes of target species is a primary goal in restoration ecology. The success of strategies for habitat restoration is often gauged by the observed distribution and abundance of key species that depend on those habitats. However, simple distribution and abundance data may mask complex mechanistic processes that impact populations. Of primary importance are dispersal, habitat use, and subsequent survival in those habitats that affect population dynamics in a number of ways. Dispersal of individuals and their offspring is important for maintaining populations in heterogeneous environments (Roff, 1974), but the spatial distribution and extent of habitats that function as population sources or sinks may be the primary determinant of population viability and persistence (Pulliam, 1988).

The historical hydropatterns in the vast watershed of the Florida Everglades, USA, have been drastically altered by flood control activities over the past half century (Light and Dineen, 1994). The historical sheetflow from the Kissimmee River and Lake Okeechobee through the Everglades to the Gulf of Mexico and Florida Bay has been greatly reduced, channelized, and redirected by numerous canals and levees for flood control, and for agricultural and urban water supply. The redirection of water, lengthening of the dry season, and lowering of groundwater levels have precipitated a number of problems for both terrestrial and aquatic communities in Everglades National Park (ENP), which encompasses the southernmost 20% of the historical ecosystem (Robertson and Frederick, 1994). In recognition of its natural value, ENP was designated as a World Heritage Site, an International Biosphere Reserve, and a Wetland of International Significance, and much effort is currently directed at restoration of the ecosystem.

One of the most severely impacted habitats is the wet marl prairie of eastern ENP, which undergoes a natural seasonal cycle of flooding and drying. Here, the dry season historically averaged 3 months or less, but, at present, the dry season has increased by one to six months in most areas (Fennema *et al.*, 1994). The resulting environmental changes are believed to have had severe repercussions throughout the food web. For example, these impacts may be linked to the 90% decline in wading bird populations over the past 50 years (Ogden, 1994). Primary impacts have also been noted in the decrease in habitat heterogeneity and productivity of basal trophic groups, that may have resulted in the disruption of key linkages between major trophic levels (Gunderson and Loftus, 1993; Turner *et al.*, 1999).

The crayfish *Procambarus alleni* Faxon is a major trophic component of the aquatic community in these marl prairie wetlands. Crayfish are often polytrophic with multiple functional roles in wetland communities (Momot *et al.*, 1978). In the Everglades, crayfish are important as prey for wading birds and other macrofauna (Frederick and Spalding, 1994), as consumers of macrophytic detritus (Gunderson and Loftus, 1993), and as predators on small invertebrates and fish. For example, Kushlan and Kushlan (1975) estimated that the 1972 white ibis population might have consumed up to 470 tons of crayfish. Like other burrowing crayfish species, *P. alleni* is well adapted for inhabiting seasonally-flooded environments by burrowing during droughts (Rhoads, 1976) and is even capable of short-term overland movement (Wygoda, 1981). The Everglades crayfish will be used as an indicator species for monitoring the progress of restoration programmes. However, it is not known how changes in hydropatterns have affected the crayfish population in these disturbed wetlands or how the proposed ecosystem restoration strategies will affect the population dynamics of this key trophic species.

Under environmental stress, burrowing crayfish are expected to have small populations dominated by small dispersing adults, widespread dispersal, and low survival (Taylor, 1983). These predictions were tested to evaluate the impacts on crayfish populations in habitats with different hydroperiods and groundwater levels over the dry season. Crayfish density and population size structure were compared in marl prairie habitats differing in local hydroperiod and minimal groundwater levels. Dispersal rates and patterns were quantified in flooded and drying habitats to compare responses with changes in hydrological conditions. Survival of resident crayfish was measured over the dry season and compared with recolonization during flooding. These data were used to explore the mechanistic basis for the effects of disrupted hydropatterns on the crayfish population in this disturbed landscape.

METHODS

Habitat characteristics and population monitoring

The marl prairie wetlands of eastern ENP consist of calcitic marl substrate with varying amounts of peat overlay and numerous soil-filled solution holes. The marl prairie is flanked by sloughs, which are large drainage basins with a slow north–south sheetflow (Figure 1). The marl prairie habitat historically underwent a seasonal drydown in spring (March–May), but currently, the dry season varies locally from November to July, depending on natural elevation, as well as the aperiodic pumping of water into the park from the canal system. Three sites (of nine used for monthly crayfish sampling) were used for dispersal and survival experiments in 1999. The average hydroperiod at these three sites lasted 3 months (Hydroperiod 'Short'), 7 months (Hydroperiod 'Medium'), and 9 months (Hydroperiod 'Long') (Table 1).

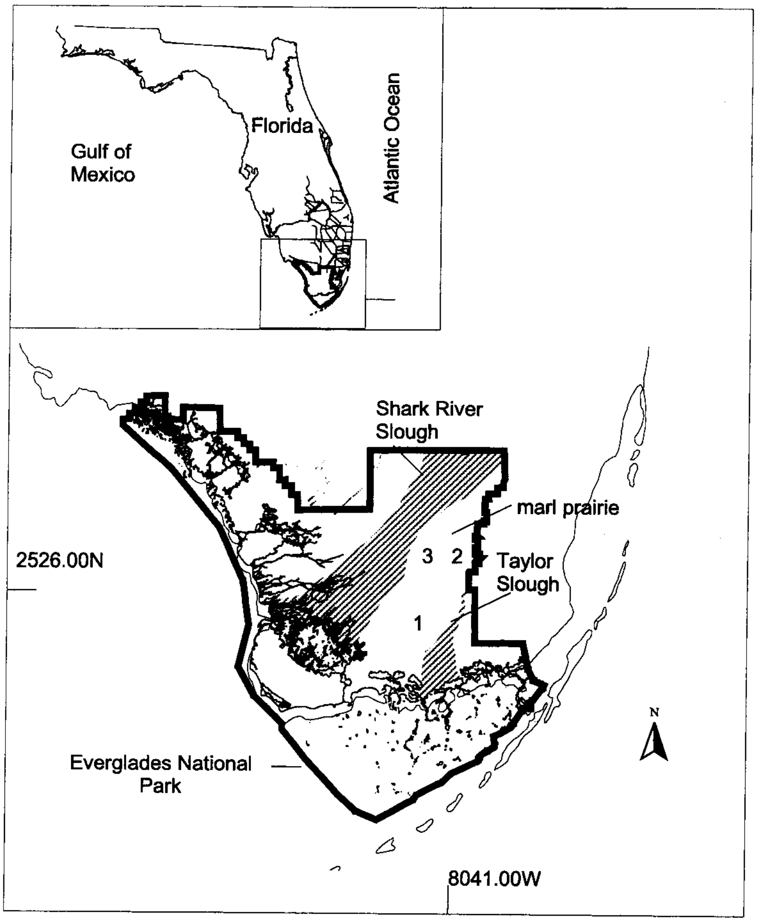

Figure 1. Map of ENP showing the extent of marl prairie habitat (experimental areas shown numbered). Inset shows the state of Florida, USA, and the extent of canals and controlled waterways (lines) used for water management.

Table 1. Characteristics of marl prairie sites in eastern Everglades National Park

Hydroperiod site	GPS[a]	GSE[b]	Habitat area	Hydroperiod (months)
Short	2525.083, 8038.391	1.12	0.40	3
Medium	2526.225, 8042.111	0.75	0.63	7
Long	2525.950, 8038.401	0.77	0.97	9

Ground surface elevation (GSE) was estimated by comparing surface water levels at sites with measurements at nearby hydrological stations. Habitat area for burrows consists of peat overlaying marl substrate and soil-filled solution holes; the proportion of area suitable for crayfish burrows is shown calculated from habitat maps.

[a] Global positioning satellite (GPS) coordinates as North and West in degrees/decimal minutes.

[b] Ground surface elevation (GSE) in metres above mean sea level, NGVD 1929.

Water levels were continuously monitored at nearby hydrological monitoring stations maintained by ENP. The area of habitat suitable for crayfish burrows was estimated by mapping and measuring soft substrate (e.g. soil-filled solution holes) in a 50 × 50 m grid in each site.

Crayfish densities were monitored during 1998–2000 on a monthly basis until the water level at the surface or in solution holes fell to < 3 cm. Crayfish, collected using cylindrical wire minnow traps baited with shrimp, were sampled at 24- and 48-h intervals. The sampling efficiency and sampling bias using this method were previously estimated from mark–recapture experiments (Acosta and Perry, 2000). Behavioural studies and data on size structure showed no significant sex- or size-related bias (except for young-of-the-year < 12 mm carapace length (CL) that could escape through the trap mesh). Relative density of crayfish at each site was estimated from measures of the sampling area (56.3 m^2) of each of six traps. All crayfish were measured (to 0.1 mm CL), weighed (to 0.1 g), sexed, marked, and released on site. Crayfish were marked using a permanent coloured latex tag inserted internally in clear abdominal segments (Acosta and Perry, 2000). With a unique colour combination for each site during each survey, groups of individuals marked during previous months and the location of tagging could be identified. Two-sample Kolmogorov–Smirnov *Z* tests were used to compare the size structure of crayfish sub-populations between pairs of sites.

Horizontal dispersal

To determine whether dispersal across the surface plane is influenced by local hydroperiod or flood stage, mass mark–recapture experiments were conducted to quantify movement rates and patterns in the three sites under flooded (July–August) or drying (December–January) conditions. Water level during flooding was typically 0.2–0.5 m above the ground surface, whereas during the drydown, water was restricted to the solution holes that were isolated by the rapidly drying surrounding ground surface.

Experiments were conducted using five concentric arrays of traps set at specific distances from the point where marked crayfish were released. With an effective sampling radius of 5 m for each trap (calculated as α, the effective sampling coefficient; Acosta and Perry, 2000), the distance between traps in a circular array was 10 m and the distance between concentric arrays was 10 m, encompassing an experimental area of approximately 1 ha. Crayfish were marked, released in the centre of the experimental area, and collected from traps after 48 h. Five replicate releases were conducted during flooding and five releases were conducted during drydowns in each of the three sites.

To describe dispersal dynamics, the diffusion model developed by Turchin and Thoeny (1993) was used to provide a mechanistic explanation for movement in terms of diffusion rates and loss of animals from the dispersing population (the settling rate). The diffusion-with-loss model is derived from the equation:

$$\frac{\partial u}{\partial t} = D\left(\frac{\partial^2 u}{\partial x^2} + \frac{\partial^2 u}{\partial y^2}\right) - \delta u$$

where D is the diffusion rate and δ is the settling rate. The Turchin–Thoeny (1993) model uses a solution that is based on an approximation of the Bessel function (Awerbuch *et al.*, 1979; Okubo, 1980) with two parameters:

$$C(r) = Ar^{1/2} \exp[-r/B]$$

where $A \equiv (\alpha N_0)/(\sqrt{8\pi}\sqrt[4]{D^3\delta})$ and $B \equiv \sqrt{D/\delta}$. The function $C(r)$ is the cumulative recaptures in all traps in a replicate at distance r, and N_0 is the number of marked crayfish released. The recaptures-with-distance data for each replicate were plotted, and the function $C(r)$ was fitted to the data. The variances of the cumulative recapture data were not homogeneous, so the data were log-transformed. The fitting equation was then of the linear form:

$$\log C(r) = \log A - \frac{1}{2}\log r - \frac{r}{B}$$

The parameter A is the recapture scale parameter, and B represents the width of the recaptures-with-distance curves. From estimates of these two parameters, rates of diffusion D and settling δ were calculated for the experimental treatments. Larger values of D indicate faster dispersal rates, and larger values of δ indicate that movement is abbreviated, leading to less population spread (Turchin and Thoeny, 1993).

Several assumptions were made about the dispersal of marked crayfish. First, there was no directional bias in movement by the dispersing population. To test this assumption, the compass directions to each trap from the release point were determined, and the mean vectors were calculated using the number of recaptured crayfish in each trap. We used the Rayleigh test with the null hypothesis that the directional movement of crayfish was random (Batschelet, 1981). Second, the diffusion equation adequately represented the dispersal dynamics of crayfish. To check this assumption, each curve fit was evaluated using analysis of variance (ANOVA) and power tests. If the model significantly underrepresented the shape of the curve, that replicate release was not used in further analyses. Third, the diffusion D and settling δ rates were constant within an experimental replicate.

Our primary interest was whether diffusion and settling differ among sites with different hydroperiods during flooding and drydown. A multivariate analysis of variance (MANOVA) was conducted with diffusion D and settling δ as dependent variables in two flood conditions (flooded and drydown) and three habitats (short, medium and long hydroperiods; Table 1) as factors. For multivariate assumptions, we used Levene's equal variances test for equality of error variances and Box's M test for equality of covariance matrices. Pillai's trace was used as the test statistic for the overall MANOVA model, the univariate F statistic was used to test the relative effects of individual response variables on significant factors, and Bonferroni tests were used for post-hoc within-site comparisons of replicates.

Vertical dispersal

To compare survival in burrows during the dry season, outplant mark–recapture experiments were conducted using field enclosures at the three sites that differed in hydroperiod (Table 1). The enclosures were constructed of 5 mm^2 polypropylene mesh that was sealed to the ground with cement; an enclosure was 20 cm high and enclosed an area with a 1 m radius. Six enclosures were built around shallow soil-filled solution holes that contained crayfish burrows in each of the three sites. Prior to the drydown, crayfish were collected from the site, marked, and released into the enclosures. During the next flooding, the emergence of survivors from burrows was monitored until water levels rose to 20 cm, generally by the second month of the flood season. Similar experiments were conducted simultaneously in six unenclosed solution holes that served as controls for each site.

The following assumptions were made about crayfish distribution and survival. First, the size of solution holes influences crayfish density, and so similar-sized solution holes (1 m radius) were sampled. Second, crayfish do not leave burrows during the dry season because this would increase mortality rates (Rhoads, 1976). Third, survival is mainly influenced by environmental factors and not by artifacts associated with the enclosures. Results from preliminary tests on survival and containment of crayfish conducted in enclosures in laboratory tanks indicated that most marked crayfish survived and remained in the enclosures as long as food was available. No recaptures were found in some of the field enclosures, and statistical assumptions of normality and homoscedasticity were not met even after transformation of the data. Therefore, we used the nonparametric Kruskal–Wallis H test on the proportion of crayfish recaptured in enclosed and non-enclosed habitats (factors). The Mann–Whitney U statistic was used for *post hoc* comparisons of survival in enclosures or in controls between pairs of sites at an adjusted α level of 0.01 (Sokal and Rohlf, 1981).

RESULTS

Density and population size structure

During first flooding, the abundance of crayfish at the medium and long hydroperiod sites quickly reached levels from the previous flood seasons, but at the short hydroperiod site, the reappearance of crayfish lagged flooding by almost two months (Figure 2). Mean crayfish densities at Hydroperiod

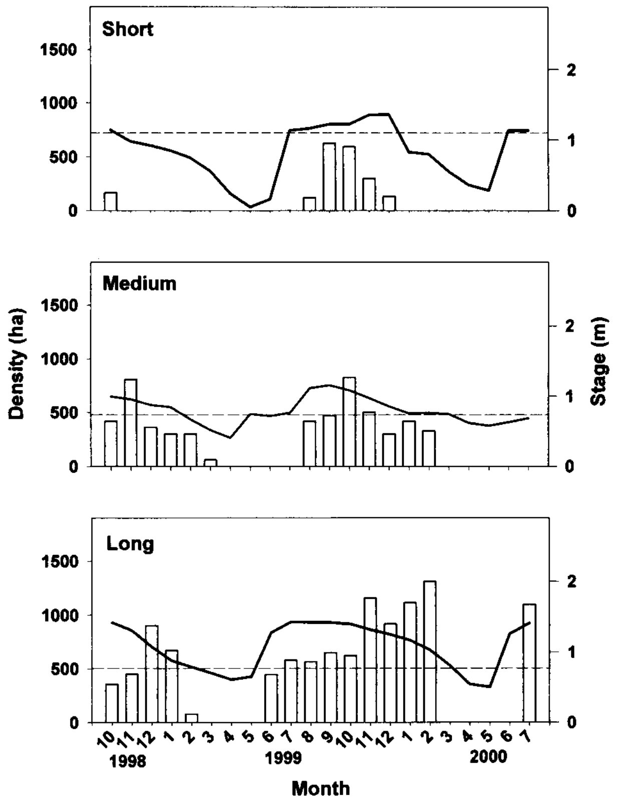

Figure 2. Densities of crayfish (bars) at three hydroperiod sites in marl prairie wetlands of eastern ENP 1998–2000. Water level (stage) is shown as a solid line, and the dashed line indicates ground surface elevation (GSE).

Medium (mean ± S.E.: 343.8 ± 65.5) and Long (mean ± S.E.: 502.4 ± 69) were also several times greater than at Hydroperiod Short (mean ± S.E.: 116.3 ± 42.8). During the drydown, the presence of crayfish at the surface decreased at all sites as they moved out of the area or retreated to burrows. From measurements of minimal groundwater levels during the dry season, burrows at Hydroperiod Short would have to be more than 1 m deep to reach lowest groundwater for crayfish to survive, whereas burrows at Hydroperiod Medium and Long would have to be about 0.5 m to reach the groundwater (Figure 2).

Crayfish population size structure at Hydroperiod Short differed significantly from that at Medium ($Z = 1.88$, $p < 0.001$) and Long ($Z = 2.98$, $p < 0.0001$). Small adults predominated at Short, whereas Medium and Long had normal distributions of size classes (Figure 3). The largest adults were more abundant at Long than at Medium, which accounted for most of the variance in size distribution at these sites ($Z = 2.59$, $p = 0.01$). The highest recruitment of small juveniles (< 18 mm CL) occurred from June to August. Crayfish *P. alleni* hatch in April–May in burrows (Rhoads, 1976), and the data indicate that the young remain with adults in home burrows for at least 2 months during the dry season.

Horizontal dispersal

The Rayleigh test for directional movement did not show any significant directional preference by crayfish at any flood stage or site (Figure 4). Polar graphs also suggest that the spread of crayfish across the ground surface was more extensive when the habitats were flooded than during the drydown. Under

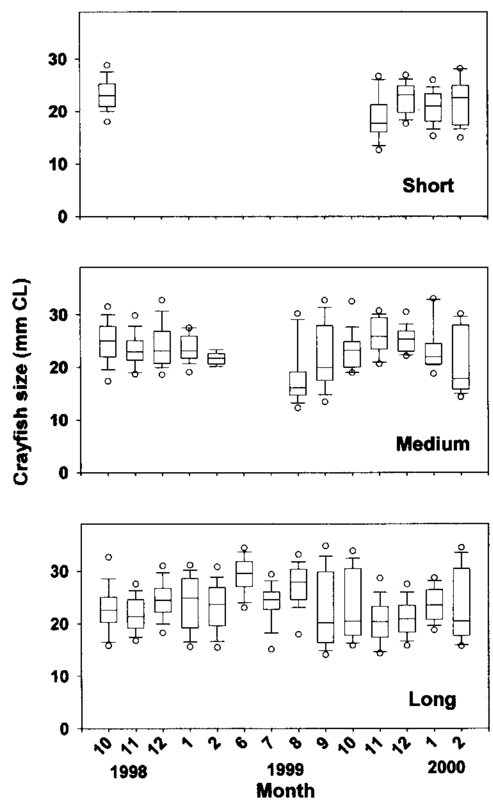

Figure 3. Population size structure at three hydroperiod sites in marl prairie wetlands 1998–2000. Box plots show mean and 25th and 75th percentiles; circles show 5th and 95th percentiles.

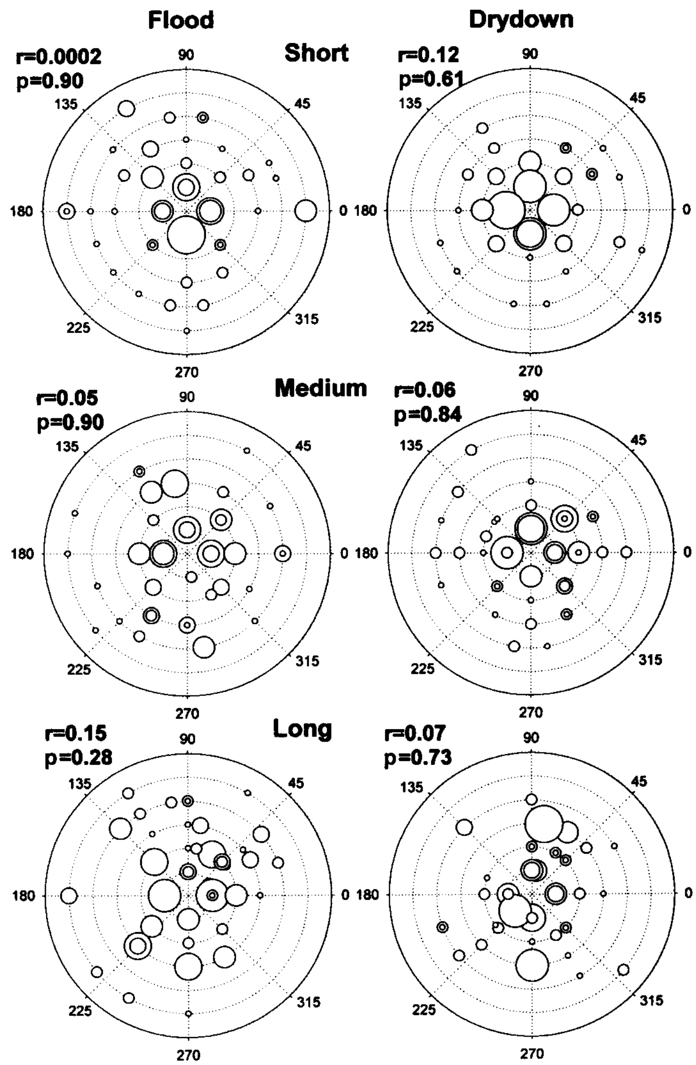

Figure 4. Directional movement of crayfish under flooded and drydown conditions at three hydroperiod sites (all replicates pooled). The size of circles represents the relative number of crayfish recaptured at that position; compass directions for movement activity are indicated by outer numbers; concentric dashed lines are 10 m intervals. The results of the Rayleigh tests for randomness in direction are shown (*r* statistics and probability values).

flooded conditions, movement occurred at a relatively even rate for the duration of the experiments (Figure 5). However, during the drydown, the spread of crayfish was reduced as movement activity was abbreviated and population spread was limited. For the flooded habitats, the diffusion model did not provide an adequate fit to two replicates at Hydroperiod Short, one replicate at Medium, and one replicate at Long that may have been due to the small number of animals used in these replicates. The model provided an adequate fit to the data for all other replicates. Power tests thus indicated a lower probability for detecting differences in the flooded experiments (mean 0.67; range 0.50–0.81) than in the drydown experiments (mean 0.88; range 0.85–0.99).

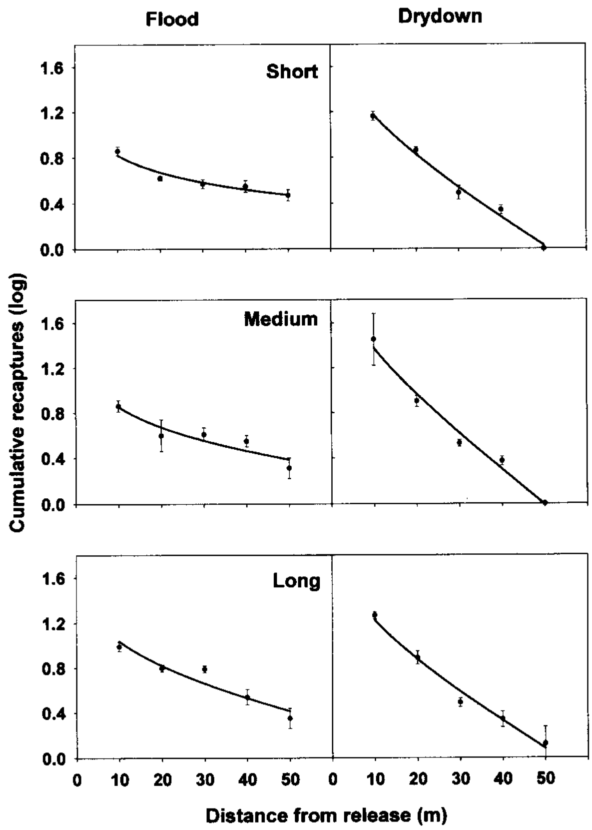

Figure 5. Recapture-with-distance curves for crayfish dispersal in flooded and drydown conditions at three hydroperiod sites. There were no statistical differences among replicates within flood treatments, so replicates are shown pooled. Circles (mean $\pm$ S.E.) are actual data; lines are fitted curves from the diffusion model.

The diffusion rate D and settling rate δ, calculated from the parameter estimates, were used in statistical comparisons of flood stage and hydroperiod effects (Table 2). In the MANOVA, variances among variables were homogeneous (Levene's test for D: $F = 1.88$, hypothesis df 5, error df 20, $p = 0.14$; for δ: $F = 3.65$, hypothesis df 5, error df 20, $p = 0.07$), and the covariance matrices were equal (Box's $M = 33.6$,

Table 2. Summary of the numbers of crayfish used in mark–recapture experiments and estimates of diffusion D and settling δ of dispersers from the fitted dispersal equation; shown are the mean ($\pm$ S.E.) for pooled experimental replicates

Stage	Hydroperiod	Released	Recaptured	Diffusion	Settling $\times 10^{-4}$
Flood	Short	210	57	1.25 (0.25)	0.0033 (0.0043)
	Medium	330	110	2.12 (0.83)	1.2 (1.6)
	Long	350	127	2.03 (0.23)	1.7 (0.089)
Drydown	Short	440	138	1.96 (0.47)	7.7 (1.3)
	Medium	430	163	1.59 (0.37)	7.4 (1.4)
	Long	415	167	1.62 (0.32)	6.7 (2.5)

The model provided an adequate fit to 11 replicates in flooded habitat and all 15 replicates in drying habitat.

$F = 1.61$, hypothesis df 15, error df 1139, $p = 0.07$). Flood stage had a significant effect on dispersal but only on the settling rate (δ) that was significantly higher during drydowns (Table 3). This confirms the observations on movement patterns indicated by the polar graphs (Figure 4). The power of the hydroperiod treatment (power = 0.12) was low due to the use of only three levels and may have precluded detection of fine-scale differences in diffusion rates. The Bonferroni multiple comparisons tests indicated that there were no significant differences in diffusion or settling rates within flooded or drydown treatments.

Vertical dispersal

Over the 1999 dry season, survival of resident crayfish in marl prairie enclosures was significantly different among sites (Kruskal–Wallis test: $H = 8.7$, df 2, $p = 0.01$). There were no survivors among all replicates at Hydroperiod Short, whereas survival was significantly higher at Medium and Long (Mann–Whitney test: $U = 51$, $p < 0.01$) (Figure 6). The proportions of survivors were similar at Hydroperiod Medium (mean $\pm$ S.E.: 0.23 ± 0.06) and Long (mean $\pm$ S.E.: 0.25 ± 0.05) (Mann–Whitney test: $U = 4$, $p > 0.05$).

Similar results occurred among the non-enclosed controls. No crayfish were recaptured at Hydroperiod Short following the dry season, but animals were recaptured at Medium and Long (Figure 6). Recapture rates at the latter sites were low because marked crayfish may have moved with flooding prior to sampling. This low but significant recapture rate occurred throughout much of the 1999–2000 sampling (Acosta and Perry, unpublished data). Although recolonization occurred at all sites, the consistent

Table 3. Multivariate analysis of variance (MANOVA) on the effects of flood stage and hydroperiod (factors) on diffusion D and settling δ of crayfish (dependent variables)

Source	Pillai's trace	F	Hypothesis df	Error df	p	Power
Stage	0.893		2	19	<0.001	1.00
diffusion		0.167		1	0.69	
settling		98.8		1	<0.001	
Hydroperiod	0.069		4	40	0.84	0.12
Stage * site	0.377		4	40	0.07	0.62
Error				20		

Pillai's trace was used to evaluate the model factors and the univariate F statistic was used to compare the relative effects of each variable on significant factors. Results of power tests are also shown.

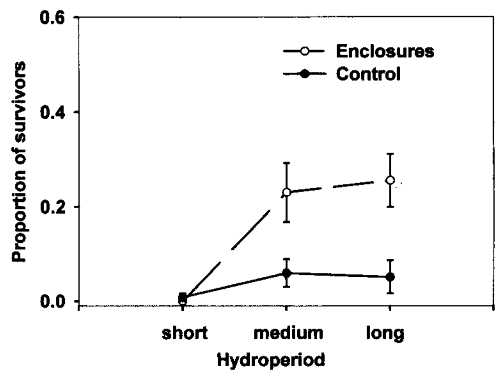

Figure 6. Survival of marked crayfish in three hydroperiod sites in field enclosures and non-enclosed controls over the 1999 dry season.

presence of marked, free-ranging crayfish from the previous flood seasons confirms the results from the enclosure experiments that some resident crayfish survived the dry season at the longer hydroperiod sites.

DISCUSSION

Hydroperiod significantly influences habitat heterogeneity and community structure in the seasonal wetlands of the Everglades, including the substrate composition, the vegetation community structure, and the dynamics of the transient aquatic fauna (Gunderson and Loftus, 1993). However, the natural hydropattern and seasonal functioning of the marl prairie have been altered by the excessive drawdown of water for urban and agricultural uses that has resulted in longer dry seasons and lower groundwater levels (Light and Dineen, 1994). The aquatic fauna must find the few refuges that remain wetted during the dry season or else die and recolonize each flood season (Loftus *et al.*, 1992). Because crayfish *P. alleni* is one of the most robust and well-adapted species for inhabiting these seasonal wetlands, any positive response to ecosystem restoration observed in this population may well indicate widespread positive effects on other more sensitive species.

Many species of crayfish respond to seasonal drought by burrowing, and no significant population changes are expected under natural flood-dry seasonality (Taylor, 1983). In stressed habitats, the expected consequences of extreme drought include smaller populations dominated by small dispersing adults, widespread dispersal for locating suitable habitats, and low survival (Taylor, 1983). During the Everglades flood season, crayfish *P. alleni* occupied marl prairie habitats with varying hydroperiods. However, in short-hydroperiod habitat, crayfish density was low with mostly small adults and few juveniles, as predicted for stressed habitats. In addition, there was a significant lag time of one to several months before crayfish occupied short-hydroperiod sites, suggesting that these small adults are not residents but are colonizers. The densities of crayfish at the longer hydroperiod sites were also substantially lower than those estimated for similar habitats in the northern range of the species (Jordan *et al.*, 1996). The crayfish population in the marl prairie wetlands of eastern Everglades National Park may be well below the carrying capacity for this habitat under conditions of more natural hydropatterns.

At the start of the flood season, crayfish dispersed to colonize newly flooded habitats where, presumably, resources were abundant. From the continuing mark–recapture studies at monitoring sites, it is estimated that the scale of seasonal population redistribution may be in the order of less than 1 km. This dispersal pattern was random with no directional movement. However, the drydown did not induce a marked reversal of this pattern, in which crayfish would retreat to habitats with deeper water as predicted. Instead, crayfish movement was abbreviated as they instead searched for burrow space, occupied existing burrows, or constructed new burrows. Moreover, increased densities of *P. alleni* have not been observed in deep slough habitats of the Everglades during the dry season, indicating that this habitat is not a dry season refuge (Rhoads, 1976; Kushlan and Kushlan, 1979; Jordan *et al.*, 1996). Retreating to shrinking pools or into the sloughs would lead to increased densities that would result in an increase in aggressive intraspecific interactions (Bovbjerg, 1959). The role of dispersal in the *P. alleni* population, instead, appears to function primarily for colonization to exploit resources in newly-flooded habitats. During drydowns, crayfish switched from horizontal movement to vertical movement by burrowing. Because the natural sheetflow has been largely replaced by artificial pumping of water into the park, the water recession rate at the end of the flood season is often abrupt, stranding crayfish that have not burrowed and leading to widespread mortality (J. Kline and S. Perry, unpublished data).

Given that crayfish switch from horizontal dispersal across the surface to vertical dispersal to the groundwater during drydowns, how is survival affected by habitat quality? Results from the enclosure study show that survival was significantly higher in habitats with longer hydroperiods and higher groundwater levels. Burrows in the short-hydroperiod areas must be more than 1 m deep to reach lowest groundwater levels, substantially deeper than the average depth of crayfish burrows (0.5 m) in this rocky substrate (Rhoads, 1976). Low or no survival in short-hydroperiod marl prairie appears to be linked to the low groundwater levels (>1 m) during the unnaturally long dry season. The threshold for mass mortality of crayfish appears to be linked to hydroperiods <7 months and groundwater levels >0.5 m below the surface during the dry season. Dispersal and survival, along with densities and population size structure in these seasonal wetlands, indicate that shortened hydroperiods and lower groundwater levels may have significant negative impacts on the viability and persistence of crayfish sub-populations.

While declines in the mega-vertebrate fauna have been well documented in this ecosystem (e.g. Robertson and Frederick, 1994), much less is known about changes in productivity of middle and lower trophic levels (but see Turner *et al.*, 1999). The aquatic invertebrate community represents the key link between primary productivity and higher trophic groups (Harris *et al.*, 1995; Laasonen *et al.*, 1998). Disruption of historical hydroperiods may have resulted in a shift in the areal distribution and extent of short-hydroperiod habitats that now function as population sinks for the aquatic fauna.

Furthermore, natural hydropatterns across this landscape are not only dependent on input by precipitation, but also on sheetflow from the northern portion of the watershed (Fennema *et al.*, 1994). Much of the northern watershed is currently managed to supply water to agricultural and urban areas and to move excessive run-off away from these areas. Conservation of this unique ecosystem may only be accomplished by accounting for the use, quality, and dynamics of the watershed outside the park boundaries. Restoration efforts for ENP should thus focus on converting aquatic population sinks to source habitats and on mitigating potential water quality problems during the re-establishment of natural pre-drainage hydrological conditions.

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