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Spatially explicit population responses of crayfish *Procambarus alleni* to potential shifts in vegetation distribution in the marl marshes of Everglades National Park, USA

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Abstract

Hydropattern disturbance has had wide-ranging impacts on wetland communities of the Florida Everglades, especially on the habitats and the aquatic biota of the seasonally flooded marl marshes. We used the Everglades crayfish *Procambarus alleni* as a model to study the associations among hydrology, vegetation distribution, and population dynamics to assess the potential impacts of hydrological changes on the aquatic faunal community in Everglades National Park. To classify benthic habitats as sources or sinks for the crayfish population, we quantified vegetation community structure using GIS maps in which dominant vegetation types were weighted by local hydroperiod (length of inundation). Regression analysis showed that this habitat classification was associated with crayfish density distribution. We then used a spatially explicit, stage-structured population model to describe crayfish population fluctuations under current environmental conditions and to simulate the potential population-level responses to habitat changes that might occur following hydrological restoration. In habitat that was initially saturated with crayfish, the crayfish population size declined under current environmental conditions and then stabilized at about 13% of the initial density over a 50-year period. A 4-month increase in hydroperiod was then simulated by converting shorter-hydroperiod *Muhlenbergia*-dominated marsh habitat to longer-hydroperiod *Cladium*-dominated marshes. The model predicted a rapid 7-fold increase in crayfish density following the simulated habitat restoration. This indicated that several functional effects may result from the restoration of historical hydropatterns in marl marshes: (1) the areal extent of habitat sinks will be reduced to isolated patches, whereas the spatial distribution of aquatic source habitats will expand; (2) crayfish population size will increase and persist over time; (3) the minimum threshold needed to increase secondary aquatic productivity may be a 7-month hydroperiod over 90% of the marl marsh landscape. Restoration of historical hydropatterns could thus have cascading positive effects throughout the Everglades aquatic food web.

Introduction

Understanding how populations of key trophic species might respond to changing environmental conditions and the resultant habitat alterations is critical for planning effective restoration strategies for stressed ecosystems. Ecosystem restoration projects involve substantial costs but are often conducted with a paucity of data on the potential population-level impacts that might occur. While the primary objective is often restoration at the ecosystem or landscape scale, the use of indicator species at a number of major trophic levels is necessary for evaluating restoration effects. To this end, spatial analyses and population simulation modeling are powerful tools that may increase the success of habitat restoration and species' recovery programs at multiple trophic levels (Dunning et al., 1995; Huxel & Hastings, 2000).

A major restoration effort is planned for the Florida Everglades, including the southern portion of the watershed in Everglades National Park (ENP). Natural hydropatterns in this vast wetland ecosystem have been disrupted by human activities for flood control and for water supply to agricultural and urban areas (Light & Dineen, 1994). The northern and eastern boundaries of ENP have been surrounded by levees, canals, and pumping stations which are used to control water in the dry season and remove excess flood waters from nearby urban and agricultural areas. Water management outside the park boundaries has resulted in longer dry seasons, lowered groundwater levels, and unnatural rates and timing of drydown and flooding inside the park, exacerbating environmental stress for both the terrestrial and aquatic biota (Gunderson & Loftus, 1993; Robertson & Frederick, 1994). For example, wading bird populations have declined over 90% from historical densities (Ogden, 1994), suggesting that major disruptions in the aquatic food web have occurred over the past 50 years.

The hydroperiod (duration of annual flooding) in eastern ENP historically averaged up to 9 months but has been shortened by 1–6 months (Fennema et al., 1994). Vegetation community structure reflects the long-term changes in hydrological and associated environmental conditions in the marl marsh (Alexander & Crook, 1984; David, 1996). In these seasonally flooded habitats, *Muhlenbergia filipes*, a species that thrives under short hydroperiods <4 months, expanded and replaced the sawgrass–spikerush community that was dominant in hydroperiods of 5–10 months (Olmstead et al., 1980). Drought-tolerant shrubs (wax myrtle *Myrica cerifera*, holly *Ilex cassine*, and saltbush *Baccharis* spp.) are replacing sawgrass *Cladium jamaicense* in shorter-hydroperiod habitat (Alexander & Crook 1984), whereas the range of *C. jamaicense* has expanded to areas that had previously longer hydroperiods (David, 1996). Dry-season refugia for fish and other aquatic fauna (e.g., solution holes that hold water through the dry season) have become increasingly rare (Loftus et al., 1992).

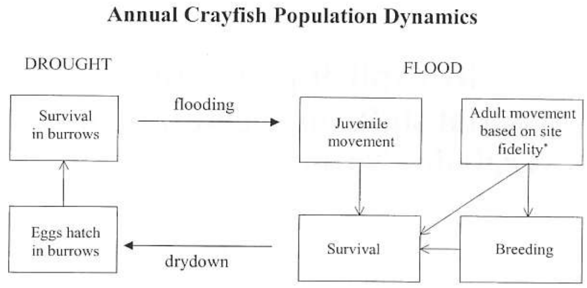

Figure 1. Conceptual model of the life history of crayfish *Procambarus alleni* in the seasonally flooded marl marshes. The spatially explicit population model was initiated at the end of the dry season.

The effects of hydropattern disturbance on much of the aquatic fauna at the mid and lower-trophic levels have not yet been quantified. Thus, the environmental conditions necessary for restoring productivity in key aquatic populations are still not clear. For example, crayfish represent an important link between multiple trophic levels in wetlands (Momot, et al., 1978), and they may be used as an indicator species for assessing environmental impacts resulting from restoration in the Florida Everglades (Science Subgroup, 1997). The crayfish *Procambarus alleni* is ubiquitous in the marl marshes of the Everglades (Kushlan & Kushlan, 1979). While differences in survival and growth of crayfish in this habitat are associated with local hydroperiod (Acosta & Perry, 2000a, 2001), it is unclear how this key population might respond to landscape-level changes resulting from proposed hydrological restoration strategies. We used the marl marsh crayfish *P. alleni* as a model to assess potential population-level responses to habitat changes that might occur if hydropatterns were to be restored to pre-drainage conditions. We developed a spatially explicit population model using parameter estimates for this species in marl marsh habitat and conducted simulations to estimate the threshold changes needed for increasing productivity in crayfish or trophically similar species.

Materials and methods

Crayfish life history and habitat requirements

The marl marsh (or marl prairie) is the primary habitat of the burrowing crayfish *P. alleni*, a robust species that is well-adapted for inhabiting seasonal wetlands (Kushlan & Kushlan, 1979). The congeneric *P. fallax* is abundant in deeper sloughs but is rare in the seasonally flooded marl marshes (Hendrix & Loftus,

Table 1. Classification of vegetation in the 638-ha block of marl marsh in eastern Everglades National Park. Habitats weights were assigned to vegetation types based on hydroperiod (length of inundation). Upland vegetation was weighted 0 (no crayfish habitat). Assemblages of mixed vegetation classes were assigned the mean of the weights

Hydroperiod in months (assigned weight)			
1–2 (1)	3–4 (3)	5–7 (4)	8–10 (5)
Pinus elliottii	*Muhlenbergia filipes*	*Cladium jamaicense*	*Taxodium* spp.
Serenoa repens	*Myrica cerifera*	*Hypericum fasciculatum*	*Eleocharis cellulosa*
	Chrysobalanus icaco	*Typha domingensis*	*Rhyncospora microcarpa*
	Conocarpus erecta	*Salix caroliniana*	*Panicum hemitomon*
	Ilex cassine	*Cephalantus occidentalis*	*Pontederia cordata*
			Sagittaria lancifolia
			Nymphaea odorata
			Bacopa caroliniana
			Utricularia spp.

2000). The life cycle of *P. alleni* is timed to coincide with the flood-dry seasonality of the marl marsh (Fig. 1). The young of the year hatch in burrows near the end of the dry season (April–May) where they remain with adult females until the next flood, generally in June–July (Rhoads, 1976). At the start of the flood season, the young juveniles disperse from natal burrows, but dispersal distances depend on population density and habitat quality (Acosta & Perry, 2001). Young adults may move up to 1 km during the flood season to colonize flooded marshes and exploit new resources. Crayfish occupying optimal habitats with longer hydroperiods generally have normal population size structures, whereas small adults dominate in shorter hydroperiod habitats, as predicted for burrowing crayfish species under stressful conditions (Taylor, 1983). During drydowns at the end of the flood season, crayfish move into existing burrows or construct new burrows in peat overlay and in soil-filled solution holes (Acosta & Perry, 2001).

No increase in crayfish density was observed in deeper slough habitats during the dry season, suggesting that this species does not undertake mass migrations from the marl marshes during drydowns (Kushlan & Kushlan, 1979; Jordan et al., 1996). Groundwater levels in the short-hydroperiod habitats may fall >1 m below the ground surface, below the average 0.5 m depth of crayfish burrows (Rhoads 1976). Mortality of crayfish that colonized short-hydroperiod habitats was often 20–30% higher than that of crayfish in longer hydroperiod habitat (Acosta & Perry, 2001). Crayfish that colonized and survived in shorter hydroperiod habitats had lower growth rates, presumably due to reduced foraging returns and shorter foraging seasons (Acosta & Perry, 2000a). The impact of local hydrology and associated environmental conditions on population dynamics may thus result in source-sink population regulation (*sensu* Pulliam 1988) in this species of Everglades crayfish.

Habitat classification

Local hydroperiod is a primary determinant of vegetation community structure in the Everglades (Schomer & Drew, 1982; Gunderson, 1994; David, 1996). As an indicator of local hydrological conditions, the spatial distribution of dominant vegetation types in a 638-ha area of the marl marsh of eastern ENP was quantified using a geographic information system (GIS). The GIS coverage was derived from vegetation analysis of the 1993/1994 Landsat TM satellite imagery with a resolution of 28 m^2 (The Nature Conservancy, 1998). Vegetation types were then weighted based on hydroperiod, from 0 for upland vegetation (no aquatic habitat) to 5 for aquatic vegetation found in longer-hydroperiod marsh (e.g., *Rhynchospora tracyi*, *Eleocharis cellulosa*, and *Panicum hemitomon*; Table 1) (Schomer & Drew, 1982; Tobe et al., 1998). The shorter hydroperiod areas of *Muhlenbergia* were weighted as 3 (hydroperiod 2–4 months), whereas sawgrass *Cladium* was weighted as 4 (hydroperiod 4–7 months).

To evaluate how well the vegetation classification represented crayfish habitat distribution, local crayfish densities were compared with the weighted vegetation of each sampling site. Crayfish were sampled monthly

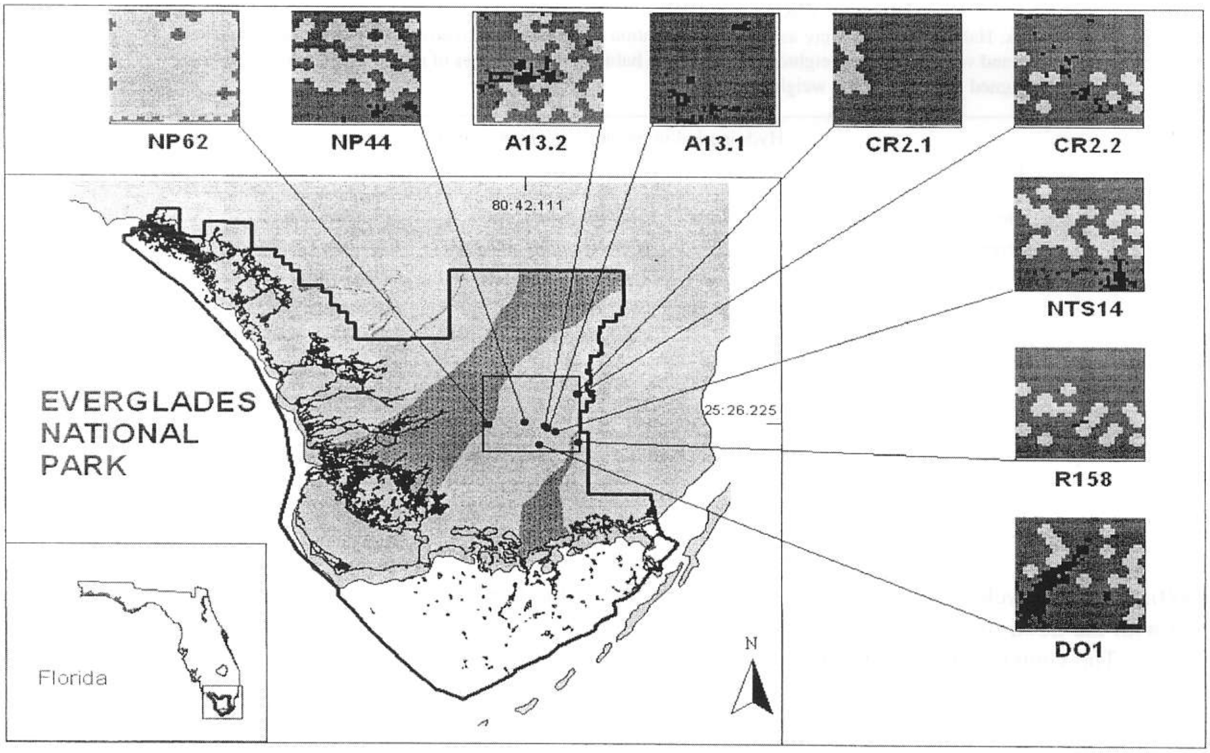

Figure 2. Maps of Florida (small inset) and Everglades National Park (large inset) showing the extent of the marl marshes between the slough habitats; shown outlined is the area used for spatial analysis and population model. Vegetation composition in 1-km^2 cells around the crayfish sampling sites are shown (outer boxes); the areal extent of vegetation types is shown weighted from best habitat (lighest shade) to no habitat (black).

during the flood season from 1998 to 2000 at nine sites across the marl marsh using standardized sampling methods (Table 2) (Acosta & Perry, 2000b). Six replicate minnow traps were used at each site to sample over 48-h periods during the first 10 days of each month. The total area of the weighted vegetation types in 1-km^2 cells around each of the nine sampling sites was then calculated from the GIS using the program PATCH (Fig. 2) (Schumaker, 1998). Spatial analysis was conducted by regressing local crayfish density on the sum of weighted vegetation in each cell. A significant fit of the least-squares regression and a slope significantly >0 indicate that the habitat classification adequately represented the range of habitat conditions that influence crayfish density.

The population model

A females-only, spatially explicit, stage-structured population model (Dunning et al., 1994; Schumaker, 1998) was used to describe population dynamics over time under current habitat conditions and to predict population-level responses to simulated changes in habitat distribution. The model uses habitat-specific demography and dispersal activity to describe population changes across habitat patches of differing quality. The GIS habitat classification of the 638-ha block of the marl marsh was used to quantify the areal distribution of population sources and sinks.

The model runs simulated a 12-month flood-dry cycle coinciding with the life history of *P. alleni*, rather than a calendar year. The population model began at the end of the dry season each year with an assessment of annual mortality (Fig. 1). At the start of the new flood season, all juveniles dispersed (i.e., natal dispersal) and adults may disperse if local habitat quality was suboptimal. Mating occurred during the flood season, and eggs hatched in the females' burrows during the following dry season. For simplicity, mortality was not associated with movement but only with the quality of the habitat in which an individual settled. Therefore, survival and fecundity were directly linked to the spatial distribution of source and sink habitats. Demographic stochasticity was incorporated into variability in survival, reproduction, and dispersal by use of a random number generator sampling from a normal distribution of field data (Table 3).

The vital rates were used in a two-stage (juveniles and adults) Leslie population projection matrix:

$$\begin{bmatrix} F_j & F_a \\ S_j & S_a \end{bmatrix},$$

where F is fecundity and S is survival of juveniles (j) and adults (a). By definition, F_j is 0. Fecundity was calculated as the mean number of female young-of-the-year (<18 mm carapace length, CL) per adult female (>28 mm CL) found at the start of the flood season across sampling sites (Table 3). Survival in each site was estimated as the ratio of the number of females at the end of the flood season (December–February) to the number at the beginning of the next flood season (June–August) (Table 3).

Parameters of the model were estimated using population data from our field studies on density, survival, fecundity, and dispersal that scaled with habitat quality and local hydroperiods (Acosta & Perry, 2000a, 2001). Parameter values varied over a three-tier range of minimum, mean, and maximum as a measure of sensitivity of each parameter (Table 3). The observed densities of crayfish and local habitat quality were assumed to be related to the space available for burrowing, the range of dispersal, and local survivorship. For example, crayfish densities were highest in optimal habitat where each individual's dispersal range was relatively small. Crayfish densities were low in marginal habitat, and individuals ranged further distances in search of optimal habitat. Habitat suitability (for breeding) was based on the threshold score of weighted vegetation in a spatial cell (Schumaker, 1998):

$$\text{Threshold score} = \text{maximum habitat weight} \times \left(\frac{\text{minimum range}}{\text{cell size}}\right).$$

Spatial cells were hexagonal with an area of 28 m^2, the highest resolution of the GIS. Breeding occurred only in cells that equaled or exceeded this threshold score.

Dispersal distances were assumed to scale with crayfish density and habitat quality (Fig. 3). Juveniles and small adults (i.e., floaters without home burrows) dispersed greater distances from optimal habitat oc-

Table 2. Sampling sites for crayfish in the marl marshes of Everglades National Park. Global positioning satellite (GPS) coordinates shown in north and west degrees–minutes. Hydroperiod represents the average annual length of inundation in months from 1998 to 2000. Site names refer to hydrological monitoring stations maintained by ENP

Site	GPS	Hydroperiod
CR2.1	2526.895 8035.716	8
CR2.2	2529.864 8036.263	8
R158	2523.753 8035.569	6
NTS14	2525.083 8038.391	4
A13.1	2525.516 8039.306	8
A13.2	2525.841 8039.619	8
NP44	2526.225 8042.111	8
NP62	2525.95 8046.662	9
DO1	2522.011 8038.401	3

Table 3. Estimates of parameters used in the spatially explicit population model for Everglades crayfish. Mean values were calculated directly from field data. Minimum and maximum values were estimated in the model

Parameter	Parameter estimate		
	Minimum	Mean	Maximum
Habitat–demography link			
Territory size (ha)	0.005	0.05	0.01
Move distance (m)	10	100	1000
Stage Matrix			
Adult fecundity	0	0.73	0.97
Adult survival	0	0.61	0.62
Juvenile survival	0	0.54	0.55

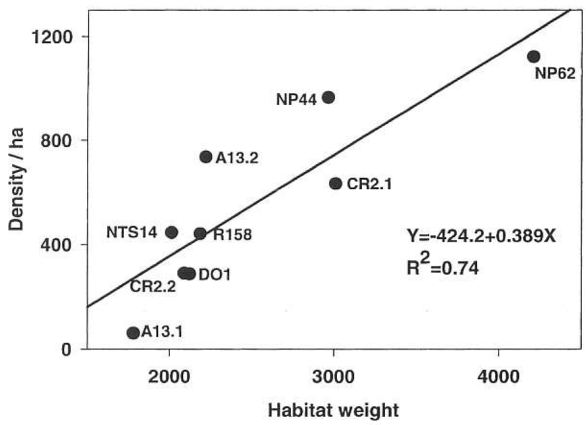

Figure 3. Regression analysis on the relationship between mean local density of female crayfish and the sum of weighted vegetation (in 1-km^2 cells) at the nine crayfish sampling sites.

cupied by large adults (breeders). The probability of settling in a habitat cell increased with the number of moves and habitat quality (i.e., the cell score) (Schumaker, 1998):

$$P_{\text{settling}} = \left(\frac{\text{cell score}}{\text{maximum score}}\right) \times \left(1 - \frac{\text{move number}}{\text{maximum moves}}\right) + \left(\frac{\text{move number}}{\text{maximum moves}}\right).$$

The range of movement distances during the flood season were estimated from field mark-recapture experiments and a random walk model (Acosta & Perry, 2001). Individuals remained longer in source habitats but appeared to move from sink habitats if they survived the dry season (Table 3).

To determine the functions that best described survival and fecundity through the range of hydroperiods at sampling sites, the estimates were plotted for all sites, and regression curves were fitted to the data (Fig. 4). These functions were then used to scale the vital rates in the population projection matrix to local habitat quality (Table 3). The minimum reproductive and survival rates were always 0 in spatial cells with no habitat. The maximum rates were calculated as:

$$\text{maximum rate} = \frac{\text{mean vital rate}}{\text{interpolation function}},$$

where the interpolation function was based on maximum rates observed in the field (Schumaker, 1998). Reproductive output in this species increased linearly with female size (Rhoads 1976), and fecundity scaled linearly with habitat conditions, such that $y = x$. Survival of both juveniles and adults was best represented by the nonlinear function $y = 1 - (1 - x)^3$.

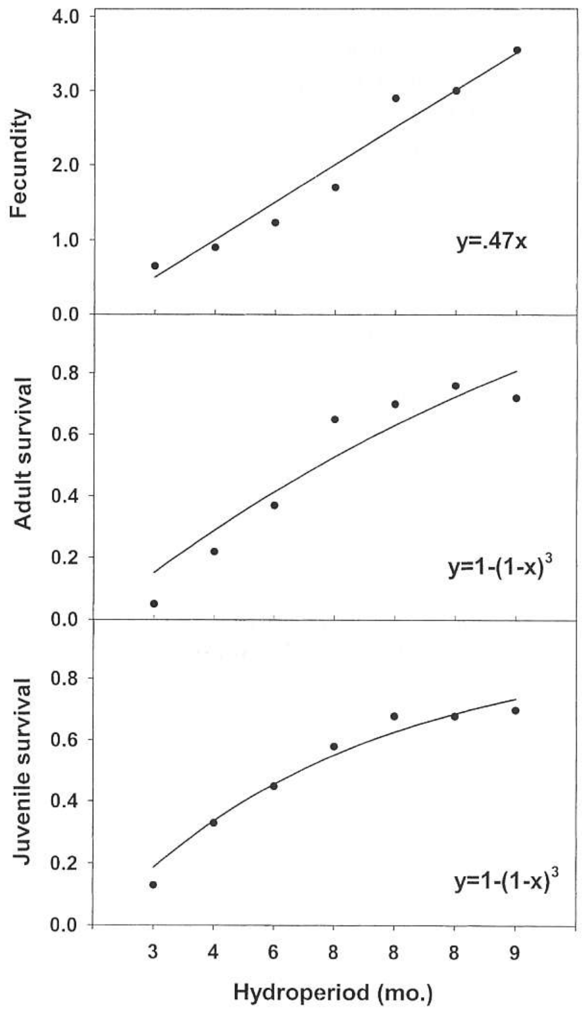

Figure 4. Functional relationships used for parameter estimation of crayfish fecundity and survival over the range of hydroperiods at nine sampling sites; two sampling sites were in close proximity in two different areas (A13 and CR2) and are shown here grouped. (A) Mean fecundity (log number of juvenile females per adult female); (B) female adult survival (proportion); (C) female juvenile survival (proportion).

Simulations

There are no data on crayfish density and distribution prior to drainage and subsequent habitat alteration occurred over 50 years ago. Therefore, the initial population size was set at the density expected if all suitable habitats were occupied by crayfish, calculated using the distribution of habitats in the GIS. The population model was then run for the first 50 years under current habitat conditions to estimate the annual population size, survival, fecundity, and changes in the dominant eigenvalues (λ) of the population projection

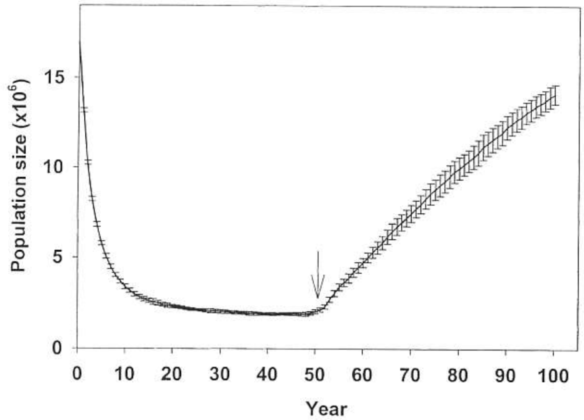

Figure 5. Model results showing fluctuation in crayfish population size under current habitat distribution (years 1–50) and simulated 4-month increase in hydroperiod (years 51–100) (arrow). A smoothing spline algorithm was used for data between years 50 and 60. Standard errors are shown for 10 replicate runs of 100 years each.

matrix. At year 50, a new GIS map of vegetation habitat distribution was inserted into the model. In this new habitat map, the effects of a 4-month increase in hydroperiod were simulated in which*Muhlenbergia*-dominated habitat (3-month hydroperiod) was converted to sawgrass-spikerush habitat (7-month hydroperiod). The distribution of all other vegetation types was assumed to be unchanged. The model was run for years 51 to 100 under these habitat conditions. The transition between habitat changes over 10 years (years 50–60) was modeled using a smoothing algorithm. Estimates of standard errors were calculated from 100 replicate runs of the simulation.

Results

The weighted classification of benthic vegetation adequately represented crayfish habitat quality (Fig. 2). Regression analysis showed that the total area of weighted vegetation types at sampling sites was significantly associated with local crayfish density (Fig. 3). Crayfish densities were consistently higher in marsh habitats dominated by *Cladium* (weight 4) and *Eleocharis* spp. (weight 5). The primary habitats (vegetation weighted 3, 4, and 5) covered 587 ha of the 638 ha or 92% of marl marsh, but the distribution of these habitats was patchy.

The model results suggested that crayfish population dynamics were influenced considerably by vegetation habitat structure and associated hydroperiods. From the areal extent of all available habitat patches,

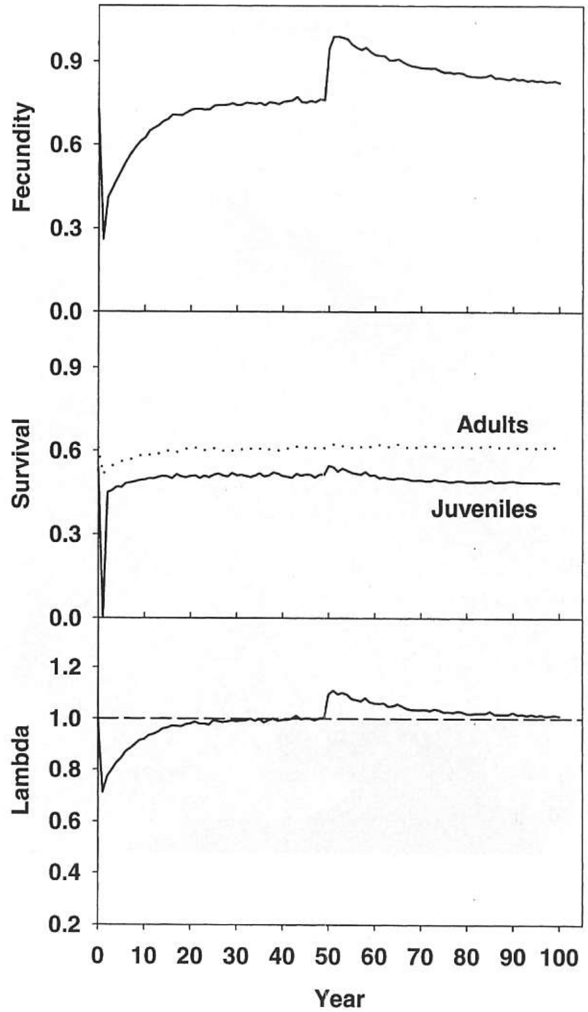

Figure 6. Model results showing fluctuations in (A) fecundity, (B) survival of adult and juvenile females, and (C) eigenvalues (λ) of the population projection matrix of which values ≥ 1 indicate habitat conditions suitable for population increase.

the initial population size in the marl marshes was estimated to be approximately 17 million crayfish, representing a rough estimate of the carrying capacity. Under current habitat conditions, however, the model showed that the crayfish population size declined to about 2.5 million crayfish by year 20, where it stabilized through year 50 (Fig. 5). Following the simulated increase in hydroperiod by 4 months and the subsequent changes in vegetation community structure, the population increased in a logistic manner over years 51–100. Although the population appeared to be approaching an asymptote, the population size had not recovered to initial densities during the 50-year habitat restoration period.

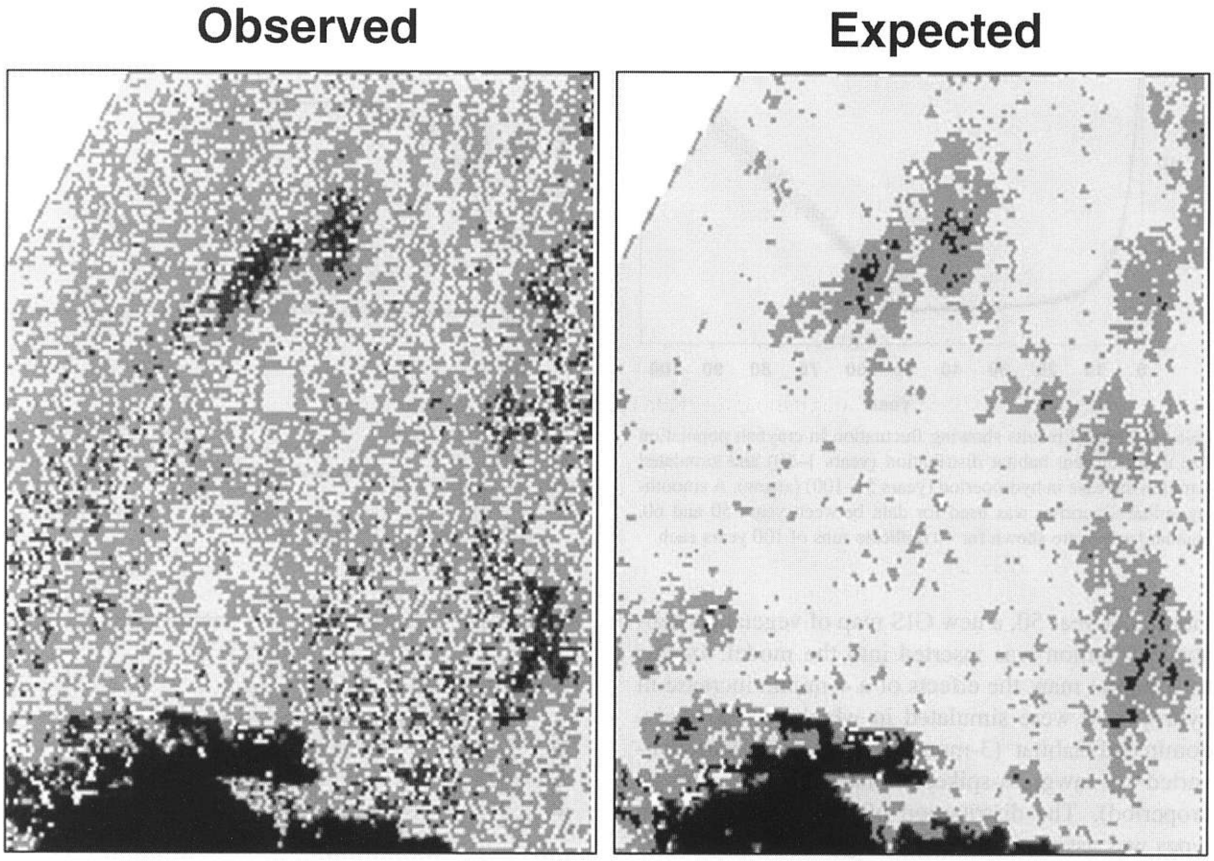

Figure 7. Source-sink dynamics in crayfish habitat across the 638-ha block of the marl marshes in Everglades National Park. The boundary of eastern Shark River Slough habitat (not included in the model) is shown in the upper left corner. The areal extent of weighted vegetation types are shown for current habitats (observed) and simulated changes in habitat with a 4-month increase in hydroperiod (expected); habitat suitability ranges from optimal habitat (lightest shade) to no habitat (black).

Following the simulated change in hydroperiod at year 50, fecundity increased rapidly in response to the greater availability of habitat suitable for breeding, then stabilized above original levels (Fig. 6A). Survival of both adults and juveniles remained relatively stable through the 100-year period after initial fluctuations (Fig. 6B). The dominant eigenvalues (λ), representing the intrinsic rate of population change in the projection matrix, initially fluctuated but stabilized at or above 1 after year 50 (Fig. 6C), indicating that the areal extent of source habitats increased following simulated habitat restoration. Represented graphically, population source habitats were seen to expand into a more continuous distribution following hydropattern restoration, whereas population sinks were reduced to isolated patches (Fig. 7). The patchy distribution of high quality habitat before simulated restoration may have contributed to the sharp decline in the initial population size.

Discussion

Disruption of hydropatterns in the Florida Everglades has resulted in longer dry seasons, lower groundwater levels during droughts, and abnormal drydown rates that directly impact aquatic productivity. These impacts are manifested in widespread environmental changes, including shifts in vegetation community structure, characteristics of the substratum, and the natural fire regime (Gunderson & Loftus, 1993; Davis & Ogden, 1994; David, 1996). Extensive stands of muhly grass *Muhlenbergia* have replaced the sawgrass–spikerush community where the hydroperiod has been reduced by at least 3–4 months (Olmstead et al., 1980). The reverse trend, in which sawgrass–spikerush was reestablished, has been observed in localized areas that have been flooded for longer periods by pumping stations near water delivery canals (T. V. Armentano, ENP, personal communication).

The distribution and structure of vegetation communities often reflect long-term environmental impacts and could be used to assess the effects of stress and restoration in associated animal populations (Holt et al., 1995). Crayfish density was highest in habitats dominated by sawgrass in medium-hydroperiod areas and spikerush in longer-hydroperiod habitat of the Everglades marl marshes. Although the Everglades crayfish opportunistically colonized and burrowed in the extensive short-hydroperiod marl marshes, survival and growth in these areas were significantly lower than in longer-hydroperiod marl marsh (Acosta & Perry, 2000a, 2001). The model results suggested that these crayfish population dynamics are associated with vegetation community structure, and consequently, hydroperiod in predictable ways. Under the current habitat conditions, the crayfish population size declined over 20 years from saturation density in all available habitats to a stable but low density that was about 13% of the original population size. The northern extent of the marl prairie wetlands in ENP is currently dominated by successional shrubs and exotic vegetation (e.g., *Melaleuca quinquenervia*) that are indicative of even drier conditions than that of the 638-ha area used in our analysis. Therefore, our results may represent the most conservative scenario for the impacts of these habitat changes.

Our results indicated that the crayfish population response to the simulated restoration of a 7-month hydroperiod would be a rapid increase up to an order of magnitude greater than the current population size. Following the simulated restoration of near pre-drainage hydroperiods, the marginal habitats that functioned as population sinks were restricted to isolated patches. Source habitats expanded into a continuous distribution, compared with the original patchy distribution that was interspersed with marginal habitats. Restoration of biotic communities in aquatic habitats may be achieved by reducing the extent of sink habitats and increasing source habitats. Source-sink dynamics exert considerable pressure on small subpopulations that are more susceptible to extinction than larger populations (Richter-Dyn & Goel, 1972; Shaffer, 1981; Akçakaya & Baur, 1996).

Everglades crayfish *P. alleni* is probably one of the more hardy species in these wetlands. Therefore, the mean 7-month hydroperiod over 90% of the marl marsh landscape that resulted in a significant positive response may represent minimal conditions for achieving historical levels of aquatic secondary productivity. The minimum threshold hydroperiod for increasing fish productivity in Everglades wetlands was estimated to be greater than 9 months (DeAngelis et al., 1997). Our model does not account for the time lag that will occur between hydropattern restoration and the shift in the vegetation community structure and detrital buildup (Brown et al., 1997). However, the model results did suggest that the response by the crayfish population might closely track ecosystem changes. Population models are tools for evaluative purposes only, and their limitations are based on data quality (Conroy et al., 1995). Our parameter estimates were based on our extensive field and experimental data over a range of hydrological conditions which may increase the reliability of this model for assessing restoration impacts in critical, degraded wetland habitats of ENP.

Restoration success criteria for heterogenous landscapes cannot be based on hydrological and geomorphological changes alone but must account for positive changes in biotic communities (e.g., Weinstein et al., 1997; Huxel & Hastings, 2000). Macroinvertebrates, such as crayfish, represent an important link between primary production and higher trophic levels in wetland ecosystems (Momot et al., 1978; Harris et al., 1995; Laasonen et al., 1998). The impacts of hydrological and associated habitat changes on such key intermediate trophic groups that influence multiple levels of the food web must be incorporated into restoration planning. Our data from field monitoring of the crayfish population, coupled with modeling at the landscape scale, provided quantitative insights into the minimal environmental changes necessary to increase crayfish productivity in the Everglades ecosystem.

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