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 res-

toration 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 salt-bush *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).

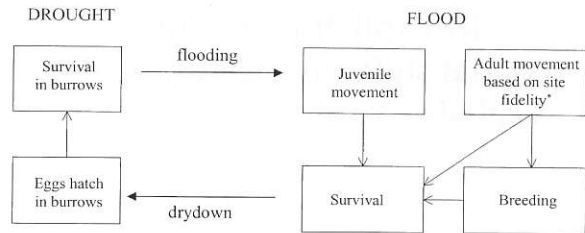**Annual Crayfish Population Dynamics**

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,