Spatio-Temporal Variation in Crayfish Production in Disturbed Marl Prairie Marshes of the Florida Everglades

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ABSTRACT

We used the burrowing crayfish *Procambarus alleni* as a model organism to compare spatial and temporal patterns of density, standing crop biomass, and size-structured productivity in the seasonal wetlands of the Florida Everglades where environmental stress has been exacerbated by hydropattern disturbance. Crayfish density was not linked to fluctuations in water temperature or dissolved oxygen and was only artifactually associated with water depth. Density and biomass within sites were similar over time but increased significantly in habitats with longer hydroperiods (duration of flooding). The effect of hydroperiod-associated habitat quality on annual crayfish production, in terms of size-structured growth and recruit production, was even more pronounced. Crayfish production in the long-hydroperiod sites was approximately two times greater than in medium-hydroperiod sites and five times greater than in short-hydroperiod sites. Turnover ratios (productivity:biomass) showed that the spatial trend in productivity consistently lagged density and biomass trends in the shorter hydroperiod habitat, indicative of population sink conditions. The long-hydroperiod sites were characterized by high productivity and appeared to function as population sources from which crayfish dispersed to nearby, often marginal, habitats. Therefore, the spatial extent and distribution of short-hydroperiod sink habitats significantly impacted crayfish density, population size structure, and productivity. Simple estimates of density or biomass that do not account for the influence of hydropattern on habitat quality may be misleading indicators of productivity because survival, growth, and reproductive output may vary substantially across disturbed landscapes.

INTRODUCTION

The use of indicator species is essential for monitoring changes in habitat quality, particularly when evaluating the effectiveness of ecosystem restoration efforts. Observations of the distribution and abundance of target species are often used for this purpose, but such measures are not always indicative of patterns of productivity. Productivity at higher trophic levels may be especially sensitive to changes in habitat quality as it affects growth, reproduction, and survival (Odum 1959). Environmental impacts on primary productivity have been studied extensively, but the dynamic influence of habitat disturbance on secondary productivity is not well understood (DeAngelis 1992). In aquatic ecosystems, the spatial and temporal dynamics of secondary productivity can be especially complex due to the interactions of the water medium with the substratum and the biota, particularly benthic vegetation and associated animal communities (Rapport 1999).

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Crayfish are good indicators for monitoring energy flow through freshwater food webs because they are efficient energy transformers, interacting with multiple trophic levels as scavengers, predators, or prey (Momot 1995). For example, *Orconectes virilis* occurred in high densities and biomasses in lakes with relatively low primary productivity (Momot and Gowing 1977). In the heterogeneous wetlands of the Florida Everglades, crayfish may represent a major food source for many fish, amphibians, reptiles, birds, and mammals (Kushlan and Kushlan 1979). For example, a rough estimate of consumption indicated that the 1972 white ibis population required up to 470 tons of crayfish annually (Kushlan and Kushlan 1975). Environmental changes in the Everglades wetlands have been linked to drastic declines in wading bird populations, by as much as 90% in some species, over the past 50 years (Ogden 1994).

Table 1. Sites in marl prairie wetlands of eastern Everglades National Park where crayfish were monitored, 1998 – 2000. Hydroperiod is shown as mean annual length of inundation in months.

Site[a]	GPS[b]	Hydroperiod	GSE[c]	Habitat
A13.1	2525.516 8039.306	9	0.594	solution holes
NP62	2525.95 8046.662	9	0.576	peat marsh; cypress domes
NP44	2526.225 8042.111	9	0.943	shallow depressions; graminoid marsh
CR2.2	2529.927 8035.450	7	1.098	solution holes
CR2.1	2526.895 8035.716	7	1.398	shallow depressions; graminoid marsh
A13.2	2525.841 8039.619	7	0.944	shallow depressions; willow heads
R158	2523.753 8035.569	5	0.458	shallow depressions; graminoid marsh
NTS14	2525.083 8038.391	5	0.989	shallow depressions; graminoid marsh
DO1	2522.011 8038.401	4	0.788	shallow depressions; graminoid marsh

[a] Site names correspond to the nearest permanent hydrological monitoring station maintained by ENP.

[b] Global positioning satellite (GPS) coordinates shown in north and west degrees/decimal minutes.

[c] Ground surface elevation (GSE) at crayfish monitoring sites adjusted from GSE (m above sea level; NGVD 1929 datum) at hydrological stations.

The declines in populations at higher trophic levels in the Everglades have been associated with disruption of historical hydropatterns (Davis and Ogden 1994). Hydrological disturbance has been particularly acute in the wetlands of Everglades National Park, encompassing the southernmost 20% of the original ecosystem (Light and Dineen 1994). A vast network of drainage canals and levees currently isolate the park, shortening the seasonal flood cycle, reducing groundwater levels during the dry season, and disrupting natural rates of flooding and drydown. These impacts have been especially severe in the marl prairie wetlands of eastern Everglades National Park where the hydroperiod (duration of annual flooding) has been reduced by one to six months from that of historical pre-drainage conditions (Loftus et al. 1990, Fennema et al. 1994).

Changes in hydroperiod have altered the dynamics of primary productivity over time. Drought-tolerant plant species have expanded their range in response to reduction of hydroperiods (Gunderson 1994), and invasive species have increased in abundance with changes in nutrient distribution (Davis 1994, Doren et al. 1997). The impacts on secondary productivity are not fully understood. Everglades crayfish *Procambarus alleni* experiences higher mortality and lower growth rates in large areas of its primary habitat in which the hydroperiod has been significantly reduced (Acosta and Perry 2000b, 2001). The impacts on the congeneric *P. fallax* are unknown (Hendricks and Loftus 2000).

We studied the spatial and temporal dynamics of secondary production of the crayfish in the seasonally-flooded marl prairie of Everglades National Park. We evaluated correlational associations between the abundance of crayfish and water quality. We then compared trends in crayfish density, standing crop biomass, and size-frequency distribution in habitats that differed in hydroperiod. These estimates were used to calculate annual productivity, in terms of size-structured growth and recruit production, for comparison with density and biomass patterns.

METHODS AND MATERIALS

Crayfish were sampled at nine sites in the marl prairie habitat of eastern Everglades National Park (ENP) from October 1998 to September 2000. The marl prairie is seasonally flooded with local hydroperiods ranging from two to 10 months, and hydroperiods ranged from four to nine months at our sampling sites (Table 1). This graminoid marsh habitat consisted of calcitic marl substratum overlaid by varying amounts of peat with numerous solution holes. The marl prairie is the primary habitat of the crayfish *P. alleni* (Kushlan and Kushlan 1979, Hendricks and Loftus 2000).

Crayfish were sampled monthly within the first 10 days of each month during which water stage above ground was > 2 cm (including inside solution holes). Crayfish were collected using six baited wire traps at each site, where the area that each trap effectively sampled (α) over 48 hr was previously estimated as 56.3 m^2 (Acosta and Perry 2000a). Crayfish density per ha at site x (D_x) was thus estimated as:

$$D_x = \left[\frac{\text{number of crayfish}}{(\alpha)(\text{number of traps})}\right] 10000 m^2 .$$

The reliability of trends in density was evaluated by examining power and coefficients of variation (CV) for the time series at each of the nine sites. The power to detect trends was estimated from Monte Carlo simulations of linear trends using means and variances of monthly samples (Gibbs 2000a,b). The power to detect trends is inversely related to the inherent variability in estimates of the density index, so the CVs were calculated by dividing the means by the detrended standard deviations obtained from the standardized residuals of linear regressions of density against time (Gerrodette 1987). The overall CV for each site was calculated as a monthly moving CV (analogous to a moving average; Gibbs 2000a).

Water depth (stage) was monitored at nearby hydrological monitoring stations maintained by ENP. Other water parameters (temperature, dissolved oxygen, pH, and conductivity) were measured at each site during monthly sampling. To assess the relationship between crayfish abundance and water conditions, we used multiple regression analysis with monthly crayfish density as the dependent variable and water temperature, dissolved oxygen, and water stage as factors. Conductivity and pH did not vary substantially among sites and were excluded from the analysis. Data series were inspected for autocorrelations using the Durbin-Watson D statistic. Tolerance and variance inflation factor statistics were used to assess collinearity among the factors. Plots of partial regression coefficients were inspected for excessive leverage of data points, and plots of the studentized deleted residuals against leverage values were used to confirm influence of such data.

During monthly sampling, all crayfish were measured (to 0.1 mm carapace length, CL), weighed (to 0.1 g), identified by sex, marked, and released. Young-of-the-year crayfish < 10 mm CL could escape through the trap mesh and were not adequately sampled. Standing crop biomass per ha at site x (B_x) was calculated from the individual wet weights (W_i) as:

$$B_x = \left[\frac{\sum_{i=1}^{x} W_i}{(\alpha)(\text{number of traps})} \right] 10000 m^2 .$$

To compare crayfish population fluctuations in space and time, a doubly multivariate repeated measures analysis of variance (RMANOVA) was conducted using density and biomass as dependent variables with sampling site (between-subjects) and month (within-subjects) as factors. Box's M test was used to test for equal variance-covariance matrices of the between-subjects factor.

Seasonal production was defined as the sum of seasonal growth production of individuals in the local population and production of recruits by adult females. Crayfish *P. alleni* have a life span of three to four years (Acosta and Perry 2000b). We assumed that energy is directed to growth in recruits (class R: < 18 mm CL), subadults (class S: 18-24 mm CL), and smaller adults (classes A_1: 25-28 mm CL; A_2: 29-32 mm CL). The largest adults (class A_3: 32-38 mm CL) were assumed to direct energy into breeding and recruit production. Growth (increase in biomass) was not significantly different between sexes and was more reliable by size class than by stage (e.g., Form I or II males) (Acosta and Perry 2000b). Furthermore, growth rates of *P. alleni* in the marl prairie varied from one site to another, so net growth during a flood season was calculated using separate growth parameters from each site. Growth production was estimated as the biomass gained by animals moving from a lower size class (W_i) to a higher size class (W_j) during a growing (flood) season; i.e., R-S; S-A_1; A_1-A_2; A_2-A_3. Growth production per ha at site x (G_x) was calculated using the density (D_i) of each size class i as:

$$G_x = \sum_{i=1}^{x} D_i \left(W_j - W_i \right).$$

Biomass W was defined from the length-weight relationship as $W_x = a_x L^{b_x}$, where W_x is the mean weight of individuals in a size class at site x, L is the median length of the size class, and a_x and b_x are growth parameters for site x.

The number of recruits produced by adult female *P. alleni* was linearly related to female size (Rhoads 1970). Production of recruits per ha at site x (R_x) was estimated for the three size classes of adult females (A_1, A_2, A_3) as:

$$R_x = 0.01 \sum_{i=1}^{x} \left(D_{Fix} E_i \right).$$

D_{Fix} is the density of adult females in size class i at site x, and E_i is the mean number of recruits produced by size class i. The multiplier 0.01 represents the average weight in g of a hatchling after it detaches from the female. Hatching success of eggs and survival rates in each size class were not known but were assumed to be expressed in the observed mean densities over a flood season. Estimates of mean density, mean standing crop biomass, mean productivity, and turnover (the ratio of production:biomass) were then graphed for visual comparisons among all sites.

RESULTS

Density at the sites with the shortest hydroperiods averaged 297 ± 58 (mean ± SE) crayfish/ha, and standing crop biomass averaged 1.023 (± 0.195) kg/ha, whereas medium hydroperiod sites had a mean density of 295 (± 38) crayfish/ha and mean biomass of 1.528 (± 0.221) kg/ha. In contrast, the two longer hydroperiod sites (NP44, NP62) averaged 635 (±85) crayfish/ha and 2.289 (±0.323) kg/ha. The density indices at all sites were reliable as indicated by estimates of high power and low coefficients of variation.

Fluctuations in crayfish density were not associated with water temperature or dissolved oxygen (Table 2). Water stage above the ground surface was only weakly related to crayfish density (partial correlation coefficient = – 0.37). However, leverage and influence statistics indicated that one site (A13.1) had a disproportionate influence on the results. At this site, density (35 ± 9) and biomass (0.222 ± 0.062) were substantially lower than all other sites, even though this habitat held water longer than other sites. The habitat at site A13.1 consisted of deep (1 m) solution holes that held low-oxygen water near the bottom for long periods of time. This site was not included in further analyses due to these confounding factors.

The patterns of density and biomass were confirmed by results of the multivariate RMANOVA. There were significant differences in density and biomass among sites (Table 3). Within sites, density appeared to fluctuate significantly among months, but biomass did not fluctuate appreciably. Therefore, a conservative interpretation of these results would suggest that density and biomass differed significantly among sites but not within sites over time.

Patterns in the size-frequency distribution of crayfish in the marl prairie followed patterns of density and biomass. Subadults and adults were most abundant at the longer

Table 2. Results of the multiple regression analysis on the relationship between local crayfish density (dependent variable) and water temperature (TEMP), dissolved oxygen (DO), and water level (STAGE) (factors). Data are from two flood seasons, 1998 – 2000. Shown are the model results and standardized coefficients for each factor.

Model: Crayfish density = 2020.7 + 14.8 DO – 19.6 TEMP – 650.3 STAGE

Source	SS	Df	F	P>F	R^2
Model	2.5×10^6	3	3.155	0.03	0.15
Error	1.3×10^7	52			
Total	1.6×10^7				

Predictors	Standardized Coefficients	t	P
DO	0.12	0.93	0.36
TEMP	–0.16	–1.237	0.22
STAGE	–0.37	2.86	0.01

Table 3. Results of the doubly multivariate repeated measures ANOVA on crayfish density and biomass (dependent variables) at nine sites (between-subjects factor) during 18 sample months (within-subject factor). Pillai's trace (Value) was used as the test statistic for the multivariate model, and mean squares were used to calculate F values for significance of the variables.

	Value	Hypothesis df	Error df	F	P
SITE	0.798	2	7	13.8	0.04
- Density	1.9×10^7		1	24.7	0.001
Error	7.8×10^5		1		
- Biomass	315.8		8	31.3	0.001
Error	80.7		8		
MONTH	0.314	34	272	1.4	0.05
- Density	6.8×10^3		17	1.8	0.04
Error	3.9×10^4		136		
- Biomass	0.925		17	1.3	0.17
Error	0.684		136		

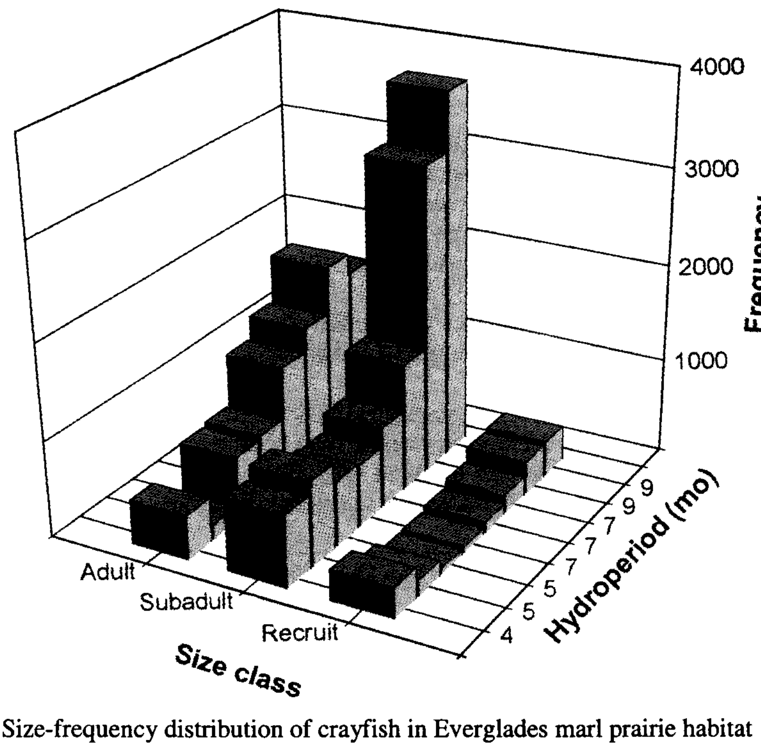

Figure. 1. Size-frequency distribution of crayfish in Everglades marl prairie habitat differing in hydroperiod and associated habitat conditions during 1998 to 2000. Size classes shown are: recruit <18 mm CL; subadult 18-24 mm CL; adult > 24 mm CL.

hydroperiod sites (Fig. 1). The mean proportions of subadults and recruits appeared to be similar in the medium and short hydroperiod sites, but large adults were more abundant in the medium hydroperiod sites. Recruitment potential could be estimated from the density of adult breeders among sites, assuming that most adults had the opportunity to reproduce at least once.

From the size-frequency distribution of crayfish among all sites, growth production was dominated by subadults moving to the adult size class, and recruit production was dominated by larger adult females (Table 4). Mean crayfish production ranged from 2.40 kg/ha at the long hydroperiod areas to 0.33 kg/ha at the short hydroperiod habitat (Table 5). Seasonal production tracked trends in density and biomass in the medium and long hydroperiod habitats but was substantially lower than density/biomass trends at the short hydroperiod sites (Fig. 3). This resulted in turnover (production:biomass) ratios that ranged from 0.98 in the longer hydroperiod site to 0.34 in one of the short hydroperiod sites.

Table 4. Parameter estimates used to calculate site-specific crayfish production in terms of growth and recruit production. Growth production is represented as the mean increase in mass expected for an individual moving from one size class to another during one flood season (i.e., recruit-subadult; subadult-small adult; small-medium adult; medium-large adult). Production of the largest adult size class (A_3) was assumed to be directed into production of recruits. Recruit production is based on mean fecundity and observed densities of three size classes of adult females (A_1,A_2,A_3).

	Mean Growth Production (in g)				Recruit Production ($\times 10^3$ g) by adult females		
Site	R-S	S-A_1	A_1-A_2	A_2-A_3	A_1	A_2	A_3
NP62	1.77	2.03	2.90	5.17	92.79	117.11	33.95
NP44	1.84	2.09	3.01	5.34	114.63	108.86	31.95
CR2.2	1.57	1.78	2.54	4.47	9.09	21.44	57.91
CR2.1	1.57	1.78	2.54	4.47	21.83	90.72	35.95
A13.2	1.66	1.87	2.67	4.68	70.96	65.98	29.96
R158	1.50	1.69	2.39	4.18	21.83	37.94	13.98
NTS14	0.87	0.96	1.39	1.34	16.38	6.59	0
DO1	0.63	0.69	0.96	1.65	12.74	14.85	1.99

DISCUSSION

Crayfish occupied all habitats that were flooded, but both density and biomass varied significantly among sites. Mean density and biomass showed increasing trends from the short- to long-hydroperiod habitats, with most variability among the medium hydroperiod sites. Deep solution holes held water for longer periods of time than the surrounding marshland. Although these were believed to be dry-season refuges for many aquatic organisms (Loftus et al. 1990, Turner et al. 1999), this habitat was marginal for crayfish because of poor water quality and the silty substratum that was unsuitable for burrow construction. While deep solution holes are potentially important habitat for aquatic fauna, factors such as water quality and the length of the dry season, impact their effectiveness as refugia. Within sites, density fluctuated during the flood season, but this variation was not consistent. However, biomass was consistently greater in longer hydroperiod habitats. Additionally, the presence of crayfish lagged flooding at the short hydroperiod sites by one to two months. These results support empirical studies that indicated that the shorter hydroperiod habitats were being colonized by crayfish from distant source populations (Acosta and Perry 2001).

The influence of environmental condition on secondary productivity is complex in nature, and observations of faunal distribution and abundance may not always reveal the full impacts on populations (Odum 1959). Habitat quality and availability impact production through influences on growth rates, fecundity, survival, and dispersal. For example, growth rates in *P. alleni* were shown to differ significantly, not only between size classes, but also among marl prairie sites that differ in hydroperiod (Acosta and Perry 2000b). Additionally, fecundity is often associated with female size, and thus, total reproductive output may be linked to size structure of the breeding population (e.g., Kuhlman and Walker 1999). The higher abundance of adult females in the longer hydroperiod habitat appeared to be the primary cause of high productivity at these sites, both in terms of growth and recruit production. The low turnover indices (<< 1) in the short hydroperiod habitats indicated that these local populations were not self-sustaining, due to low growth rates, low survival, and low reproductive output by few adults. Low turnover ratios are indicative of adverse environmental conditions, low food availability and quality, or lack of suitable habitat (Griffith et al. 1996, Momot and Gowing 1977, Mitchell and Smock 1991, Roell and Orth 1992). The turnover indices at the long hydroperiod sites (≈ 1) suggested that local crayfish production was stable but may be limited by the carrying capacity of these isolated habitat patches (Acosta and Perry in press).

Although the Everglades ecosystem is characterized as an oligotrophic, low productivity system (Turner et al. 1999), secondary productivity may have declined several-fold from historical levels. The precipitous declines in some animal populations at higher trophic levels (e.g., wading birds, Ogden 1994; snail kite, Beissenger 1995) may be linked to decreased secondary productivity in aquatic habitats across the Everglades landscape. There is substantial correlational evidence that habitat changes associated with hydropattern disturbance may be the proximal cause of stress on vertebrate populations in these wetlands (Davis and Ogden 1994). In this regard, the shallow seasonally-flooded marl prairie wetlands of eastern Everglades National Park may be the most endangered habitat in this ecosystem. One of the primary goals of the large-scale restoration efforts planned for the greater Everglades ecosystem is aimed at the re-establishment of historical hydropatterns (Davis and Ogden 1994). Monitoring the spatial and temporal changes in secondary productivity of key trophic groups to further environmental and habitat alterations will be essential for ensuring that the desired impacts are being achieved.

Table 5. Spatial distribution of density, biomass, and production of crayfish in marl prairie wetlands. Production was calculated as the mean sum of size-structured growth and recruit production. Turnover is the ratio of production to mean standing crop biomass. Shown are estimates of power and coefficients of variation (CV) for trend detection in the time series data of monthly crayfish density at each site, 1998 - 2000.

Site	Production (kg/ha)	Biomass (kg/ha)	Turnover	Density (no./ha)	Power	CV
NP62	2.058	2.094	0.983	631	0.96	0.02
NP44	2.399	2.484	0.966	638	0.91	0.11
A13.2	1.490	2.038	0.731	431	0.90	0.11
CR2.1	1.135	1.647	0.689	331	0.62	0.30
CR2.2	0.544	0.899	0.605	122	0.89	0.19
R158	0.499	1.091	0.457	243	0.78	0.26
NTS14	0.330	0.702	0.470	273	0.75	0.25
DO1	0.428	1.276	0.335	376	0.86	0.22

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