Aquatic Ecology **34:** 389–395, 2000.

Differential growth of crayfish *Procambarus alleni* in relation to hydrological conditions in marl prairie wetlands of Everglades National Park, USA

Charles A. Acosta and Sue A. Perry
South Florida Natural Resources Center, Everglades National Park, 40001 State Road 9336, Homestead, FL 33034, USA (Phone: 305-242-7800; Fax: 305-242-7808; E-mail: sue_perry@nps.gov)

Accepted 23 November 2000

Key words: crayfish, *Procambarus alleni*, growth, Florida Everglades, hydroperiod

Abstract

Environmental conditions influence crustacean growth by affecting molt intervals and incremental increases in length and weight. In the seasonally-flooded marl prairie wetlands of eastern Everglades National Park, U.S.A., hydropattern exerts considerable influence on aquatic primary productivity, and so may influence the availability of food resources for higher trophic levels. The seasonal hydroperiod has been drastically altered by anthropogenic factors, but the impacts on the aquatic community are not well known. We studied whether differences in growth of crayfish *Procambarus alleni* could be detected in habitats with different hydroperiods. We first described growth patterns based on incremental increases in length and weight of crayfish on a high protein diet in the laboratory. Regression analyses indicated that growth patterns in males and females were similar. Although the intermolt period increased with age, the proportional increases in length and weight were similar through successive molts. The relationship between length and weight of crayfish was best described by a power equation for allometric growth. We then compared growth curves for crayfish subpopulations from different areas of the marl prairie. In habitats with the longest hydroperiods, crayfish weight-at-size was not significantly different from that in laboratory crayfish on the high protein diet. However, weight gain per unit increase in length in short hydroperiod sites was significantly less than in long hydroperiod sites or in the laboratory. These results indicate that crayfish productivity may be associated with hydroperiod in these stressed wetlands, and this may contribute to observed source-sink population regulation.

Introduction

Growth in crustaceans is a highly complex and asynchronous process that is often impacted by environmental conditions. Protein synthesis and cellular growth occur primarily during intervals between molts, but size increases directly follow ecdysis (Aiken & Waddy, 1987). Furthermore, molt frequency and increases in size-at-age may be highly variable within a species and between species due to a number of abiotic factors (Hartnoll, 1982; Huner, 1984; France, 1985; Griffith et al., 1996). Environmental factors may impact crayfish growth by affecting feeding behavior, foraging efficiency, and the availability and quality of food resources (Momot & Gowing, 1977; France, 1985). The relationship between premolt and post-molt length has been used to describe growth and the effects of environmental conditions on growth patterns, but the functional relationships vary among species (Hiatt, 1948; Kurata, 1962; Mauchline, 1976). Additionally, simple length-weight patterns may have the potential for indicating differential growth (Austin, 1995) that may be associated with the severity of environmental stress across the range of a species.

The crayfish *Procambarus alleni* Faxon is one of the most ubiquitous inhabitants of the seasonally-flooded marl prairie wetlands of eastern Everglades

National Park, Florida, U.S.A. Environmental conditions across much of the Everglades landscape, however, have been altered by the disruption of natural hydropatterns due to water management and other anthropogenic impacts (Light & Dineen, 1994). The shortening of the hydroperiod, the rapid rate of drydowns, and lowered groundwater levels during the dry season impact the aquatic community by increasing mortality in the aquatic fauna, changing algal community composition, and reducing primary productivity (Gunderson & Loftus, 1993; Davis et al., 1994). While crayfish *P. alleni* are well-adapted to seasonal drought by burrowing, mortality is excessively high in areas where the hydroperiod is greatly reduced (Acosta & Perry, in press).

To assess whether differing hydrological conditions impact growth of crayfish, we compared growth dynamics of crayfish in the marl prairie wetlands. Our objectives were: (1) to describe growth of *P. alleni* on a high protein diet in the laboratory, (2) to determine the functional relationship between length and weight, and (3) to compare length-weight patterns between crayfish subpopulations from marl prairie habitat with different hydroperiods. If growth dynamics can be quantified, the impacts of environmental stress on growth can be quickly evaluated over a species' range.

Table 1. Crayfish sampling sites in the marl prairie wetlands of eastern Everglades National Park. Site names correspond to nearest hydrological monitoring station in the park. Location of sites shown as north and west Global Positioning Satellite (GPS) coordinates (degrees/decimal minutes). Ground surface elevation (GSE) estimated from water depth at hydrological stations. Hydroperiod is the mean 1998–2000 flood season

Crayfish Site	GPS (N/W)	GSE (m)	Hydroperiod (mo)
NP62	2525.950 8046.662	0.576	9
NP44	2526.225 8042.111	0.943	9
A13.2	2525.841 8039.619	0.944	7
CR2.1	2525.895 803.716	1.398	7
R158	2523.753 8035.569	0.458	5
N14	2525.083 8038.391	0.989	5
DO1	2522.011 8038.401	0.788	4

Methods

Laboratory growth

We measured growth of crayfish in the laboratory as a benchmark for comparison to growth in the field. Juvenile crayfish were collected in 1998–1999 from flooded marl prairie habitat with an average hydroperiod of 9–10 mo (the longest hydroperiod among all sites; Table 1). Because protein in the diet has been associated with optimal crayfish growth (Huner, 1984; Momot, 1995), crayfish *P. alleni* were held in 3 m^2 mesocosms with natural sand-algal substrates and were fed a high-protein diet (shrimp) every two days in proportions of 100% of the total wet weight of crayfish in a mesocosm. Food remaining was removed the following day, and 50% of the water was changed on a weekly basis. Crayfish were grown out in five size classes to reduce aggressive and cannabalistic interactions (Bovberg, 1959).

Animals were measured (to 0.01 mm carapace length, CL), weighed (to 0.1 g), and identified by sex. For identification, individuals were marked using two methods: a permanent colored latex plug inserted under the clear abdominal exoskeleton (Acosta & Perry, 2000) and an external number painted with acrylic nail polish on the dorsal carapace. Crayfish that molted were easily identified by the absence of the external mark, and the molted individual could then be identified by the unique color-coded internal mark. The other crayfish in the mesocosm were not disturbed during sampling of molted individuals. Post-molt measurements were taken only after complete hardening of the exoskeleton, about three days after ecdysis.

To analyze incremental growth patterns in male and female crayfish, we used Hiatt growth diagrams in which pre-molt and post-molt carapace lengths were plotted for all molts (Hiatt, 1948). Inflections in the distribution of lengths may indicate differences in growth associated with different life history stages or maturity states (Mauchline, 1976). To determine the function that provided the best description of the growth pattern, we compared the fit of linear and quadratic regression equations, and then used the regression coefficients and analysis of variance (ANOVA) to determine which regression provided the best fit to the data. Linear regression provided the most parsimonious description of the association between pre-molt (Y_t) and post-molt (Y_{t+1}) measurements:

$$Y_{t+1} = a + bY_t,$$

where a is the Y-intercept and b is the growth constant. Similar analyses were conducted on the pre-molt and post-molt weights.

We postulate that if the incremental increase in length is proportional to the incremental increase in weight per molt, the slopes of the regressions (growth constant b) of the Hiatt growth curves should be the same. To evaluate the relationship between incremental increases in length and weight over successive molts, regression analyses of Hiatt growth curves were conducted on length and on weight of males and females. We then tested for differences in pairs of regression slopes (male and female length, male and female weight, male length-weight, and female length-weight) using t-tests (Zar, 1984). We compared the length-weight relationship of crayfish fed a high protein diet in laboratory mesocosms containing natural substrate and algae to crayfish from the marl prairie wetland.

Field growth

Crayfish were collected from seven sites in the marl prairie wetland of eastern Everglades National Park during an on-going monitoring project (Figure 1). The marl prairie sites differed in hydroperiod ranging from near normal to greatly reduced, compared to pre-disturbance hydropatterns (Light & Dineen, 1994). For example, site P62 nearest Shark River Valley Slough is inundated for an average of nine months, whereas sites DO1 and N14 near the eastern boundary of the park are inundated for only three months (Table 1). Crayfish were collected using standardized sampling methods and were identified by sex, measured, weighed, and released on site (Acosta & Perry, 2000).

Regression analyses were used to determine if the length-weight relationships differed among the marl prairie sites and between these and the laboratory subpopulations. The carapace length (independent variable) and the wet weight (dependent variable) were plotted for males and females at each site. We fitted the power equation for allometric growth to the data:

$$Y = aX^b,$$

where Y is the weight, X is the carapace length, and a and b are constants. The regression coefficients and analysis of variance (ANOVA) were used to evaluate the fit to the data.

To compare the length-weight relationships for the different subpopulations, we first linearized the power curves by taking the logarithms of lengths and weights:

$$\log Y = \log a + b \log X.$$

We then conducted linear regression analyses on male and female growth at each site. To test for growth differences, we used an analysis of covariance (ANCOVA) to test the null hypothesis that the regression slopes are not significantly different (Zar, 1984). If the null hypothesis was rejected, multiple comparisons were conducted on pairs of sites using the Tukey q-test (Zar, 1984).

Results

A total of 122 female and 85 male crayfish were grown in the laboratory. Growth measurements on individual crayfish ranged from a minimum of two months on 15 crayfish to 18 months on 21 crayfish. Growth was recorded for all life history stages from young-of-the-year juveniles (12 mm CL) to Form I and Form II males and adult females (Thorpe & Covitch, 1991). The frequency of molting in crayfish decreased with increasing age (range: 1–3 wk in juveniles; 4–6 wk in adults), but the incremental increases in length and weight following ecdysis were greater in older individuals. Incremental increases in length were similar between males ($Y = 0.172 + 1.051X$; $R^2 = 0.98$) and females ($Y = 0.38 + 1.088X$; $R^2 = 0.98$) fed a high protein diet in the laboratory ($t = 1.2$, df 167, $P > 0.05$) (Figure 2). Similarly, the incremental increases in weight was not significantly different between males ($Y = 0.224 + 1.136X$; $R^2 = 0.99$) and females ($Y = 0.073 + 1.24X$; $R^2 = 0.97$) ($t = 1.7$, df 137, $P > 0.05$).

The Hiatt growth diagrams for pre-molt versus post-molt measurements showed no major inflections that would suggest changes in growth patterns in either males or females (Figure 3). The incremental growth increases followed similar linear patterns in which the increases in weight-at-age were proportionately similar to increases in length-at-age. These length-weight increases were also not significantly different between males ($t = 1.7$, df 116, $P > 0.05$) and females ($t = 1.8$, df 167, $P > 0.05$) (Figure 3).

Although growth patterns were similar among males and females in the laboratory subpopulation, we

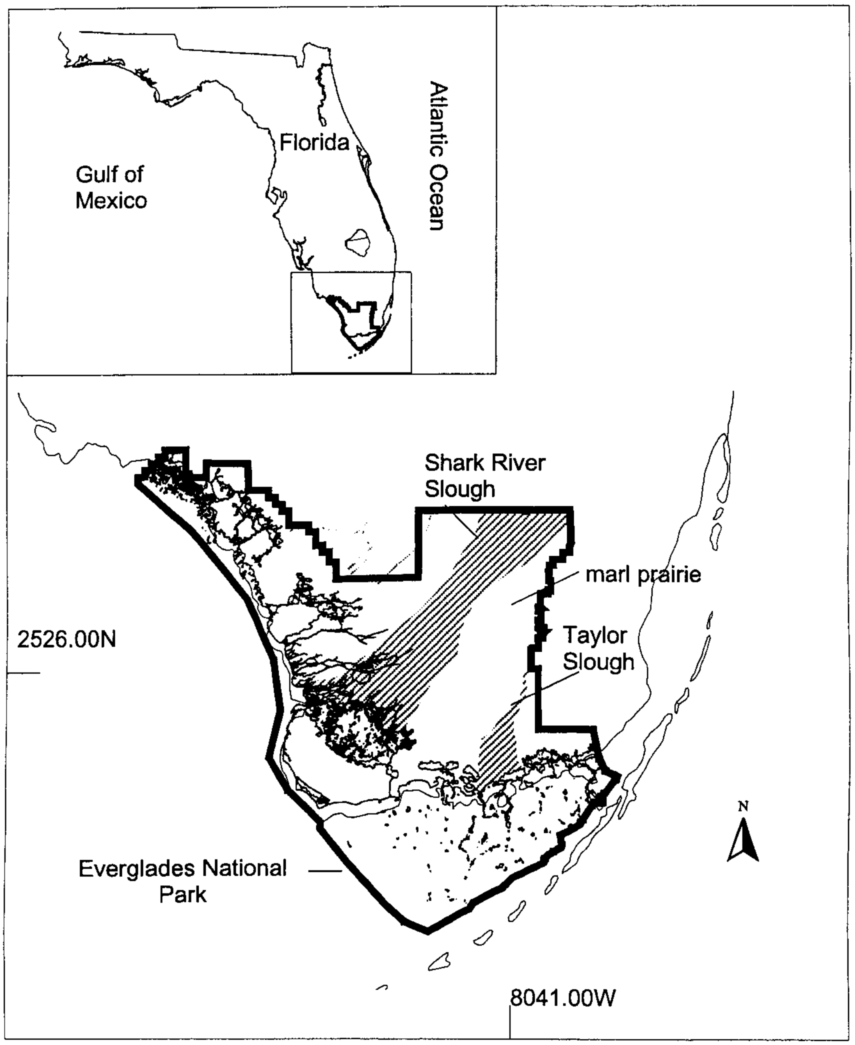

Figure 1. Map of Everglades National Park in Florida, U.S.A. (inset) showing the areal extent of the marl prairie wetlands.

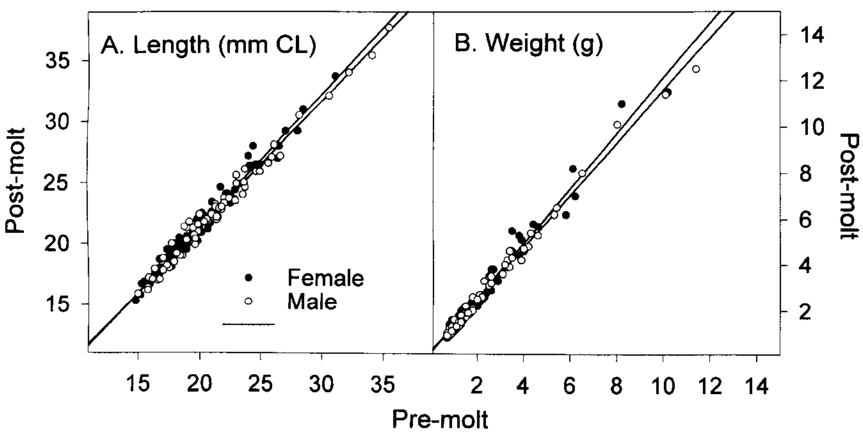

Figure 2. Hiatt growth diagrams showing pre-molt and post-molt incremental growth in crayfish *Procambarus alleni*. A. Carapace length (mm) of males and females. B. Wet weight (g) of males and females.

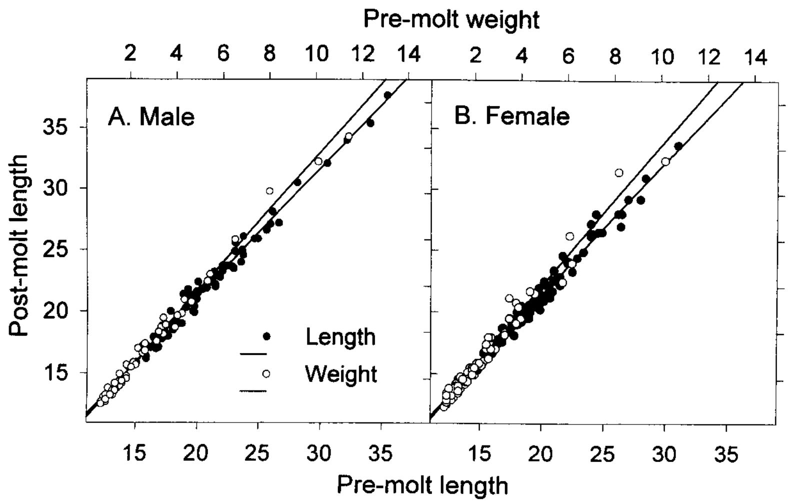

Figure 3. Hiatt growth diagrams showing pre-molt and post-molt incremental growth in crayfish *Procambarus alleni*. A. Carapace length (mm) versus weight (g) in males. B. Carapace length (mm) versus weight (g) in females.

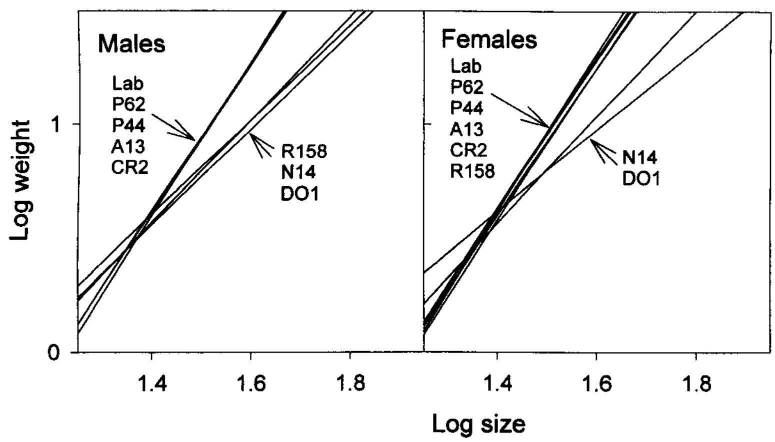

Figure 4. Linearized growth curves of length-weight data and linear regressions on male and female crayfish *Procambarus alleni* in field and laboratory subpopulations. Sites are grouped by regression slopes that are not statistically different.

took a conservative approach to analysis of the field subpopulations and continued to analyze the data separately for males and females. The allometric growth constants (b) of the power equation ranged from highest in animals from the laboratory and longer-hydroperiod sites to lowest in the short-hydroperiod sites (Table 2). The slopes of the linear regressions of the log-transformed data were significantly different among subpopulations (males: $F = 17.9$, df 1380, $P < 0.01$; females: $F = 21.5$, df 1487, $P < 0.01$) (Figure 4). Multiple comparison tests indicated that growth slopes were significantly steeper at sites with longer hydroperiods than sites with shorter hydroperiods (Table 2). Furthermore, growth in the laboratory subpopulation was similar to that of crayfish growth in sites with longer hydroperiods.

Discussion

Growth rates and patterns are highly variable among crayfish species and within a species under different environmental conditions (Hartnoll, 1982; Aiken & Waddy, 1987). Growth in crayfish *Procambarus alleni* on an optimal diet in the laboratory followed a progressive growth pattern in which linear increment increased with animal size (Kurata, 1962). Hiatt growth curves showed no significant differences in the rate of change in carapace length and weight over successive molts in both males and females. This was somewhat

Table 2. A. Parameter estimates and regression coefficients of the power equations for growth in length and weight of crayfish; the coefficient b represents the allometric growth constant and a is the y-intercept. B. Results of Tukey's multiple comparisons on slopes of linear regressions of log-transformed data between pairs of sites; underlined sites indicate no significant differences in growth. Field sites are arranged from longest (P62) to shortest (DO1) hydroperiods.

A.		Lab	P62	P44	A13	CR2	R158	N14	DO1
Males:	a	9.4E-5	8.1E-5	7.8E-5	9.7E-5	8.5E-5	0.0001	0.0001	5.8E-5
	b	3.302	3.332	3.362	3.316	3.345	3.247	3.248	3.163
	R^2	0.96	0.95	0.96	0.96	0.97	0.96	0.95	0.97
	N	85	443	304	118	176	75	95	92
Females:	a	9.8E-5	9.4E-5	0.0001	0.0001	9.5E-5	9.7E-5	4.3E-5	6.5E-5
	b	3.289	3.277	3.278	3.272	3.304	3.275	3.149	3.115
	R^2	0.97	0.97	0.96	0.98	0.97	0.97	0.94	0.98
	N	122	508	337	142	183	65	80	49

<table>
<tr><td>B.</td><td>Lab</td><td>P62</td><td>P44</td><td>A13</td><td>CR2</td><td>R158</td><td>N14</td><td>DO1</td></tr>
<tr><td>Males</td><td colspan="5">____________________</td><td colspan="2">__________</td><td>_____</td></tr>
<tr><td>Females</td><td colspan="6">________________________</td><td>_____</td><td>_____</td></tr>
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unexpected because this species exhibits allometric growth in which sexual differences are pronounced following maturity; e.g., Form I males develop large claws. However, these morphometric differences were not translated into significant differences in carapace length and wet weight.

The incremental increases in length were proportionally similar to incremental increases in weight. This suggests that the relationship between length and weight may be indicative of the effects of external factors on growth. For example, growth in marginal habitat may be reflected in a lower weight gain per step increase in length following ecdysis than in optimal habitat. Growth of crayfish on a high-protein diet in the laboratory was similar to growth in marl prairie habitat with longer hydroperiods (>7 months of inundation). These growth patterns were significantly different from those for crayfish in habitats where the hydroperiod was less than 6 months.

The duration of flooding impacts productivity in the marl prairie wetlands by influencing substrate composition, algal growth, and marl deposition (Davis et al., 1994). These factors, in turn, may impact higher trophic levels, including the abundance of fish and other aquatic fauna (Gunderson & Loftus, 1993; DeAngelis et al., 1997). Our data suggest that crayfish growth was adversely impacted by locally shortened hydroperiods and associated habitat quality. These growth patterns might be linked to the availability and quantity of animal protein in the aquatic food web. Crayfish growth has been shown to be optimal on a high protein diet (Huner, 1984; Momot, 1995). Momot (1995) noted that many species of crayfish may not be primarily detritivorous or herbivorous as previously classified, but in fact, may be primarily carnivorous becoming facultative herbivores as animal protein becomes scarce. In our study, the increase in weight per increase in length in *P. alleni* was highest in marl prairie habitat with longer, more natural hydroperiods where the highest biomass of fish and other aquatic fauna occurred (DeAngelis et al., 1997). Because crayfish interact with multiple trophic levels as prey, predator, and scavenger, they have important multi-functional roles in energy flow in many freshwater aquatic ecosystems (Momot & Gowing, 1977; Kushlan & Kushlan, 1979; Momot, 1995).

Furthermore, crayfish density, population size structure, dispersal, and mortality are also linked to local hydrological conditions (Acosta & Perry, in press). Crayfish do not disperse long distances to avoid the long period of drought in short-hydroperiod sites, but instead, burrow in local substratum during the dry-downs (Kushlan & Kushlan, 1979). Because crayfish are inactive in burrows during the dry season, feeding and growth are greatly reduced during this stressful period (Rhoads, 1976). Therefore, most growth occurs during the flood season of which the duration (i.e., local hydroperiod) impacts the time available for foraging and foraging returns in terms of resource availability and quality. Growth rates may thus be suboptimal in crayfish occupying or colonizing habitats with shortened hydroperiods, consistent with observations that these habitats function as population sinks.

Acknowledgements

We thank all those who fed or measured thousands of crayfish: Christophe Blanc, Cristina Bruno, Kate Grenouillou, Jeff Kline, Eric Nelson, and Guila Sagnotti. C. Acosta was funded through Cooperative Agreement No. 5280-8-9015 from Everglades National Park to Kelsey Downum, Florida International University. This study was funded by the Critical Ecosystems Science Initiative (project 5284-3807-388) of the National Park Service, U.S.A.

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