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Larval Development of *Aratus pisonii* (Milne Edwards) (Brachyura, Grapsidae) From Marine and Estuarine Environments Reared Under Different Salinity Conditions[1]

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ABSTRACT

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Larval development of the mangrove crab, *Aratus pisonii*, reared under three salinity conditions were studied using larvae hatched from females collected from two populations off the Venezuelan coast: one located at mangrove swamps associated with an estuarine coastal lagoon and the other at a marine bay. Laboratory rearings were performed using offshore sea water diluted to 15, 25, and 35 ‰S. Results were analyzed in terms of survival and mean duration per larval stage throughout the whole larval phase of the life cycle. Salinity and larval origin have a significant effect only upon survival of zoea I. Only the mean duration of zoea I of marine larvae proved to be significantly affected by salinity. A differential response was found for the whole larval phase associated with salinity; this response was similar for marine and estuarine larvae. The detected differences in larval survival are interpreted as an adaptation of the species to the environmental conditions of localities where adults were collected.

ADDITIONAL INDEX WORDS: *Estuarine, larval development, mangrove crab, salinity tolerance.*

INTRODUCTION

The roles of physical and chemical factors in decapod larval development have been analyzed through studies on the effects of those factors, individualized or in combination. Temperature, salinity, diet, and light have been tested and found to influence duration and number of larval stages, total development time, and both total and per-stage survival (COSTLOW *et al.*, 1960, 1962, 1966; COSTLOW and BOOKHOUT, 1962, 1968; ROBERTS, 1974; CHRISTIANSEN and COSTLOW, 1975; CHRISTIANSEN and YANG, 1976; SULKIN, 1978; ANGER, 1984, among others). Results from laboratory rearings have been related to the environment normally inhabited by the species. Differences in tolerance to temperature and salinity have been observed, depending on the species and its habitat (COSTLOW and BOOKHOUT, 1962; COSTLOW *et al.*, 1960, 1962, 1966). Seasonal changes of environmental conditions seem to affect larval life of species subjected to such changes (DÍAZ, 1974; JONES, 1981). However, comparative studies on larval stages obtained from adults inhabiting different environments have not been emphasized.

Tolerance to a single parameter, shown by individuals of a given population, should not be extrapolated to the entire species. This can only be concluded after comparative studies have been made on tolerance using specimens from different habitats representing the distributional range of the species (KINNE, 1971).

Among the factors influencing estuarine organisms, salinity fluctuations seem to be important in molding adaptive trends of a species. The range of salinity fluctuation in estuarine waters is greater than that in marine environments. Therefore, it seems reasonable to expect differences in the larval development of species commonly inhabiting marine and estuarine ecosystems, when larvae from these

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environments are reared under similar salinity conditions. Changes in larval developmental pattern might be manifested as changes in the number of instars, intermolt duration, size, survival, etc., as data presented by COSTLOW (1965), COSTLOW and BOOKHOUT (1962), COSTLOW *et al.* (1960, 1962, 1966) show for a single species from one type of ecosystem, but reared under different combinations of salinity and temperature.

The purpose of the present investigation was to assess the responses of *Aratus pisonii* larvae to various levels of salinity associated with those experienced by *A. pisonii* adults inhabiting marine and estuarine ecosystems. This species commonly inhabits seaward-facing borders of mangrove forests from the exposed littoral zone of roots to the canopy. *Aratus pisonii* is distributed from the central eastern coast of Florida (USA) throughout the Caribbean Islands to the northern Brazilian coast in South America (WARNER, 1968). The larval phase of *A. pisonii* consists of four zoeal stages and one megalopa, the juvenile stage being attained in about 24 to 30 days at 25°C (WARNER, 1968).

MATERIALS AND METHODS

Ovigerous females of *Aratus pisonii* were manually collected from two geographically separated locations on the Venezuelan coast. The species lives under different salinity regimens: (1) mangrove swamps influenced mainly by the ocean (Morrocoy National Park, 10°52'N — 68°16'W), where salinity fluctuates little (36±2 °/₀₀S), and (2) swamps associated with an estuarine coastal lagoon (Tacarigua Lagoon National Park, 10°20'N — 68°55'W). Here in location 2 the salinity ranges are extensive (from 1 to 40 °/₀₀S) caused by variable riverine input as well as a seasonal rain regime (GAMBOA *et al.*, 1971).

Only females with late-stage eggs were collected and transported individually in plastic bags containing water from the collection site. In the laboratory, females were transferred to large glass bowls and kept under controlled temperature (26±1°C) and light (12L:12Dh) conditions until hatching, which commonly occurred on the night of collection. Ovigerous females were maintained in filtered water from respective collection sites. The salinity corresponded to the yearly mean value at each locality (36±1 °/₀₀S for Morrocoy Bay and 20 °/₀₀S for Tacarigua Lagoon).

Zoeae released simultaneously from at least five females from the same locality, were pooled. Only vigorously swimming healthy-appearing zoeae were used. They were solitarily placed in small fingerbowls in order to follow separately their development. Each culture set was structured with at least 40 of those larvae

Considering the salinity range of the Tacarigua Lagoon (1 to 40 °/₀₀S), three salinity values of seawater were used in the rearings: 35, 25, and 15 °/₀₀. Seawater was collected offshore in an attempt to minimize possible effects on larval development of substances dissolved in the waters surrounding the mangrove swamps. Culture temperature and light conditions were similar to those for adults. Not less than five culture sets were structured for each treatment (salinity) and locality (larval origin). Table 1 shows the initial rearing conditions. In order to prevent seawater evaporation, fingerbowls containing larvae and food were placed into covered plastic boxes and maintained in culture cabinets. Larvae were daily offered freshly hatched *Artemia salina* nauplii from the San Francisco area. Larvae were transferred daily to freshly filtered seawater in clean fingerbowls, and counted for live individuals of each stage; exuviae and dead individuals were removed and preserved. No antibiotics or fungicides were used.

The effects of salinity on survival and mean duration of each larval stage, and on mortality and duration of total larval development, were analyzed by one- and two- way analyses of variance (ANOVA), *a posteriori* multiple comparison of means (SNK), test of independence (G), and an *a posteriori* test (STP) (SOKAL and ROHLF, 1969). Non-parametric tests were used in cases when heterogeneity of variance was detected and/or when there were insufficient data for application of a parametric test (SIEGEL, 1956).

RESULTS

Table 1 shows the total number of larvae reaching each developmental stage under the various treatments; also, it presents the variable number of zoeal stages detected for both marine and estuarine larvae. The culture of isolated larvae in each fingerbowl allowed us to follow their development independently.

Mean Specific Survival per Larval Stage

This is considered as the survival of a particular larval stage estimated as the percent number of individuals of that stage reaching the following stage (Table 2). The mean was obtained from results of culture sets used in each treatment. Because rearings at the 15 °/₀₀S treatment showed no further development beyond zoea III for marine larvae and

Table 1. Number of larvae from marine and estuarine localities reaching each larval stage under three salinity treatments.

Larvae Origin	Marine (n = 6)			Estuarine (n = 5)		
	Salinity Treatment (S ‰)					
Larval Stages	15	25	35	15	25	35
Zoea I	292	288	288	238	231	227
Zoea II	15	96	84	63	133	67
Zoea III	2	14	12	5	41	19
Zoea IV	—	6	6	1	17	9
Megalopa[a]	—	2	—	—	—	—
Megalopa[b]	—	2	3	1	5	3
Megalopa[c]	—	6	4	—	11	7
% Larvae Reaching Megalopa	0	3.47	2.43	0.42	6.93	4.41

The first line indicates the initial number of larvae used in each condition. Numbers represent the sum of results from culture sets (n) used according to larvae origin.
[a]from zoea II.
[b]from zoea III.
[c]from zoea IV.

Table 2 Percentage of *Aratus pisonii* larvae in stage x_i reaching stage x_{i+1} reared at three salinity treatments using marine and estuarine larvae.

Larval Stages	Salinity treatments (‰S) 15 $\bar{x}\pm SE$	25 $\bar{x}\pm SE$	35 $\bar{x}\pm SE$
Marine Larvae (n = 6)			
Zoea I	5.28±2.57	33.09±5.41	29.04±9.04
Zoea II	8.33±5.69	17.15±4.42	8.33±5.27
Zoea III	—	64.45±18.19	25.00±15.95
Zoea IV	—	66.67±21.08	22.22±16.48
Megalopa	—	5.56±5.56	9.76±6.24
Estuarine Larvae (n= 5)			
Zoea I	26.47±4.17	57.31±5.25	29.78±6.67
Zoea II	9.17±2.00	32.86±7.42	25.88±11.19
Zoea III	40.00±24.49	48.95±13.45	37.50±19.36
Zoea IV	—	43.33±17.95	31.00±19.00
Megalopa	—	5.00±5.00	—

beyond zoea IV for estuarine larvae (only one estuarine larvae reached the megalopa in all cultures at 15 ‰S), data from this treatment beyond zoea III were disregarded for both types of ANOVA. Similarly, no estuarine larvae reached the juvenile stage in the 35 ‰S treatment (see Table 1); therefore, the megalopa stage was not included in the ANOVA. Prior to test differences among larval survival by means of two-way ANOVA an arcsine transformation was given to the percentages.

As shown in Table 3, two-way ANOVA for each larval stage indicated that salinity and locality have a significant effect only upon survival of zoea I, without any interaction. Responses were not additive. Kruskal-Wallis one-way analyses of variance for each larval stage indicated a significant effect of salinity on zoea I of both estuarine and marine larvae ($H_{|2|} = 9.140$ and 7.365 respectively, $P<0.05$).

Multiple comparisons of means, using an *a posteriori* test (STP), indicated the existence of a survival gradient respect to salinity: 25 ‰S > 35‰S > 15‰S, ($P<0.05$).

Mean Duration of Larval Stages

Table 4 shows mean duration of each larval stage for each salinity treatment and locality. A series of one-way ANOVA indicated a significant effect of salinity $F_{s[2, 11]} = 4.20^*$ ($P<0.05$) only on mean duration of the first zoeal stage of the marine larvae. As shown in Table 4, zoeae I tends to prolong their duration as the culture water is less saline. Though it was not statistically significant, this trend was also observed for the other zoeal stages. Data from the zoea III stage of marine larvae, and zoea IV and megalopa of marine and estuarine larvae, reared at 15 ‰S, were not included in the analysis because of massive mortality of these stages in the culture and/or the low number of megalopa obtained (see Tables 1 and 2).

Mean duration of *Aratus pisonii* zoeal stages was similar regardless of treatment and locality of origin. For those treatments in which juveniles were obtained, an increase in the duration of the megalopa stage was detected in respect to the duration of the zoeal stages (Table 4).

Larval Development as a Whole

Comparing the sum of dead larvae in culture sets by means of a G test of independence, significant differences ($G_{(\alpha, 20)} = 90.200^*$, $P<0.05$) were detected among the mortality patterns found for each treatment. An *a posteriori* STP test allowed testing homogeneity of grouped mortality patterns. Larval mortality corresponding to the treatments at 35 ‰S (marine and estuarine larvae), 25 ‰S (marine larvae) and 15 ‰S (estuarine larvae) were statistically similar ($G_{(\alpha, 20)} = 17.876$ N.S., $P>0.05$.

Figure 1 (a and b) shows percent survival per larval stage, taking the initial number of larvae in each series as 100%; replicate values from the same treatment were pooled together. In both marine and estuarine larvae there is a rapid decrease in the percentage reaching the zoea II, continuing the zoeal stages III and IV, and decreasing to near zero percent as the megalopa stage is reached. For a similar salinity condition, percent survival appears to be slightly higher for the estuarine larvae. Highest survival is shown by estuarine larvae reared at 25 ‰S, and lowest by marine larvae cultured at 15 ‰S.

Table 3. Values and its significance for *Aratus pisonii* larval stages survival for marine and estuarine larvae reared under different salinity conditions.

Source	df	ZOEAL STAGES I	II	III	IV[a]
Subgroups	5,27	3.19[b]	1.93 NS	2.03 NS	(3,18) 1.30 NS
Locality	1,27	7.09[b]	3.27 NS	0.82 NS	(1,18) 0.46 NS
Treatment	2,27	4.11[b]	2.69 NS	2.87 NS	(1,18) 2.62 NS
Interaction	2,27	0.66 NS	0.29 NS	1.80 NS	(1,18) 0.83 NS

[a]Data from 15 °/∞S treatment disregarded for this stage, see text for explanation.

[b]$P<0.05$; NS = not significant; degrees of freedom in parentheses.

Values were obtained from two-way ANOVA with inequal but proportional subclass numbers using percent survival transformed into arcsine.

Table 4 Mean duration in days $\bar{x}\pm$SD/and number of molting larvae (n) for each larval stage of *Aratus pisonii* reared at three salinity treatments using marine and estuarine larvae.

Larval Stages	Salinity treatments (°/∞S) 15 $\bar{x}\pm$SD (n)	25 $\bar{x}\pm$SD (n)	35 $\bar{x}\pm$SD (n)
Marine Larvae			
Zoea I	5.50±1.02 (15)	4.64±0.55 (96)	4.26±0.23 (84)
Zoea II	6.25± — (2)	6.23±3.42 (14)	5.86±1.97 (12)
Zoea III	— (0)	4.23±1.25 (6)	3.67±0.47 (6)
Zoea IV	— (0)	3.29±1.53 (6)	3.75±1.53 (4)
Megalopa	— (0)	6.00± — (1)	8.50± — (2)
Estuarine Larvae			
Zoea I	4.57±0.47 (63)	4.21±0.26 (133)	4.81±0.36 (67)
Zoea II	4.43±1.34 (5)	4.13±0.82 (41)	3.95±0.88 (19)
Zoea III	6.00± — (1)	4.42±0.74 (17)	3.44±0.80 (9)
Zoea IV	— (0)	5.54±0.71 (11)	4.70±0.42 (7)
Megalopa	— (0)	10.00± — (2)	— (0)

Kruskall-Wallis one-way analyses of variance indicated no significant differences ($H=2.49$ N.S., $P<0.05$) for the total duration of development among treatments.

Variability in the number of larval stages was detected for *A. pisonii* (see Table 1). The megalopa stage can be reached from the zoea III or IV, and rarely, from the zoea II. Megalopa were most often obtained from zoea IV. Such variability seems not to be related to salinity of water used nor the locality from which larvae originated ($G_{(3)} = 0.517$ N.S., $P<0.05$).

DISCUSSION

Our results indicate that salinity appears to have a significant effect on the mean survival of the first zoeal stage of *Aratus pisonii* from both marine and estuarine environments.

In general, larvae did not attain the megalopa stage at 15 °/∞S (only one estuarine larva reached the megalopa). There were more estuarine larvae reaching the zoea IV stage while the marine larvae (at 15°/∞S) stopped developing at zoea III. Furthermore, there was a higher percent of estuarine larvae reaching the megalopa in all treatments (see Table 1). Those results suggest tolerance to a wider range of salinity among estuarine larvae.

Based on the survival observed in each treatment, a similar gradient of responses for marine and estuarine larvae was found when homogeneous response sets were determined. However, survival of estuarine larvae was found to be higher for all treatments (Figure 2). We interpret the higher survival showed by the estuarine larvae as reflective of a wider range of tolerance to salinity within the interval used during the laboratory rearings. A wide range of salinity tolerance is not uncommon for larvae of euryhaline crabs as shown in previous works, *i.e.* COSTLOW *et al.* (1966), FOSKETT (1977), YOUNG (1979), and RABALAIS and CAMERON (1985). Such increased tolerance would be an adaptation to the fluctuating estuarine salinity. From results obtained for *Uca subcylindrica*, RABALAIS and CAMERON (1985) suggest that a wide larval salinity tolerance range would be advantageous for this species which inhabits extremely saline habitats.

Because a 15 °/∞S is often encountered under estuarine conditions, a higher survival at 15 °/∞S would be expected for the *A. pisonii* estuarine larvae. However, our results invalidate this expectation (see Table 2).

Our results indicate that salinity does not have an obvious affect upon mean duration of larval stages except perhaps for zoea I originating from marine adults. Each zoeal stage lasted from 4 to 6 days, while the megalopa lasted from 6 to 10 days (see Table 4). These results are in agreement with those of other species reported by COSTLOW and BOOKHOUT (1962, 1968), KNOWLTON (1970), ONG and COSTLOW (1970), KINNE (1971), and SCHLOTTERBECK (1976). Their work showed that salinity affected survival while mean duration of each stage appeared to be influenced mostly by temperature. An increase in temperature caused increase in molting rate, but at the same time an increase in mortality had been reported. Thus, optimal conditions for larval development of a given species are determined within a narrow combination of temperature and salinity ranges.

The observed trend to increase duration of the *A. pisonii* megalopal stage with respect to that of the zoeal stages, could be related to several factors other than salinity, such as (1) temperature, (2) inability of the megalopa to prey on *Artemia nauplii*, and (3) absence of appropriate substratum for

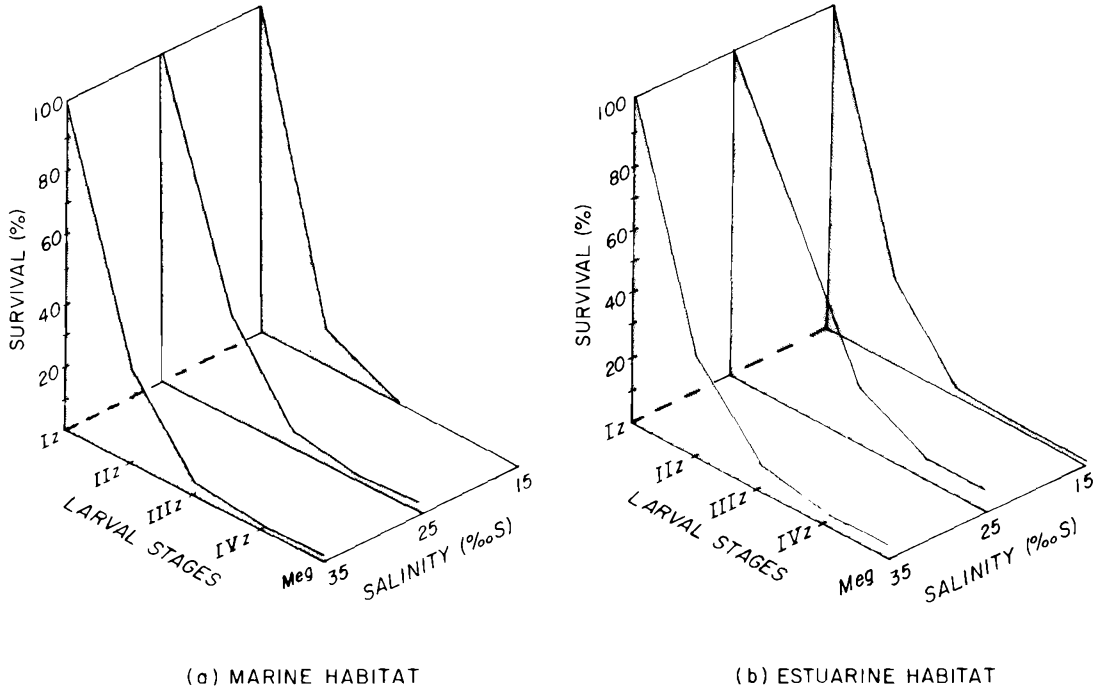

Figure 1. Survival of *Aratus pisonii* larval stages in three salinity conditions using larvae from (a) marine and (b) estuarine habitats.

settlement. If starvation is suffered during premolt, the molting process would be delayed (ANGER and DAWIRS, 1981).

A longer period as megalopae increases the individual's probability to spread and reach an appropriate substratum prior to metamorphosis (JACKSON and STRATHMANN, 1981). Despite the cost of spreading, as analyzed by PALMER and STRATHMANN (1981), extension of the duration of late larval stages might allow the species to colonize new areas or repopulate already colonized ones. This might enhance the possibilities of gene flow among local populations, even though such spreading would increase probabilities of larval mortality. If spread were accidental it would not have short term advantage (MILEIKOVSKY, 1971; SCHELTEMA, 1971; SANDIFER, 1973; STRATHMAN, 1978, 1982).

The physical aspects of an estuary are such that salinity fluctuations, in spatial and temporal scales, do not last as long as required for *A. pisonii* larvae to reach the megalopa stage (about 30 days) in waters having a small salinity range. In an estuary such as Tacarigua Lagoon (GAMBOA *et al.*, 1971), larvae would be exposed to extreme salinities during relatively short periods of time, depending on the duration of tidal flow and freshwater influx. If exposure time to salinities of 25 ‰S or less is shorter than the duration of any particular larval stage, *A. pisonii* larvae might resist such fluctuations. If estuarine larvae are exposed to salinities higher than 25 ‰S, they can be expected to have higher tolerance during prolonged periods of time, owing to their higher tolerance to the upper salinity range. Such differential tolerance to salinity might cause differential recruitment in areas showing contrasting and persistent salinity ranges, *i.e.* inlet of the estuary (15 to 35 ‰S) versus areas adjacent to river discharges (0 to 15 ‰S). The circulation process, concomitant with a behavioral pattern, might explain estuarine larval retention within each estuary area, as proposed by SULKIN and VAN HEUKELEM (1982) for *Callinectes sapidus*. In the Tacarigua coastal lagoon we have observed a consistently higher density of *A. pisonii* adults in areas closer to the inlet than in areas under the direct influence of the river's discharge. This might be interpreted as a consequence of low larval survival in persistently low-salinity waters and larval retention in the areas. However, possible other

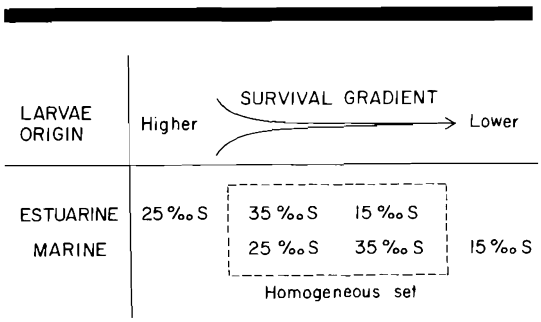

Figure 2. Survival gradient and homogeneous sets found in the larval development of *Aratus pisonii* from marine and estuarine habitats reared under three salinity conditions.

factors due to river input which might affect larvae survival can not be overlooked.

Along the Morrocoy National Park, where salinity range is close to 35 °/₀₀S year round, *A. pisonii* adults show an homogeneous distribution. Our results showed higher survival of larvae from this locality when reared at 25 °/₀₀S. In spite of the fact that in Morrocoy National Park the larvae might not encounter water with this salinity level, the salinity there allows the larvae to reach postlarval stages in sufficient number to maintain the adult population.

In spite of constraints imposed by the laboratory conditions, such as lack of biological interactions, quality and amount of food and controlled salinity and/or temperature, laboratory rearings reveal important information about the larval process. Our results indicate that *A. pisonii* larvae from estuarine waters exhibit a greater range of tolerance to water salinity, being able to survive salinity of 15 °/₀₀S for longer periods of time than larvae from marine waters. However, if that salinity level is maintained for extended periods of time, the probability of reaching postlarval stages diminishes.

The larval response to dominating physical and chemical factors could be related to responses of the adult. From another study on adult *A. pisonii* at the same locations, Díaz and Conde (unpublished) found that estuarine ovigerous females of similar body size produce almost twice as many eggs per clutch as those from marine swamps. Such differential reproductive output (clutch size) might be related to the relative stability encountered in the marine system compared to the estuarine one. The larval mortality risk in estuarine waters would be compensated by higher larval tolerance to salinity variations and by greater production of larvae by the adults. Greater egg production in the estuary might be enhanced by a qualitatively better diet based upon nutrient availability in estuarine waters (SIMONS and JONES, 1981). In contrast, the relative stability of the marine locality appears to be a contributing factor to lower larval production per clutch and to a narrower larval tolerance to salinity fluctuations.

CONCLUSIONS

(1). A significant effect of water salinity used in rearings upon survival of zoea I from both marine and estuarine origin was detected. For these cases, a differential response (gradient) in survival was detected for the three salinities used: 25 °/₀₀S > 35°/₀₀S > 15°/₀₀S. Differences in mean specific survival were not significant among most estuarine larval stages when reared in the three salinities suggesting a greater tolerance to salinity.

(2). Survival of estuarine larvae was found to be higher than that of marine larvae for all treatments, being higher for those reared at 25 °/₀₀S.

(3). A significant effect of salinity used in rearings was detected upon the mean duration of zoea I, larvae spent more time at this stage as culture salinity was lower. In general, duration of the megalopa stage was longer than any of the zoeal stages.

(4). The higher range of tolerance to water salinity exhibited by estuarine larvae, in terms of mean survival and mean duration, might be related to the observed greater production of larvae by estuarine adults. These characteristics of *Aratus pisonii* complex life cycle might compensate for the mortality risk derived from the relative unstability of the estuarine environment.

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