

Seasonal Developmental Sequences of *Emerita talpoida* (Say) (Anomura, Hippidae)¹

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ABSTRACT

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The larval development of the sand crab *Emerita talpoida* (Say) was studied under similar laboratory conditions using larvae hatched from eggs produced in a single locality during spring and summer. Two developmental sequences were found, larvae hatched in May went through five or six developmental stages while those hatched in August showed six or seven stages and took longer to metamorphose. These developmental sequences were ascribed to environmental conditions to which adults and embryos were exposed. The role of factors such as temperature, salinity, amount of yolk in the eggs are discussed in relation to ecological models of larval development.

ADDITIONAL INDEX WORDS: Larval development, sand crab, *Emerita*, sandy beach, seasonality.



INTRODUCTION

Emerita talpoida (Say), the only species of this genus found in North Carolina, USA, commonly inhabits the intertidal zone of sandy beaches. Its complete geographic range extends from Harwich, Massachusetts, USA, to Progreso, Yucatán, México (WILLIAMS, 1965). The larval development of *E. talpoida* was described by REES (1959), indicating variability in its number of zoeal stages.

Changing environmental factors to which the larvae are seasonally subjected, such as salinity, temperature, photoperiod and diet, have generally been suggested as responsible for variabilities during the larval development of several species of Crustacea. However, it appears that there is not enough evidence in favor of any single factor. COSTLOW (1965) suggests that endocrine mechanisms associated with the molting process could be affected by environmental factors inducing larval variability in terms of duration and number of instars. The endocrine system can be assumed as a

phenotypical expression of the genetic load.

According to SANDIFER and SMITH (1979) the instar of metamorphosis may be inheritable, but not the specific duration of larval development. Ample reviews on larval development variability are presented in WENNER (1985).

Along Bogue Banks, North Carolina, *E. talpoida* presents a life history pattern which varies according to seasonal changes of environmental conditions. Early year breeding pulse starts in January ending by June, when the second pulse starts, which ends by late September. Seasonal environmental changes affect fecundity, duration of the embryonic period and the amount of yolk supplied to eggs (DIAZ, 1980), consequentially, could be speculated, the amount of energy supplied to each larva at hatching also would be affected. Therefore, the life cycle should be considered as a whole, studying the relationship between the adult phase and larval phase, as suggested by ISTOCK (1967).

Here, we present a study aimed to test if variable developmental sequences presented by *E. talpoida* (REES, 1959) could be related to the seasonal environmental changes to which adults and embryos of this species are exposed in North Carolina

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beaches and, apparently associated with reported changes in its life history. Our tests can not allow differentiation between effects of embryonic development, seasonal variation independent of environmental conditions, or nutritional effects on adults reflected in status of larvae. Our tests can show developmental differences in larvae from the two seasons of the year, also that variability in larval stages occurs within and between larval populations originated from adults inhabiting a single locality subjected to seasonal variations of environmental conditions. Speculations are presented on the ecological implications of such seasonally changing developmental sequences.

MATERIALS AND METHODS

Ovigerous females of *Emerita talpoida* with late-stage egg masses were manually collected at Bogue Banks, North Carolina, during the second week of May and during the first week of August. They were individually placed in containers with seawater and a constant supply of bubbling air in a 25 °C constant temperature cabinet until hatching, which generally occurred on the night of collection.

As the larvae hatched, those vigorously swimming healthy appearing zoeae were selected for rearing. Groups of ten larvae were placed in glass bowls containing filtered seawater and recently hatched *Artemia salina* nauplii. Larvae were changed daily to clean bowls with seawater, counted for live individuals of each stage and new *A. salina* nauplii added. Exuviae and dead individuals were identified, counted and preserved. In view of possible effects of *Artemia* from different sources on the larval development (BOOKHOUT and COSTLOW, 1970), only *Artemia* from the San Francisco area were used.

Water temperature along Bogue Banks from March to June might increase from 15 to 25 °C, with daily oscillations. From July through September, for the same area, water temperature oscillate around 25 ± 1 °C (DIAZ, personal observations). At the Beaufort Channel, Beaufort, North Carolina, monthly mean water temperatures registered for the same periods oscillated from 12.7 to 25.9 °C and from 27.4 to 25.4 °C respectively (KIRBY-SMITH, personal communication). In an attempt to maintain the larvae in a rearing condition as near as possible to the field conditions, a 20-25 °C temperature cycle was chosen for maintaining the larvae with 12 hours difference between maximum and minimum temperatures. The extreme tem-

peratures were maintained for approximately six hours. Parallel culture series from the same females were also maintained in 25 ± 1 °C controlled cabinets. The salinity range of water used was 35 ± 1 ‰, while a 14L:10D photoperiod was set for cultures. No antibiotics or fungicides were used.

For the spring rearings, larvae from three females were selected, while five ovigerous females provided the larvae for summer culturing. The total number of larvae in each experiment is shown in Table 1.

RESULTS

Rearings were terminated when larvae reached the juvenile stage. Since in natural conditions embryos and larvae are subjected to different temperature ranges during the spring and summer reproductive pulses (DIAZ, 1980), the parallel 25 °C cultures allowed for comparing results of rearings from both seasons, having in mind the environmental temperature changes to which natural populations are subjected in the study area. Kruskal-Wallis one-way analyses of variance (SIEGEL, 1956) revealed no significant differences ($P > 0.05$) in survival and mean duration of larval stages among culture series from different females at each of the temperature conditions. Thus, these series were considered as replicates and their results were pooled allowing comparisons by means of Kruskal-Wallis tests.

Figure 1 shows the relative daily survival at each stage respective to the initial number of larvae in rearings, and duration per stage in respect to the initial number of larvae in rearings and duration per stage, according to its frequency distribution as a function of time. Variability in the number of stages prior to the megalopa was observed within season and between seasons. In the spring, the megalopa stage was reached after a fifth and/or a sixth zoeal stage, while in the summer cultures, after a sixth and/or a seventh zoeal stage. Figure 2 shows the

Table 1. Initial number of *Emerita talpoida* larvae for each temperature condition of rearings performed at two different seasons of the year.

Hatching day	Number of larvae per temperature condition	
	20-25 °C	25 °C
Spring		
May 9	98	99
May 9	96	98
May 9	96	96
Summer		
August 2	47	41
August 3	50	47
August 3	48	48
August 10	74	--
August 10	76	--

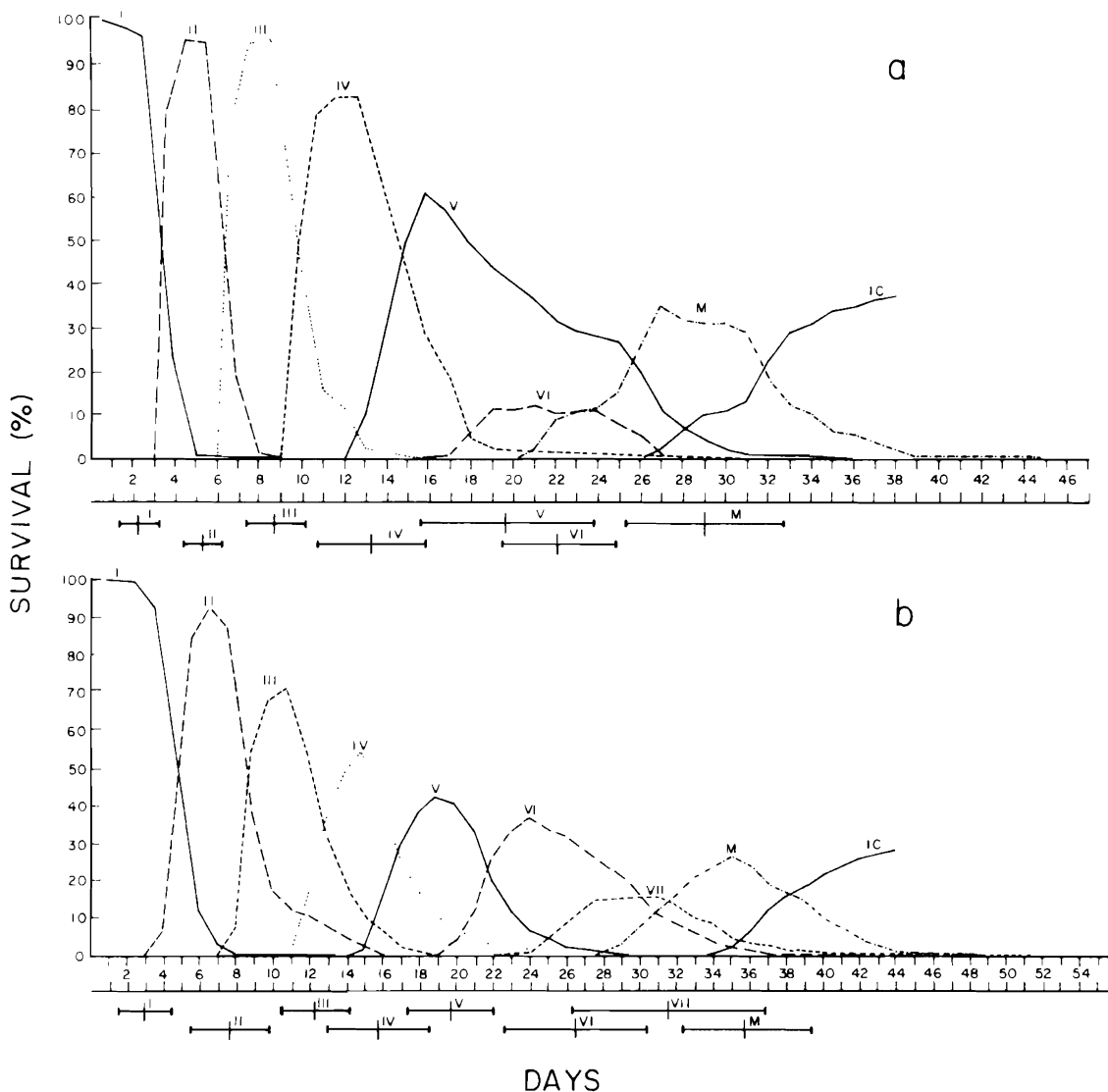


Figure 1. Rearing record of *Emerita talpoida* at the 20-25 °C temperature cycle. Daily percent survival at each instar. Bars: mean and standard deviation of the duration of each instar. Symbols I to VII, M and IC: zoeal stages I to VII, megalopa and first juvenile crab, respectively. (a) Culture from spring eggs; (b) culture from summer eggs.

proportion of larvae passing through the developmental sequences for each season. Variability in the morphological characteristics within individuals of the stages prior to megalopa was observed. Generally it consisted of instars showing mixed characteristics of the two last zoeal stages. However, megalopae obtained from different zoeal stages in spring and summer, were morphologically similar.

Survival proportions per stage were calculated for each season culture (Fig. 3). The survival (1_x) from the III to the IV zoeal stage was considerably higher in cultures of larvae hatched from spring eggs when compared to the 1_x obtained from summer batches; whereas, 1_x of the stages immediately prior to megalopa was found to be lower. From the spring rearings, the V zoeal stage produced twice

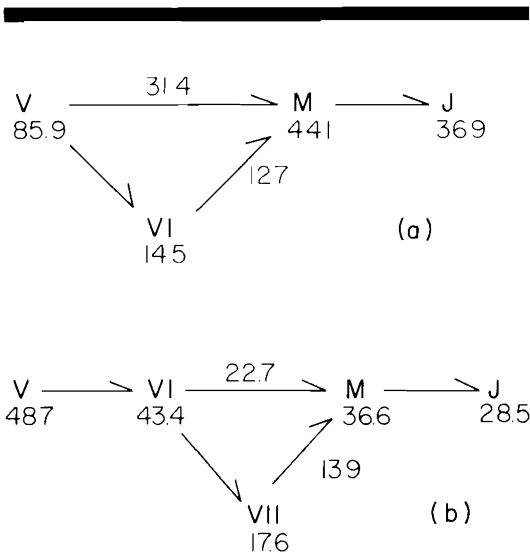


Figure 2. Seasonal developmental sequences of *Emerita talpoida* larvae reared at 20-25 °C temperature cycle. (a) Spring cultures; (b) summer cultures. Symbols V to VII, M and J: zoeal stages V to VII, megalopa and first juvenile crab, respectively. Arabic numerals: proportion of larvae that molted to a particular stage as percent of the number of larvae at the start of the rearings.

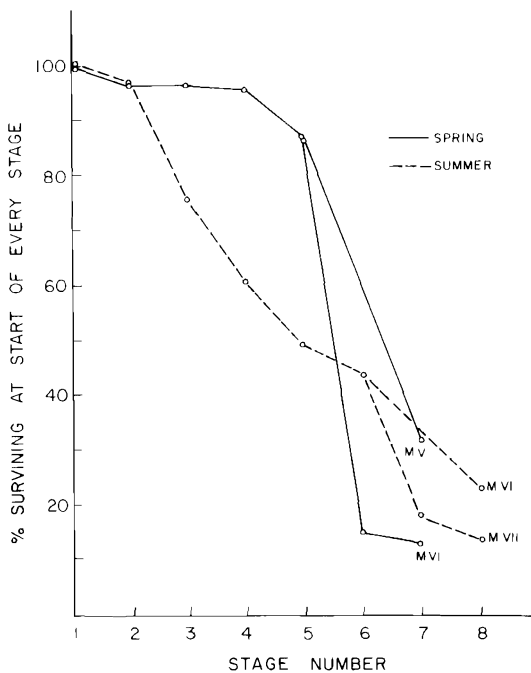


Figure 3. Percent survival of *Emerita talpoida* larvae at the beginning of each larval stage for spring and summer rearings at 20-25 °C cyclic temperature, M-V to M-VII: megalopa molted from zoeae V to VII, respectively.

the number of megalopae than the VI zoeal stage. However, the proportion of megalopa obtained from the VI zoeal stage was found to be twice as large as those from V zoeal stage. These proportions are affected by differential mortality rates exhibited by the V and VI stages (see Tables 2 and 3). In the summer cultures, the proportions of megalopae and VII zoeal stage produced from the VI zoea were found not to be strikingly different.

For the summer rearings the occurrence of an extra zoeal stage, together with the longer duration of the larval stages, resulted in a complete larval development of one week longer in duration, when compared with the spring rearings. Duration of the megalopa was found to be similar for both seasons (Tables 2 and 3).

DISCUSSION

The occurrence of a non-fixed number of instars, changes in the rates of molt and survival, or morphological variations among larvae of the same stage, have been regarded as expressions of variability in the larval history of several groups of Crustacea (COSTLOW, 1965; WENNER, 1985). Within the Hippidae, HANSON (1969) observed variability for *Hippa cubensis* in the number of larval stages, in the molting rate and in some morphological features. For *Emerita analoga* in the USA west coast, JOHNSON and LEWIS (1942) observed variations in the setation and development of appendages of larvae collected from the plankton. For the same species, EFFORD (1970) found 8 to 11 molts before the megalopa stage was attained, and suggested that *E. analoga* larvae go through fewer molts in the plankton than under laboratory conditions. Laboratory rearings of *E. rathbunae* from the Baja California coast (USA) showed variations in the number of stages and its morphology (KNIGHT, 1967). REES (1959) found that most of *E. talpoida* reared at 30 °C and 32.2 ‰ S, mean salinity, passed through six zoeal stages and only few individuals went through a seventh zoea before the megalopa, with a total mean duration of 28 days. Using the number of setae on the maxillipeds as an indication of the number of molts. REES (1959) suggested that planktonic *E. talpoida* larvae studied by SMITH (1877) could reach the megalopa stage after five zoea stages. No indication of seasonal variation was given. From planktonic material KNIGHT (1967) found morphological evidences suggesting seasonal variation in the molting pattern of *E. rathbunae*. In this study, we found two seasonal

Table 2. Pooled data of larvae cultures from three different *Emerita talpoida* females, reared from hatching to juvenile stage (J) at the 20-25 °C temperature cycle during spring.

Stage x	Observed alive n	Mortality rate ($1_{x+1}-1_x$)/1	Molting rate $1_{x+1}/1_x$	Duration range (obs. days)	Mean duration (days)
I	290	0.041	0.959	(1-8)	2.2
II	278	0.004	0.996	(4-8)	2.2
III	277	0.015	0.986	(6-18)	3.7
IV	273	0.087	0.912	(10-30)	4.2
V	249	0.466	0.167 ^a	(13-37)	7.6
VI	42	0.124	0.365 ^b	(17-31)	6.1
M-V ^c	91	-	-	(21-?)	-
M-VI ^c	37	-	-	(22-?)	-
M ^d	128	0.163	0.836	(21-45)	9.0
J	107	-	-	(26-?)	-

1_x . Proportion of survivors at start of stage x

a. Molting to sixth zoeal stage

b. Molting to Megalopa

c. M-V, M-VI Megalopa originated from V and VI zoeal stage respectively

d. Total number of Megalopa produced

Table 3. Pooled data of larvae cultures from five different *Emerita talpoida* females, reared from hatching to juvenile stage (J) at the 20-25 °C temperature cycle during summer.

Stage x	Observed alive n	Mortality rate ($1_{x+1}-1_x$)/1	Molting rate $1_{x+1}/1_x$	Duration range (obs. days)	Mean duration (days)
I	295	0.034	0.966	(1-11)	2.9
II	285	0.220	0.779	(4-16)	4.5
III	222	0.203	0.792	(7-19)	5.2
IV	177	0.198	0.802	(11-30)	5.7
V	142	0.098	0.901	(15-30)	5.7
VI	128	0.071	0.406 ^a	(20-46)	7.5
VII	52	0.210	0.523 ^b	(23-54)	9.5
M-VI ^c	67	-	-	(28-?)	-
M-VII ^c	41	-	-	(31-?)	-
M ^d	108	0.213	0.778	(28-48)	8.7
J	84	-	-	(34-?)	-

1_x . Proportion of survivors at start of stage x

a. Molting to seventh zoeal stage

b. Molting to Megalopa

c. M-VI, M-VII Megalopa originated from sixth and seventh zoeal stage respectively

d. Total number of Megalopa produced

developmental sequences for *E. talpoida*. Larvae cultured from eggs laid during spring presented five or six zoeal stages while those reared from summer eggs showed six or seven stages before molting to megalopa. The occurrence of a different number of stages in each season account for an increase of one week in the mean duration of the total larval development shown by summer rearings in respect to the spring cultures. The duration and mortality of each stage of development proved to be different in the seasonal sequences, as well as the proportion of individuals reaching a particular stage.

Several authors have reported evidences on the effect of temperature on the larval development of species subjected to temperature changes in a seasonal or geographical scales, such results are pertinent to our findings. COSTLOW (1967) postulated that survival and duration of *Callinectes sapidus* megalopae in nature are directly associated with the time of hatching and final zoeal molt, coupled with seasonal temperature and local salinity changes. Geographical distribution of the species might account for differential effects of temperature on the number of larval stages. Laboratory

studies on the larval development of the Galatheid *Pleuroncodes planipes* from California, USA (BOYD and JOHNSON, 1963) and on its equivalent species, *P. monodon* from Southern Chile (FAGETTI and CAMPODONICO, 1971), have revealed that relatively high temperatures increased the number of intermoult for both species. However, an inverse relationship was detected for the tropical caridean shrimp *Tozeuma carolinense* (EWALD, 1969). While both *P. planipes* and *P. monodon* inhabit areas where the water temperatures do not often reach 20 °C, *T. carolinense* is rarely exposed to temperatures below 20 °C. Furthermore, results from others studies (see reviews presented in KINNE, 1971 and WENNER, 1985) indicated that both salinity and temperature affect the rate of larval development as well as survival. Larvae subjected to transport by currents might encounter changes of the salinity and temperature while being transported. Such changes might, in turn, affect populational parameters of wide geographical range species as *E. talpoida*.

The number of larval stages appears to be affected by environmental surrounding conditions of the habitat of the adult population or by the conditions to which embryos are exposed. Molting frequency of larvae from two separated populations of *T. carolinense* was found to be different by a factor of two, when reared under similar laboratory conditions (EWALD, 1969). The temperature effect on the variability of the number of instars does not explain the differences between larvae rearing from the two *T. carolinense* populations. This might be an indication of genetic differences in the mechanisms controlling the molting process in larvae from the species' populations living under different environmental conditions. Acclimation temperature during the embryonic development influences significantly the survival and the mean duration of *Halicarcinus paralacustris* (LUCAS, 1972). At Bogue Banks, North Carolina (USA), *E. talpoida* eggs laid early in the year are kept attached to the female for a considerably longer time than those laid during summer (DIAZ, 1980). Therefore, the spring brood is exposed to a gradual increase in temperature during its embryonic development, while the summer clutches are developed at relatively constant temperatures.

Seasonal changes seem to play a role in the amount of yolk accumulated, thus affecting egg size. DIAZ (1980) found that *E. talpoida* eggs laid during the spring were significantly larger than those laid during summer. EFFORD (1967), working

with several species of the genus *Emerita* of the Americas, found a tendency towards increasing egg volume with a decrease in temperature. On a geographical scale, variations in egg size could also be connected to changes in temperature from North to South. Efford also found that "egg size (of *E. analoga*) decreases with progress through the summer to autumn as with passage from North to South". From his findings and the reported temperature development time relationship (HANSON, 1969), Efford proposes that large eggs produced in colder waters may provide zoeae with more food which may help them to survive longer in the plankton, inferring that *Emerita* larvae are lecithotrophic to some extent. Observations made by LUCAS (1972), DIAZ (1980), EFFORD (1969), together with those mentioned previously on the larval development of *E. analoga* (EFFORD, 1970) and *E. rathbunae* (KNIGHT, 1987), and the findings presented here, argue in favor of VANCE's (1973a, b) model and its "intuitive appeal" referred to by STRATHMANN (1977:373). Vance proposes that larger eggs would produce larvae which spend less time feeding and "the animal can spend more time as an embryo". Our results, show that larvae resulting from larger eggs, with a long embryonic period (spring broods) had fewer number of instars and spent shorter time as zoeae. Also, they showed a lower mortality rate during the early stages of development. The contrary was found for the summer rearings. However, the proportion of megalopae or juveniles produced from both broods was similar (Figures 2 and 3).

The 20-25 daily cycle and the 25 °C constant temperature used during rearings are, respectively, slightly above the spring water temperature for the region, and slightly below the recorded during summer. Despite that, the similarities observed between cultures under both temperature conditions suggest that the developmental sequences for each season are not induced by the temperature used. Since external food supply was kept well above the larval ingestion rate, the registered mortality rates do not necessarily reflect natural mortality due to starvation or planktonic predation.

The advantage or disadvantage of having changing developmental sequences can be envisioned when the adult population is examined (*i.e.*, studies on fecundity changes and recruitment rates) and when considerations are made on larval dispersal and its effects on the species' distribution and genetic exchange between geographically separated populations (MILEIKOVSKY, 1971; SCHELTEMA, 1971; STRATHMANN, 1974). More-

over, the seasonal and regional water temperature changes, the larval dispersal and the reported effects of temperature, salinity, photoperiod and diet on the length of larval life suggest that VANCE's (1973 a, b) model is still lacking those variables which appear to result in a more efficient reproductive mechanism. However, Vance's model has already initiated new arguments for the interpretation of the main directions followed by marine invertebrates during their larval development.

During the planktonic drift, larvae are subjected to predation, starvation, variations in food supply and unpredictable changes of abiotic factors which, as shown, might affect the length of the larval cycle. In such a case, an increase in planktonic life would increase death probabilities (STRATHMANN, 1978), the contrary would decrease dispersion (PALMER and STRATHMANN, 1981). Death risk would emerge from the probability of becoming a suitable prey for the other zooplankters, also, from physiological malfunctioning or from nutritional vulnerability (*sensu* SULKIN, 1978). According to ANGER and DAWIRS (1981) starvation resistance varies in relation to temperature and stage. In general, starvation resistance decreases as temperature increases; there is an optimal temperature at which starved decapod larvae achieve their longest survival (REGNAULT, 1969 a, b; RICE and PROVENZANO, 1966; GORE, 1968). Larval development is affected by starvation, if suffered during premolt (ANGER and DAWIRS, 1981). However, nutritional deficiencies affect number and duration of zoeal stages (SULKIN and NORMAN, 1976). FREEMAN and COSTLOW (1980) suggested that the Molt Inhibiting Hormone (MIH) is probably secreted during the post-molt, independently of feeding. If MIH secretion is prevented by extirpation of eyestalk, but food availability is not restricted, supernumerary larval stages may be induced (COSTLOW, 1963, 1966).

GURNEY (1942) has questioned the normality of larval history pattern obtained under laboratory conditions, suggesting that, abnormal stages might be induced by the artificial conditions. However, examples cited above in relation to variable developmental sequences during planktonic life, and reviews presented by Gore, and Rabalais and Gore in WENNER (1985) aim towards the consolidation of an information body in support of an evolutionary envisage.

The occurrence of seasonal developmental sequences has been somewhat disregarded, mainly because most of the words describing crustacean

larval development are based upon rearings carried out during one season of the year without considering the conditions to which the adult population is subjected prior or during the breeding season.

The number and duration of larval stages might be determined by genetic characters as suggested by SANDIFER and SMITH (1979), which would be expressed by internal factors, such as endocrine control of the molt, but they might also be affected by environmental factors at the time when the development of the embryo is occurring as well as during the process of larval development. Such interactions would generate short term changes in the interval sequence, adequate to the conditions surrounding the adult and/or the larval population. Thus, the ability of changing the larval cycle pattern can be considered as a characteristic which enhances fitness of organisms subjected to a changing environment.

CONCLUSIONS

- (1) *Emerita talpoida* larvae from a single locality, reared under similar laboratory conditions, showed two different developmental sequences along two seasons of the year. Egg extruded since the beginning of the year produced larvae in spring which went through five or six zoeal stages, while those produced and hatched in midsummer showed six or seven zoeae.
- (2) Within each developmental sequence, variability in the number of zoeal stages was detected as well as among sibling larvae.
- (3) The summer developmental sequence extended its mean duration in one week in respect to the spring sequence. This time elongation is ascribed to the existence of one additional zoeal stage. Despite differences detected for survival per zoeal stage between seasonal sequences, the number of megalopaeas well as duration of this stage were found to be similar for both seasonal sequences.
- (4) The seasonal developmental sequences observed for *E. talpoida* appear not to be induced by the rearing conditions but by the environmental conditions to which embryos and larvae are exposed. Thus, interactions between external and internal factors, such as temperature, amount of yolk in eggs and those controlling the molting process, would generate short term changes in the larval sequence. These changes are adequate to the changing environment, even among sibling larvae produced in two seasons when considerable environmental

changes occur. Our results and published works suggest the genetic character of the seasonality observed for the developmental sequences.

(5) The seasonal developmental sequences shown by *E. talpoida* larvae seem to be in concordance with reproductive pulses and the changing life history pattern presented by adults of this species in the same study area.

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□ RESUMEN □

El desarrollo larval del cangrejo hipido *Emerita talpoida* (Say) ha sido estudiado bajo condiciones de laboratorio similares, usando larvas obtenidas de huevos producidos en una localidad única durante primavera y verano. Se han observado dos secuencias en el desarrollo, las larvas obtenidas en Mayo atravesaron cinco o seis estados de desarrollo mientras que las obtenidas en Agosto mostraron seis o siete estados y necesitaron más tiempo para realizar la metamorfosis. Estas secuencias en el desarrollo han sido imputadas a las condiciones ambientales a las que fueron expuestas los adultos y embriones. Se discute la importancia de factores como temperatura, salinidad y cantidad de vema del huevo en relación con los modelos ecológicos de desarrollo larval.--Miguel A. Losada, Universidad de Santander, Santander, Spain

□ ZUSAMMENFASSUNG □

Die Larvalentwicklung der Sandkrabbe *Emerita talpoida* (Say) wurde unter ähnlichen Bedingungen untersucht mit der Verwendung von Larven aus Eiern gezüchtet, die aus einer einzigen Lokalität stammten, während Frühling und Sommer. Zwei Entwicklungsfolgen wurden bestimmt: die Larven, die in Mai erzeugt wurden, gingen durch fünf oder sechs Entwicklungsfolgen, während solche die im August erzeugt wurden wiesen sechs oder sieben Etappen und eine verzögerte Metamorphose auf. Diese Entwicklungsfolgen wurden auf Umweltverhältnisse, denen die Erwachsenen und Embryos ausgesetzt wurden, zugeteilt. Die Rollen die Faktoren wie Temperatur, Salinität und Eidotterquantität spielen, werden besprochen in Verbindung mit ökologischen Larvalentwicklungsmodellen.--Carlos Schubert, IVIC, Caracas, Venezuela

