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Occurrence of an alternative pathway in the larval development of the crab *Chasmagnathus granulata* Dana, 1851 under laboratory conditions

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Abstract

Larvae of the crab *Chasmagnathus granulata* were collected in a salt marsh located in the Lagoa dos Patos, Brazil and reared from eclosion to metamorphosis under different dietary regimes. Larvae reared individually in beakers of 40 ml and fed *Tetraselmis chuii* (zoea III and zoea IV), showed a supplementary stage, here designated as zoea V, with morphological characteristics intermediary between zoea IV and megalopa. No zoeae V molted to megalopa stage. To confirm the occurrence of the supplementary stage, mass cultures of larvae of *C. granulata* were fed *Artemia* sp. at high densities, we again detected the fifth zoeal instar. However, when zoeae V were individually placed in beakers and fed *Artemia* nauplii, they succeeded in molting into megalopae. We observed the occurrence of two types of zoeae IV — a smaller type (from which originated the zoeae V) and a larger type (which directly developed into megalopae). We conclude that stressful nutritional/environmental conditions were responsible for the occurrence of this alternative path of development.

Introduction

The variability in nuber of the larval stages of decapod crustaceans has motivated many studies on the influence of ecological factors. The number of larval stages in Brachyura was initially considered constant (Gurney, 1942). Some authors considered the 'extra' stages 'artifacts of the laboratory' (Boyd & Johnson, 1963), because they were less frequent, did not evolve into megalopa and, in most cases, did not occur in nature (Knowlton, 1974).

This concept was questioned, principally in larvae of *Calinectes sapidus* (Sulkin, 1978; Millikin *et al.* 1980) and some from other Brachyura (Porter, 1960; Costlow, 1966; McConaugha, 1982; Rodrigues, 1982; Rieger, 1986; Montu *et al.*, 1990).

Recent works show that these forms considered 'abnormal' are frequently found in the laboratory and in field samples. It has been observed that the Caridea show variations in the number of larval stages under laboratory conditions as well as in nature (Knowlton, 1974; Criales & Anger, 1986; Goyanes, 1987). With Anomura, it is also common to observe a variation in the number of stages in larvae collected from natural populations (Johnson & Lewis, 1942; Veloso, 1988) or reared in the laboratory (Roberts, 1974; Carvalho, 1991).

The present work owes its existence to a supplementary zoeal stage of the crab *Chasmagnathus granulata* observed during an experiment which had as objective the quantification of the ammonia-nitrogen excretion rates in larvae submitted to different diets (Pestana *et al.*, in press).

During these experiments, we observed two paths of larval development, a 'normal' path, described by Boschi *et al.* (1967), with four zoeal stages and one megalopa, and an 'alternative' path, with one additional zoeal stage. We also observed the existence of two types of zoeae IV — one of smaller size (from which originated the zoeae V) and a larger one (which develops directly into megalopa). In the present work the two paths of development are discussed. We describe, for the first time, the zoea V of *C. granulata*. This study is important because, despite the fact that *C. granulata* adults and juveniles have been relatively well studied (Rieger & Nakagawa, 1988; Santos *et al.*, 1987; Santos & Nery, 1987; D'Incao *et al.*, 1990; D'Incao *et al.*, 1992), the larvae are not yet so well known and many doubts persist regarding their larval biology and ecology.

Material and methods

In the summer of 1990/91, ovigerous females of *C. granulata* were collected manually from a salt marsh located in the Lagoa dos Patos, Brazil. These females were kept in the laboratory in a 5 liter aerated aquarium, at 25‰ seawater, until their larvae were almost ready to hatch. The adults were fed with small pieces of fresh fish and water was changed daily.

After eclosion, the larvae of *C. granulata* were removed from the aquarium with a glass protozoan pipette and reared individually in B.O.D. incubators, in numbered glass beakers containing 40 ml of filtered water, at 25‰. This salinity was obtained by mixing filtered seawater with sufficient amounts of deionized freshwater, and was checked by means of a refractometer. All experiments were carried out in the incubators, at a constant-temperature (25 °C), and 12:12 L:D.

Three types of food were tested in the experiments: microalgae (*Tetraselmis chuii*), rotifers (*Brachionus plicatilis*) and newly hatched *Artemia* nauplii. The larvae remained in the incubators in contact with the food for a two-hour period, after which they were transferred to beakers containing clean water. Afterwards, the series returned to the incubator until the following day.

In the experiments with microalgae it was necessary to keep the larvae fed with *Artemia* nauplii until the desired stage. We observed that the group maintained with *T. chuii* would never succeed in completing its development with only this type of food.

We detected, initially, the alternative path of development in individual cultures fed with *T. chuii* from zoea III. To effectively confirm the existence of this alternative path, we made mass cultures with approximately 100 newly hatched larvae, in flasks of 1 liter, and fed with *Artemia* nauplii. From these cultures, we took 15 zoeae IV of smaller size and placed them in individual cultures in beakers of 40 ml. A control was maintained with 20 larval from the same females, individually reared from zoea and fed with *Artemia* nauplii in beakers of 40 ml, from eclosion to metamorphosis to the juvenile stage. No attemps were made to rear juvenile further.

Table 1. C. granulata. Biometric relationships between the zoea IVa and zoea IVb stages. The average values are presented in mm (standard deviation in parentheses).

Measurement	ZIVa	ZIVb	*t*	*p*
RS-DS	1.800 (0.2307)	1.6323 (0.0951)	2.0326	<0.05
Cephalothorax	0.9545 (0.0765)	0.8475 (0.0682)	3.2060	<0.05
Total length	2.8955 (0.0954)	2.6325 (0.1068)	5.6690	<0.05

RS- Rostal spine.
DS- Dorsal spine

From the mass cultures we took zoeae IV of the two sizes for comparison, by performing dissections under a stereomicroscope (Wild and Zeiss), comparing the results with the description made by Boschi *et al.* (1967). The zoeae V were also dissected for better observations of morphological differences. We measured the larvae to verify if the biometric differences were significant between the stages (zoeae IV of both types and zoeae V). The three measurements used were based on the work of Montu *et al.* (1988): the length between the rostral spine and the tip of the dorsal spine (RS-DS); carapace length (cephalothorax — from the orbit to the posterior carapace border); total length (distance from the tip of the rostrum to the posterior border of the telson, excluding the processes of the telson).

Differences between mean values were tested after comparing their variance (*F*-test) by means of Student's t statistic. They were considered statistically significant if p (two-tailed) was <0.05.

Results

In the series fed with *T. chuii* from zoea III in individual cultures, 45% of the larvae molted to zoea IV, we observed here the appearance of a supernumerical zoea V stage (Fig. 1) first with a frequency of 5%. No zoeae V molted to megalopae. In the series fed with *T. chuii* from zoea IV onward, 65% of the larvae molted to zoea V and only 15% molted directly to megalopae. Again, no zoeae V molted to megalopae.

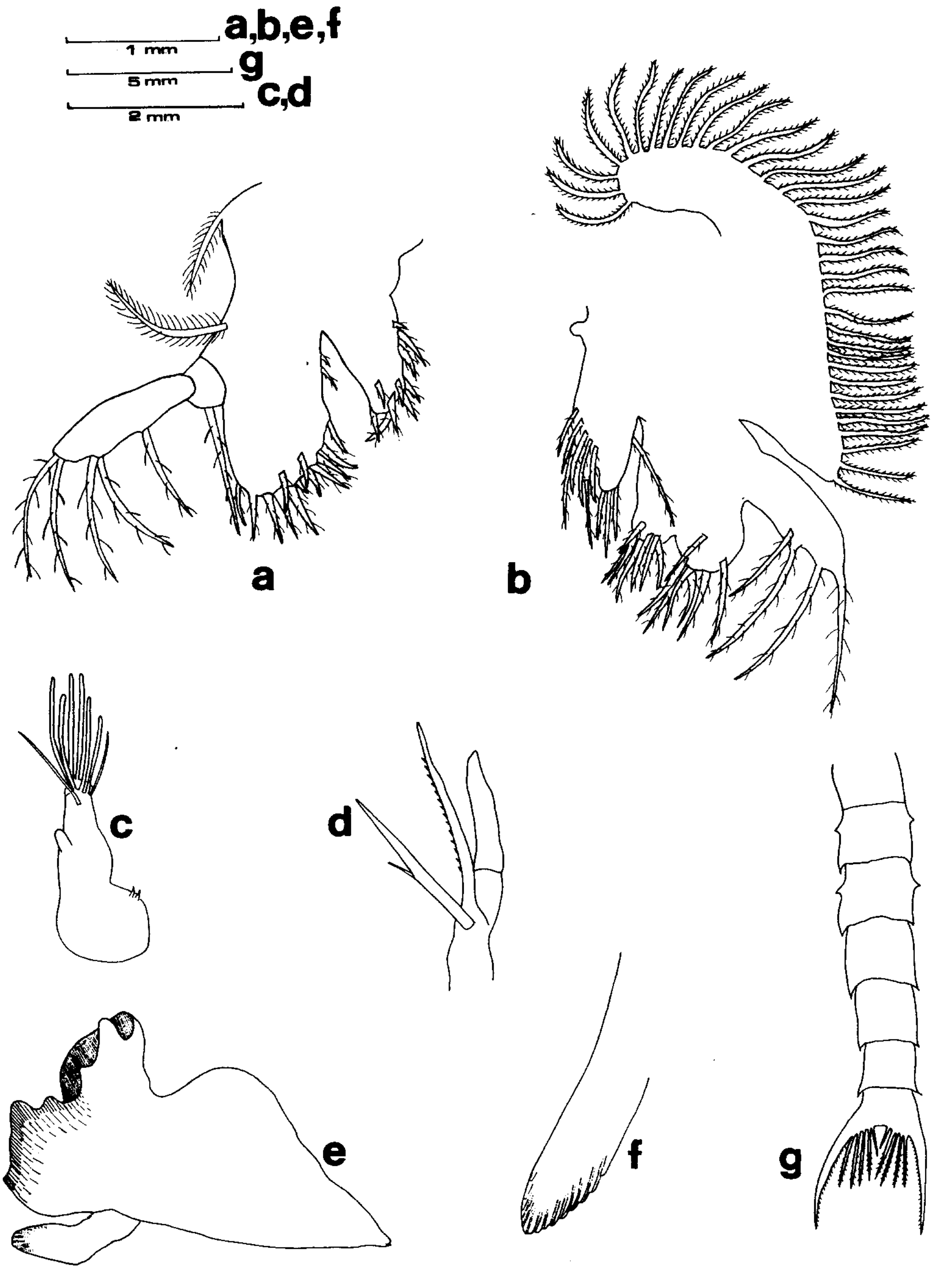

Fig. 1. C. granulata. Zoea V: A- Maxillule; C- Antennule; D- Antenna; Mandible; F- Pleods (vision of exopod setae); G- Abdomen and Telson (dorsal view).

In the individual cultures in which the larvae were fed exclusively with *Artemia* nauplii or with rotifers, it was possible to complete the whole larval phase using just one type of food and, in this case, there occurred no the alternative pathway of development.

In the mass cultures both paths of development occurred, and observed two types of zoeae IV,

Table 2. C. granulata. Description of the two types of zoeae IV identified in the present study.

	Zoea IVa (larger)	Zoea IVb (smaller)
Antenna	Endopod: almost the same length of spinous process	Endopod: half of the length of spinous process
Antennule	6 aestethascs + 2 setae	5 aestathascs + 2 setae
Mandible	Mandibular palp well developed	Without mandibular palp
Maxilla	Scaphognathite: 25 ps	Scaphognathite: 25 ps
	Endopod: 4 ps	Endopod: 4ps
	Basal endite: 14 ps	Basal endite: 11 ps
	Coxal endite: 7 ps	Coxal endite: 7 ps
Maxillule	Endopod bisegmented: 1–4 ps	Endopod bisegmented: 1–4 ps
	Basal endite: 12 ps	Basal endite: 8 ps
	Coxal endite: 6 ps - 1 spine in the basis	Coxal endite: 6 ps
Maxilliped 1	Basis: 10 ps	Basis: 8 ps
	Endopod 2-2-2-2-6 ps	Endopod: 2-2-2-2-6 ps
	Exopod: 10 ps	Exopod: 10 ps
Maxilliped 2	Basis: 4 ps	Basis: 4 ps
	Exopod: 10 pns	Exopod: 10 pns
	Endopod 0-1-6 ps	Endopod: 0-1-6 ps
Maxilliped 3	Developed (pereiopods)-start of visible segmentation under the cuticle.	Rudimentary
		Pereiopods: chelae rudimentary without segmentation
	Chelae well formed	
Telson	Last somite: 4 pairs of spines: 2 small spines	4 pairs of spines in the center
Abdomen	Long pleopods - setae visible through transparent carapace	Short pleopods, without indication of setae
Carapace	12 ps postero-lateral	12 ps postero-lateral
	3 ps postero-dorsal	3 ps postero-dorsal

PS: plumose setae
PNS: Plumose and natatory setae

that differed significantly ($P<0.05$) in measurements (Table 1). We named the 'most developed' stage (of larger size) as zoea IVa and the 'least developed', zoea IVb (following the process used by Criales & Anger, 1986).

Besides differences in biometric relationships, we also noted morphological differences between the two zoea IV stages, mainly in relation to the setation and morphology of the pereiopods (Table 2 and Fig. 2).

Of the 15 zoeae IVb separated in individual cultures, 14 molted to zoea V (one of which died on the 1st. day of the experiment). Of those surviving 10 reached the stage of megalopa, with a mean intermolt period of 5.2 days (from zoea V to megalopa). In the control group initiated with 20 zoeae I, none of the larvae presented an alternative path, molting directly from zoeae to megalopae.

The zoeae V showed morphological characteristics that were almost intermediate between those of zoeae IV and megalopae (Table 3). These characteristics can be seen in Figs 1 and 2.

Discussion

Various factors are considered responsible for the appearance of the supernumerical stage in the larvae of decapod crustaceans, for example, temperature (Wickins, 1972; Criales & Anger, 1986); salinity (Wickins, 1972; Knowlton, 1974; Criales & Anger, 1986), photoperiod (Wickens, 1972; Knowlton, 1974) and antibiotics (Criales & Anger, 1986) amongst others.

In the present work, environmental factors such as temperature, salinity, and photoperiod were main-

Table 3. C. granulata. Morphological differences between the zoea IV and zoea V stages.

	Zoea IV (Boschi *et al.*, 1967)	Zoea V (present study)
Carapace	Posterior border: 3 small setae	Posterior border: 3 ps (on each side)
	Postero-lateral border: ?	Postero-lateral border: 18 ps (on each side)
Abdomen	Somite 1: 2 or 3 dorsal setae	Processes with setae
	Somites 2 and 3: with spines	Somites 2 and 3: with lateral spines
	Pleopods: well visible	Pleopods: very developed
	Setae: ?	Setae of the exopod are visible under the cuticle
Telson	Processes: sides with 5 minute spines	Processes with a row of spines on the border
	4 pairs of larger spines with setae	
	2 pairs of smaller spines without setae	4 pars of larger spines with setae
		2 central spines, larger than in zoea IV, with setae
Antenna	Spinous process with small lateral spines	Spinous process with small lateral spines
	Exopod with one spine in the middle distal region	Exopod with one spine in the middle distal region
	Endopod: bisegmented	Endopod: bisegmented
Antennule	3 large aestethascs + 2 smooth setae	6 large aestethascs + 2 smooth setae
	Endopod: ?	Endopod: well visible
Mandible	Mandibular palp small and without setae	Mandibular palp well developed and without setae
Maxilla	Scaphognathite: 17–19 ps	Scaphognathite: 32–36 ps
	Endopod: bisegmented, with 4 ps	Endopod: 4 ps
	Basal endite: 12 ps	Basal endite: bilobed with 14 ps
	Coxal endite: 5 ps	Coxal endite: bilobate with spine at the basis
Maxillule	Endopod bisegmented: larger segment with 4 setae; smaller segment	Endopod bisegmented: larger segment with 5 ps; smaller segment with
a with one internal setae	1 internal ps well developed	
	Basal endite: 12 ps	Basal endite: 13 ps
	Coxal endite: 5 ps	Coxal endite: 10 ps
	Protopod: ?	Protopod: 2 ps well developed
Maxilliped 1	Basis: 6 ps in the internal region	Basis: 10 ps in the internal region
	Endopod: 5 somites: 2-2-2-2-6	Endopod: 5 somites: 2-4-2-2-6 ps
	Exopod: 10 ps	Exopod: 10 ps
Maxilliped 2	Basis: 3 ps	Basis: 4 ps
	Exopod: 10 pns	Exopod: 12 pns
	Endopod: 3 somites: 0-1-6 ps	Endopod: 3 somites: 0-1-5 ps
Maxilliped 3	Observed by transparency through carapace	Well developed, forming large volume under the carapace
Pereiopods	Well developed; 1st. pair with chelae well formed	Chelae well formed, with segmentation

PS: plumose setae
PNS: Plumose and natatory setae

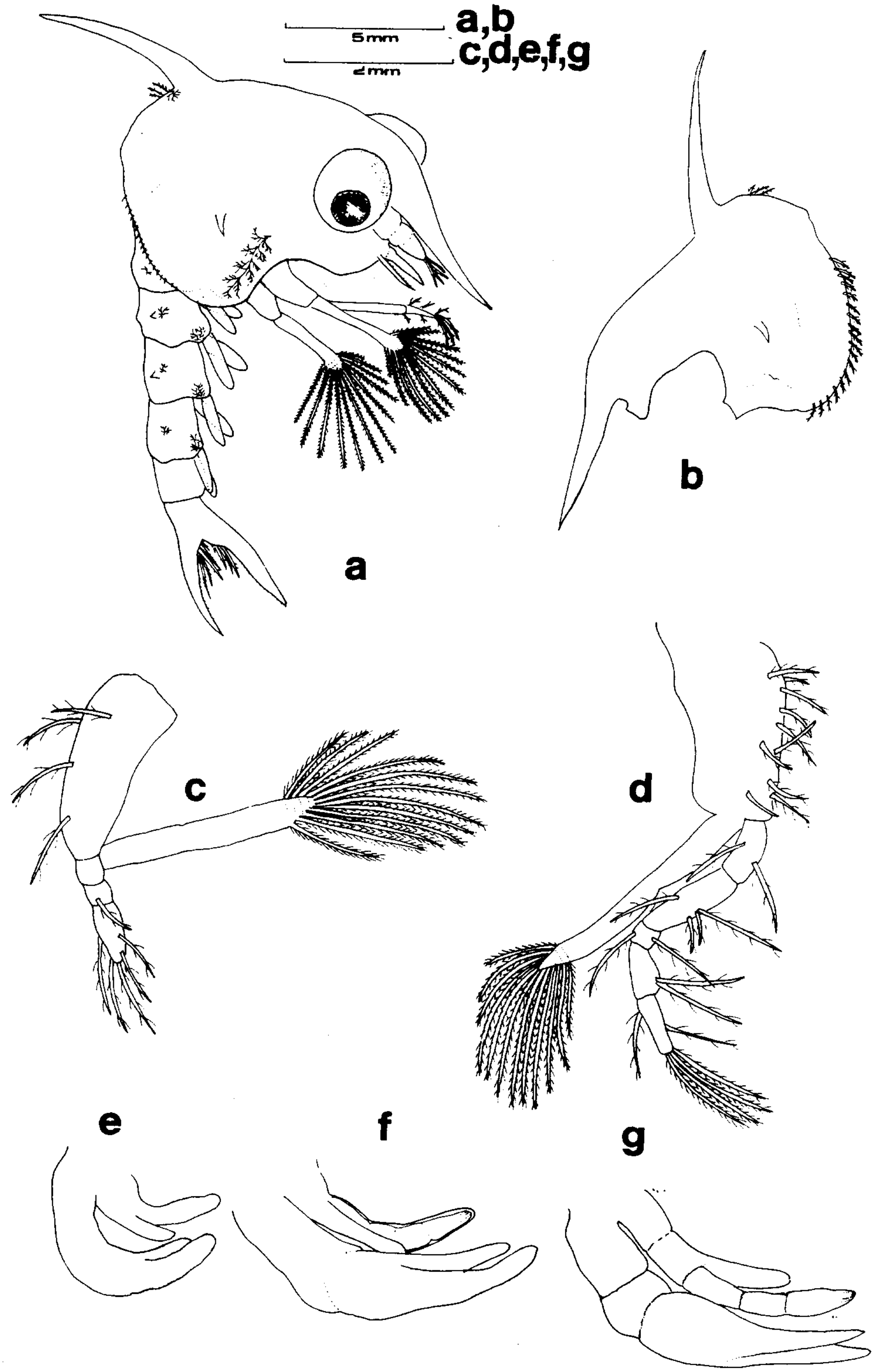

Fig. 2. *C. granulata.* Zoea V: A- Lateral view; B- Carapace; C- Maxilliped 1. Comparison among pereiopods: E- Zoea IVb; F- Zoea IVa; G- Zoea V.

tained constant, but variables such as feeding period (availability of food) and quality of diet could have interfered with the results.

Alterations in diet have already been reported as being capable of modifying the number of stages in larval development. Broad (1957), working with two species of Palaemonetes, concluded that the number of stages varied according to the quantity of food available. Costlow (1965) observed that when food was insufficient a variation in the number of stages or in small morphological characteristics could occur in *Calinectes sapidus* larvae.

In addition to the quantity of food available, the quality of diet is considered a cause of alteration in the number of larval stages. McConaugha (1982) concluded that diets with low and medium levels of lipids produced a high percentage of 'extra-numerous' stages in *Rithropanopeus harrissi*. Such premises were proved also for *Macrobrachium carcinus* larvae (Choudhury, 1971); *Palemon serratus* (Wickens, 1972; Goyanes, 1987); *Leander squilla* (Schulte, 1975); *Palaemonetes* spp. (Broad, 1957; Knowlton, 1974); *Crangon* spp. (Criales & Anger, 1986).

Besides nutritional/environmental factors, studied by Harms & Anger (1990), tendency of the larvae to pass through a defined number of stages could be hereditary. Sandifer & Smith (1979) suggested that variation in development could bring advantages in a prolonged planktonic larval phase. These advantages include a great potential for dispersion and an ability to colonize new habitats, in case unfavorable conditions arise. A variable planktonic existence time could permit a wider distribution of individuals of the same descendent. An extension of the molt cycle, with the addition of 'extra' stages, could be interpreted as a possible adaptation to extremely variable environments, increasing the possibility to find an appropriate habitat for metamorphosis (Forster, 1951; Montu *et al.*, 1990). As a rule, the variation of the planktonic larval phase incraeses the distribution area of the determined species and perhaps a reduction of the over-population in a determined area.

In the present study, with occurrence of a large percentage of zoea V in cultures fed with microalgae, we admit that the quality of the food and its possible nutritional deficiency for the larvae of *C. granulata* caused the alterations that we observed in the larval development. As a result, the larvae needed one more stage before completing their metamorphosis to megalopa. The majority (65%) of the series initiated with zoeae IV and fed with microalgae molted into this extra stage. This suggests that the later the stage, the larger the nutritional requirements of the larvae. We related this fact with the ecological role of megalopa: to select an adequate biotope for adult life.

In the mass cultures, where larval densities were elevated, inadequate and unfavorable conditions were created, which, according to Criales & Anger (1986), tend to increase the number of stages. Despite the larvae originating from various females, which diminished the possibility described by Montu *et al.*, (1990) that the nutritional state of the female could interfere in the development of the larvae, the hypothesis of heredity could still be considered. However, for satisfactory conclusions to be drawn, it would be necessary to make more experiments with various generations.

In contrast to some works that refer to the variability in larval development (Broad, 1957; Costlow, 1965; Montu *et al.*, 1990), the zoeae V from individual cultures did not evolve into megalopae. This could be explained by the probable nutritional deficiency of the diet (microalgae), because in the later experiments, initiated with 15 zoeae IVb, withdrawn from the mass cultures and fed since the eclosion with *Artemia* sp. nauplii, almost all (14) passed to the fifth zoeal stage and 66% of the initial number molted into megalopae.

Despite the initial inadequate conditions in mass cultures, causing the appearance of two types of zoeae IV, the subsequent separation of larvae into individual cultures and feeding with *Artemia* nauplii apparently created favorable conditions so that they succeeded in completing their development into megalopa.

It is concluded that the appearance of the supranumeral stage, zoea V is due to stressful conditions rather than to genetic factors. These conditions could arise due to nutritional factors (in terms of quantity-quality), causing irreversible harm (the larvae not succeeding to molt to megalopa stage), or by overcrowding, the damages in this case being reversible.

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