Juvenile development and growth patterns in the mud crab *Eurytium limosum* (Say, 1818) (Decapoda, Brachyura, Xanthidae) under laboratory conditions

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Abstract
The post-larval development of the mud crab *Eurytium limosum* was studied under laboratory conditions by using the offspring of ovigerous females collected at the Comprido River mangrove, SP, Brazil. The first crab stage is fully described and the juvenile development, until crab stage 10, is examined with emphasis on morphological change, sexual differentiation and growth patterns. The carapace of the first crab stage is nearly square as observed in other xanthids, becoming similar to adults only at stage 15. The sexes can be distinguished from stage four, based on the number of pleopods and their morphology. While the intermoult period increases, the moult percentage decreases at each stage. The abdominal allometric growth is sex-dependent, with males showing a negative \( b=0.71 \) and females an isometric \( b=0.95 \) relative growth pattern. Male gonopods undergo a positive allometric growth, and their shape changes remarkably until sexual maturity. The cheliped dentition can be observed after stage 4. Regardless of sex, most crabs have a molariform right cheliped, which is thought to aid the handling of asymmetric prey such as gastropods.

Keywords: Decapoda, Eurytium limosum, juvenile development, morphology, relative growth, Xanthidae

Introduction
A very particular kind of growth is found in crustaceans due to their rigid exoskeleton. The increase in body size occurs only during the moulting period, after ecdysis and before hardening of the tegument as a result of water uptake (Negreiros-Fransozo and Fransozo 1991). Ecdysis prevents any growth records, making impossible age determination by direct methods, such as counting the growth increment in fish otoliths or scales. Tagging methods are also limited due to ecdysis.

Laboratory rearing provides relevant information on the sequence of stages, moult increment, variation of size within each stage, intermoult period, and ontogenetic variations.
(Flores et al. 2002). Owing to rearing difficulties and low survival of juvenile crabs in the laboratory, the available information on post-larval ontogeny is much reduced compared to larval development. Also, according to Hebling et al. (1982), most authors who have reared larvae did not go further than from the megalop stage.

Most characters used in brachyuran crab identification are based upon mature adult morphology, because other growth phases are largely unknown (Franzoso and Negreiros-Fransozo 1987). Therefore, it is difficult and sometimes impossible to identify planktonic larvae, juvenile and immature stages of crabs. This lack of information makes larval and juvenile studies important, as they provide a greater knowledge for systematic classification and phylogenetics.

As far as xanthids are concerned, publications on juvenile post-larval stages are available for *Panopeus austrobesus* Williams, 1983 (described as *Panopeus herbstii* H. Milne Edwards, 1834) by Hebling et al. (1982); *Panopeus bermudensis* Benedict and Rathbun, 1891, *P. herbstii*, *Panopeus turgidus* (Rathbun, 1930) and *Eurypanopeus depressus* (Smith, 1869) by Martin et al. (1984); *Eriphia gonagra* (Fabricius, 1775) and *Eurypanopeus abbreviatus* (Smith, 1860) by Franzoso and Negreiros-Fransozo (1987); *Menippe nodifrons* Stimpson, 1859 by Franzoso et al. (1988), *Menippe mercenaria* (Say, 1819) by Tweedale et al. (1993); *Panopeus rugosus* H. Milne Edwards, 1880, *Hexapanopeus heblingii* Rodrigues and Loyola e Silva, 1998 and *Panopeus occidentalis* Saussure, 1857 by Rodrigues (1997); and, recently, *Hexapanopeus caribbaeus* (Stimpson, 1871) by Vieira (2000).

All larval stages and the first juvenile stage of the mud crab *Eurytium limosum* (Say, 1818) were studied by Kurata et al. (1981) and the tolerance of these larvae to salinity variation was studied by Messerknecht et al. (1991).

The aim of the present study is to provide a detailed morphological description, including sexual differentiation, and to provide estimates of age, carapace mean increment and relative growth patterns through the early juvenile stage sequence of *E. limosum*.

**Material and methods**

Ovigerous females of *E. limosum* were collected at the Rio Comprido mangrove (23°29′20″S, 45°09′53″W), Ubatuba, São Paulo, Brazil and taken to the laboratory in February 1999. They were kept in individual aquaria under natural environment conditions until larval hatching. The zoeae were reared in mass culture, with seawater salinity of 25‰, as suggested by Messerknecht et al. (1991), and at 24 ± 1°C temperature. After the moult to the megalop stage, the specimens were removed and held separately in 100-ml acrylic recipients containing 50 ml of filtered seawater under the same environmental conditions.

The water was changed, all acrylic containers were washed with fresh water and air dried before being used the following day; the larvae and early juvenile stages were fed on live *Artemia* nauplii. Shrimp and mussel were incorporated in the diet of more advanced stages. The specimens were checked for moults daily. The intermoult period was recorded and both exuviae and dead specimens were preserved in 70% ethanol. Exuviae were stained with chlorazol black and used for morphological examination, illustrations and measurements. The morphology of first juvenile crabs was illustrated and changes of carapace, antenna, antennule, mouthparts, pleopods, and pereiopods were recorded for each stage and sex.

The measurements included carapace width (CW) and length (CL); molariform cheliped propod length (ML) and height (MH); serriform cheliped propod length (SL) and height (SH), abdominal width (AW) and gonopod length (GL).
The ratio CW/CL was plotted against juvenile stage, and a logarithmic equation was fitted to this relationship in order to estimate the stage at which the shape of the juvenile carapace would become similar to the adult form. The average age at each stage, the carapace growth and the moult increment were also observed.

The relative growth of body parts was determined using the allometric equation:

\[ Y = aX^b \]  

(1)

The carapace width was considered the independent variable. Analysis of the allometric growth constant \( b \) gives information about the increase of a given organ in relation to a reference measure of size. When \( b=1 \) a condition of isometry applies, whereas negative and positive allometric growth are verified when \( b>1 \) and \( b<1 \), respectively.

Between-sex and between-growth phase comparisons of allometric relationships were carried out using covariance analyses (Zar 1996). If differences were not significant the data were grouped and the overall was calculated. Isometry was tested using a Student’s \( t \) test (\( H_0: b=1, \alpha=0.05 \)).

Voucher specimens have been deposited at the NEBECC (Group of Studies on Crustacean Biology, Ecology and Culture) collections, under the reference \( E. \limosum—\#0073 \).

**Results**

*Description of first juvenile stage (C1)*

The dorsal view of the first juvenile stage is shown in Figure 1.

**Carapace (Figure 1a, b).** Square; orbital and concave anterolateral margin with two anterolateral spinules (the anterior larger than the posterior), and bilobed front.

**Antennule (Figure 2a).** Peduncle three-segmented: proximal segment well developed with 15 simple setae; segment 2 with three simple setae; distal segment with three short, three sub-terminal long, and three terminal long simple setae. Endopod two-segmented: proximal segment without setae; distal segment with one subterminal, and two terminal simple setae. Exopod five-segmented: proximal segment with six aesthetascs; segment 2 with five aesthetascs, one long, and one short simple setae; segment 3 with four aesthetascs, and one simple seta; segment 4 with one subterminal simple seta; distal segment with one terminal simple seta.

**Antenna (Figure 2b).** Peduncle three-segmented; segments of peduncle larger than those of flagellum. Proximal segment with three marginal plumose, and one simple setae; segment 2 with three subterminal plumose setae; distal segment with one simple seta. Flagellum seven-segmented with 0, 3, 0, 4, 0, 4, 3 simple setae from proximal to distal segment.

**Mandible (Figure 3a).** With median tooth on differentiated inner margin. Palp two-segmented with three subterminal and five terminal plumose setae on distal segment.

**Maxillule (Figure 3b).** Endopod unsegmented with two marginal simple, and one terminal cuspidate setae. Basal endite with 12 terminal (three plumose and nine cuspidate), four intermediate plumose, four proximal plumose, and two basal plumose setae. Coxal endite
Figure 1. *Eurytium limosum*. Dorsal view of the first juvenile stage and carapace shape of early juvenile stages.
Figure 2. *Eurytium limosum*. First juvenile stage. (a) Antennula; (b) antenna.
with seven plumodenticulate and seven plumose setae. Protopodite with two simple and one plumose setae.

Maxilla (Figure 3c). Endopod unsegmented, with one long plumose seta. Basal endite bilobed: proximal lobe with one subterminal short simple, and six terminal long simple setae; distal lobe with one subterminal long and eight terminal setae. Coxal endite bilobed: proximal lobe with three simple, and one plumose setae; distal lobe with two marginal, two subterminal, and two terminal simple setae. Scaphognathite with 49–56 marginal plumose setae and 9–12 simple setae on lateral surface.

Maxilliped 1 (Figure 4a). Endopod unsegmented with three marginal plumose, and five or six terminal simple setae. Basal endite with four proximal simple, eight intermediate
simple and one plumodenticulate), and 13 terminal (11 plumose, one plumodenticulate, and one simple) setae. Coxal endite with 11 simple setae. Exopod two-segmented, proximal segment with two subterminal plumose setae; distal segment with six terminal long plumose setae. Epipod with 15 marginal long filamentous simple setae.

Maxilliped 2 (Figure 4b). Endopod four-segmented: proximal segment with nine (three plumose and six simple) setae; segment 2 with one short simple setae; segment 3 with one proximal simple, four subterminal plumose and one terminal simple setae; distal segment with two simple subterminal, and eight terminal cuspidate setae. Exopod two-segmented: proximal segment with 10 simple setae; distal segment with five simple setae. Protopod with one simple seta. Epipod with two simple setae.

Maxilliped 3 (Figure 4c). Endopod five-segmented, proximal segment with 19 simple setae; segment 2 with 19 simple, and two plumodenticulate setae; segment 3 with four simple, and seven plumodenticulate setae; segment 4 with three simple, and six plumodenticulate setae; distal segment with two simple, and four plumodenticulate setae. Exopod two-segmented: proximal segment with five simple setae; distal segment with two subterminal simple and four terminal long simple setae. Protopod with 36 simple setae. Epipod with eight simple and 20 marginal long filamentous simple setae.

Pleopods (Figure 5). Four pairs of pleopods without setae, and located ventrally from abdominal somites 2 to 5.

Pereopods (Figure 6). Chelipeds similar to those of adults, but without defined dentition, all segments stronger and larger than other pereopods; walking legs with scattered short simple setae.

Abdomen (Figure 7). Composed of six somites plus telson; all somites are wider than long and lateral margin is rounded with short scattered plumose setae.

The identification of early juvenile stages of xanthid species is difficult owing to their great similarity. Thus, several characters that might make it easier to identify the first 10 E. limosum stages among other xanthids are listed in Table I.

Figure 1b shows the changes of carapace shape throughout the stage sequence. Carapace measurements for each stage are given in Table II. It is apparent that at each ecdysis the carapace grows wider. The relationship between the ratio CW/CL and stage duration can be expressed by:

\[ R = 0.1638 \ln(S) + 1.05077 \]

suggesting that early post-larval E. limosum crabs can reach a carapace shape similar to that of the adults around stage 15.

Mean accumulated duration of each stage increases according to the logarithmic equation (Figure 8):

\[ S = 2.7186 \ln(D) - 4.95585 \]

Carapace size (Figure 9) also increases at each stage. On the other hand, moult increment decreases at each moult (Figure 10).

Based on pleopod morphology, sexual differentiation becomes recognizable from stage 4, as shown in Figure 4 (C4). Four pleopod pairs on abdominal somites 2–5 are found in crab
Figure 4. *Eurytium limosum*. First juvenile stage. (a) Maxilliped 1; (b) maxilliped 1; (c) maxilliped 3.
Figure 5. *Eurytium limosum*. Pleopods of early juvenile stages.

|                | PL$_2$ | PL$_3$ | PL$_4$ | PL$_5$ | PL$_6$ | PL$_7$ | PL$_8$ |
|----------------|--------|--------|--------|--------|--------|--------|--------|
| **Unsexed**    |        |        |        |        |        |        |        |
| C 1            |        |        |        |        |        |        |        |
| C 2            |        |        |        |        |        |        |        |
| C 3            |        |        |        |        |        |        |        |

|                |        |        |        |        |        |        |        |
| **Females**    |        |        |        |        |        |        |        |
| C 4            |        |        |        |        |        |        |        |
| C 5            |        |        |        |        |        |        |        |
| C 6            |        |        |        |        |        |        |        |

|                |        |        |        |        |        |
| **Males**      |        |        |        |        |        |
| C 7            |        |        |        |        |        |
| C 8            |        |        |        |        |        | 0.1 mm |

*Juvenile development of Eurytium limosum*
Figure 6. *Eurytium limosum*. Pereopods of first juvenile stage.
stages 1–3. After moulting to crab stage 4, females retain the four appendage pairs, which become biramous, while they are reduced to two pairs in males, located on the first and second abdominal somites.

The relative growth equations for early *E. limosum* stages are shown in Table III. As may be noticed in the relationship between CW and CL, changes in the carapace shape are similar between sexes and between early and late stages examined.

Sex-related differences can be also detected by examining the AW versus CW relationship. For early unsexable crab stages, a single equation indicating a negative allometric growth can be fitted. Females, however, showed an isometric growth after stage 4.

The allometric growth of cheliped propodus did not differ between sexes (*P* > 0.05), showing an isometric growth for all relationships analysed. However, after stage 4 the cheliped dentition can be clearly observed. Chelipeds were either molariform bearing crusher teeth, or serratiform with cutting teeth. Most crabs, regardless of sex, were right-handed for the molariform chela (85%). Handedness, however, was not frequent for both sexes.

**Discussion**

A carapace nearly as long as wide, with a slightly bilobed front, characterizes the first crab stage of *E. limosum*, as observed in other xanthid first crab stages. A dorsal view of the first crab carapace was described by Kurata et al. (1981) and Messerknecht et al. (1991). The carapace shape was comparable with the description provided herein, but carapace measurements differed among these reports. Other morphological differences from the description given by Messerknecht et al. (1991) could also be observed in the present study, probably due to natural differences between these populations.
Table I. *Eurytium limosum*: main morphological characters used in the identification of early juvenile stages.

|                | C1  | C2  | C3  | C4  | C5  | C6  | C7  | C8  | C9  | C10 |
|----------------|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|
| **Antennula**  |     |     |     |     |     |     |     |     |     |     |
| Endopod segment number | 2   | 2   | 2   | 2   | 3   | 3   | 3   | 3   | 3   | 3   |
| Exopod segment number  | 5   | 6   | 7   | 8   | 9   | 10  | 12  | 13  | 13  | 14  |
| **Antenna**     |     |     |     |     |     |     |     |     |     |     |
| Segment number   | 10  | 11  | 12  | 12  | 13  | 16  | 17  | 18  | 20  | 22  |
| Length (mm)      | 0.65| 0.76| 1.04| 1.26| 1.39| 1.67| 1.98| 2.11| 2.37| 2.66|
| **Maxillula**   |     |     |     |     |     |     |     |     |     |     |
| Number of setae on protopod base | 2   | 3   | 3   | 5   | 6   | 8   | 10  | 12  | 14  | 16  |
| **Maxilla**     |     |     |     |     |     |     |     |     |     |     |
| Number of marginal setae on exopod | 49–56 | 60–65 | 83–97 | 108–125 | 145–164 | 161–179 | 180–213 | 205–234 | 159–259 | 263–291 |
| Exopod length (mm) | 0.38 | 0.43 | 0.56 | 0.76 | 0.95 | 1.04 | 1.26 | 1.43 | 1.54 | 1.62 |
| **Maxilliped 1** |     |     |     |     |     |     |     |     |     |     |
| Number of terminal setae on endopod | 5–6  | 7   | 10–15| 18–22| 22–24| 27–30| 31–32| 41–42| 39–42| 48–50|
| Number of subterminal setae on endopod | 0   | 0   | 0   | 0   | 7–9 | 10–13| 17–20| 20–22| 27–28| 30–38|
| Exopod basal segment length (mm) | 0.35 | 0.41 | 0.55 | 0.67 | 0.82 | 0.96 | 1.13 | 1.29 | 1.41 | 1.49 |
| **Maxilliped 2** |     |     |     |     |     |     |     |     |     |     |
| Exopod basal segment length (mm) | 0.36 | 0.46 | 0.57 | 0.74 | 0.93 | 0.98 | 1.16 | 1.27 | 1.39 | 1.61 |
| **Maxilliped 3** |     |     |     |     |     |     |     |     |     |     |
| Exopod basal segment length (mm) | 0.34 | 0.39 | 0.52 | 0.70 | 0.78 | 0.92 | 1.08 | 1.18 | 1.28 | 1.47 |
As shown in Table IV, the adult carapace shape is reached later in the stage sequence compared to other xanthids. Growth patterns are, however, similar to those found in other crustaceans (Kurata 1962; Hartnoll 1982), in which the intermoult period and carapace size increase, while the percentage moult increment decreases at each stage. One such example is the crab *M. mercenaria*. Yet, in this case the intermoult period was shown to be influenced by environmental conditions (Savage 1971; Yang and Krantz 1976; Tweedale et al. 1993).

Any conclusion on natural growth patterns based on laboratory rearing should be interpreted with caution (Hartnoll 1982; Tweedale et al. 1993). Field and laboratory

### Table II. *Eurytium limosum*: average values of carapace size.

| Juvenile stages | Carapace measurements (mm) | CW/CL |
|-----------------|----------------------------|-------|
| C1              | CW 1.27 CL 1.20            |       |
| C2              | CW 1.62 CL 1.41            |       |
| C3              | CW 2.06 CL 1.78            |       |
| C4              | CW 2.74 CL 2.17            |       |
| C5              | CW 3.66 CL 2.83            |       |
| C6              | CW 4.16 CL 3.06            |       |
| C7              | CW 5.11 CL 3.68            |       |
| C8              | CW 5.55 CL 3.96            |       |
| C9              | CW 7.03 CL 4.95            |       |
| C10             | CW 7.18 CL 5.02            |       |
| Adults\(^a\)    | CW 22.78 CL 15.24          |       |

CW, carapace width; CL, carapace length; CW/CL: ratio between carapace width and length. \(^a\)Based on crabs collected in the field.

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Any conclusion on natural growth patterns based on laboratory rearing should be interpreted with caution (Hartnoll 1982; Tweedale et al. 1993). Field and laboratory

### Figure 8. *Eurytium limosum*. Age at the different juvenile stages.
conditions differ in many ways, and it is known that environmental factors affect growth rate (Hartnoll and Gould 1988; Hines 1989; O'Connor 1990). In this case, moult increment percentage of individuals reared in the laboratory may be equivalent to (Kurata

![Figure 9. Eurytium limosum. Growth curve for early juvenile stages.](image)

![Figure 10. Eurytium limosum. Percentage moult increment against juvenile stage.](image)

Table III. *Eurytium limosum*: allometric growth results.

| Variable | Sex | N  | Linear regression              | $r^2$ | Allometric coefficient$^a$ |
|----------|-----|----|--------------------------------|-------|---------------------------|
| CL       | US  | 49 | $\log CL = 0.75 \log CW - 0.01$ | 0.98  | -                         |
|          | S   | 83 | $\log CL = 0.83 \log CW - 0.02$ | 0.98  | -                         |
|          | US  | 42 | $\log AW = 0.77 \log CW - 0.54$ | 0.85  | -                         |
|          | ♂   | 30 | $\log AW = 0.71 \log CW - 0.48$ | 0.77  | -                         |
|          | ♀   | 55 | $\log AW = 0.95 \log CW - 0.61$ | 0.96  | 0                         |
| MP       | Length | S  | $\log MPL = 0.99 \log CW - 0.21$ | 0.97  | 0                         |
|          | Height | S  | $\log MPH = 1.01 \log CW - 0.56$ | 0.96  | 0                         |
| SP       | Length | S  | $\log SPL = 0.99 \log CW - 0.23$ | 0.97  | 0                         |
|          | Height | S  | $\log SPF = 1.03 \log CW - 0.62$ | 0.96  | 0                         |
|          | GL   | ♀  | $\log GL = 1.79 \log CW - 1.29$ | 0.96  | +                         |

CL, carapace length; AW, abdomen width; MP, molariform propodus; SP, serratiform propodus; GL, gonopod length; US, unsexed; S, sexed; $r^2$, determination coefficient. $^a$Results of tests against the isometric condition ($P<0.05$): 0, isometry; −, negative allometry; +, positive allometry.
Table IV. Juvenile stage at which the carapace shape reaches the adult morphology for Brazilian xanthid species.

| Species                  | Stage | Author                                      |
|--------------------------|-------|---------------------------------------------|
| Eriphia gonagra          | I     | Fransozo and Negreiros-Fransozo (1987)      |
| Eurypanopeus abbreviatus | VII   | Fransozo and Negreiros-Fransozo (1987)      |
| Panopeus austrobesus     | XI    | Hebling et al. (1982)                       |
| Hexapanopeus caribbeaus  | XI    | Vieira (2000)                               |
| Eurytium limosum         | XV    | Present study                               |

1962; Tagatz 1968), smaller (Hiatt 1948; Savage and McMathan 1968; Savage 1971; Hogarth 1975) or larger than moult increments of animals in the field (Chittleborough 1976).

Dimorphic abdominal growth is commonly reported in studies on the relative growth of brachyurans. Positive allometric growth of the female abdomen has usually been associated with morphological requirements for reproduction in adults. In this manner, the greater allometric level recorded for young females leads to a broad abdomen, in which the incubation of eggs take place. The larger the female, the larger capacity for carrying eggs thus increasing its reproductive potential (Hartnoll 1974).

The prevalence of a right molariform cheliped was also observed in early *M. mercenaria* juveniles (Savage and McMathan 1968) and *E. limosum* adult crabs (Guimaraes 2002), which is probably related to the feeding habit of some predatory crabs, namely to handle asymmetric prey such as gastropods (Abby-Kalio and Warner 1989; Lee 1995). Vernberg and Costlow (1966) found similar results for *Uca* and verified by running breeding experiments that handedness is probably inherited. Hamilton et al. (1976) observed that, early in its post-larval ontogenesis, the blue crab *Callinectes sapidus* Rathbun, 1896 bears a right molariform and a left serratiform claw, but the incidence of right-handedness decreased in later stages.

The higher allometric coefficient of gonopods in males suggests a fast initial development of these appendages, which will undergo further remarkable changes until sexual maturity.

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