Morphology and growth of the larval stages of *Geograpsus lividus* (Crustacea, Brachyura), with the descriptions of new larval characters for the Grapsidae and an undescribed setation pattern in extended developments

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Abstract

Among the eight currently recognized genera and forty species belonging to the brachyuran crab family Grapsidae (Thoracotremata), the complete larval development is only known for three species of *Metopograpsus*. In the present study, we investigated the larval development of *Geograpsus lividus* originating from Jamaica and reared under controlled conditions in the laboratory. It consists of 8 zoeal stages and the megalopa, representing the longest recorded developmental pathway for any brachyuran. Although long developments had been suggested for some species, based on specimens collected from the plankton, these were never confirmed by laboratory culture. In the present study, zoeal growth (measured as increase in body size, dry mass, and contents of carbon, nitrogen and hydrogen) is quantified, and morphological and meristic characters of the larval stages of *G. lividus* are described and illustrated. The development from hatching to the end of the zoeal phase took two months. During this time span, larval size (cephalothorax length) increased 4.4-fold, while the various measures of biomass increased by factors of 57-72. Morphologically, the larvae present most characters previously established for the family Grapsidae. However, the two last zoeal stages show new features which differ from the typical setation pattern known from grapsid species with only 5 zoeal stages. These were found in the number of natatory setae on the exopods of the maxillipeds, and in the setation of the basis of the first maxilliped. Other characters, which had previously only been described for zoeae of *Pachygrapsus* and attributed to *Planes*, were observed also in *G. lividus* and could be confirmed as common features for the Grapsidae. Moreover, the larvae of *G. lividus* present a spinulation on the lateral and rostral spines of the cephalotorax. This character is recorded for the first time in grapsid crabs. A comparison of these observations is made with those based on terminal zoeal stages of species belonging to other brachyuran families, where similar characters have been documented.

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Introduction

The family Grapsidae MacLeay, 1838 presently consists of 40 species distributed among 8 genera according to Ng *et al*. (2008): *Geograpsus* Stimpson, 1858; *Goniopsis* De Haan, 1833; *Grapsus* Lamarck, 1801; *Leptograpsodes* Montgomery, 1931; *Leptograpsus* H. Milne Edwards, 1853; *Metopograpsus* H. Milne Edwards, 1853; *Pachygrapsus* Randall, 1840; and *Planes* Bowdich, 1825. For this family, data on larval development and growth are scarce and most larval descriptions deal only with the first zoeal stages, while complete larval developments are only known for three species of *Metopograpsus* (see Kakati 1982; Fielder and Greenwood 1983; Pasupathi and Kannupandi 1986). According to Ingle (1987) this lack of complete larval developments observed in the laboratory is probably due to the difficulties of rearing these small larvae.

Despite the fact that knowledge on larval morphology of the family Grapsidae is far from complete, Cuesta *et al.* (1997), Cuesta and Schubart (1999) and Cuesta *et al*. (2006) showed that zoeal and megalopa stages of all grapsid genera (except *Leptograpsodes* with no larval data known) presents a combination of consistent morphological characters that allows their distinction from the rest of "grapsoid" families. This morphological set of characters had been corroborated in all known first zoeal and megalopa stages, but due to the lack of descriptions of the complete zoeal phase for 6 out of the 8 grapsid genera, the rest of proposed zoeal characters, are awaiting confirmation.

The number of larval stages is variable in many decapod species, but has usually been considered constant and species-specific in Brachyura (see Anger 2001). However, there are reports of additional zoeal stages in Brachyura, especially in estuarine intertidal species, belonging to Portunoidea, Xanthoidea, Calappoidea, Parthenopoidea, Grapsoidea and Ocypodoidea (see Montu *et al.* 1990; Anger 1991, 2001; Rieger 1998, Spivak and Cuesta 2009, and references therein). In both cases, additional last stages and for the last zoeal stage of long developmental pathways, the corresponding zoeal stages show changes in the expected setation pattern. Until now this feature had only been reported in Grapsidae for the species *Pachygrapsus marmoratus* (Cuesta and Rodríguez 2000).

The first zoeal stage of *Geograpsus lividus* from the Pacific coast of Panama and Gulf of Mexico were described by Cuesta and Schubart (1999) and Guerao *et al.* (2001), respectively. In the present study, the complete larval development of *G. lividus* originating from Jamaican material is described and illustrated in detail from laboratory-reared material, zoeal growth rates (measured as increments in body size and biomass) are provided and compared with those previously observed in other brachyuran crab species with an extended mode of larval development, and larval morphology is compared with that known from other Grapsidae and further brachyuran families that pass through 6 or more zoeal stages.

Material and Methods

An ovigerous female *Geograpsus lividus* was collected on March 20, 2003, on a sandy beach with scattered rocks in Discovery Bay (Jamaica) and transported live to the Helgoland Marine Biological Station (Germany). Larvae hatched on March 29th. They were mass-reared at constant temperature (24°C), salinity (32‰) and an artificial 12:12 h light:dark cycle, using unaerated bowls (400 ml) at initial densities of 70 (zoea I-II), 50 (zoea III-IV), 30 (zoea V-VI) or 20 (zoea VII-VIII) individuals per bowl, respectively. In daily intervals, water and food (*Artemia* spp., ca. 10 freshly hatched nauplii / ml) were changed, and the larvae were checked for moulting and mortality. Freshly moulted larvae were separated from those moulting later and transferred to another rearing bowl, so that each bowl exclusively contained larvae being in the same stage and having the same age within a given stage. Samples of larvae and exuviae were fixed in 4 % formaldehyde in seawater.

Larval biomass was measured immediately after hatching (zoea I, 0 days) and at the end of the zoeal phase (zoea VIII, 11 days; or 60 days after hatching), so that zoeal growth could be expressed in terms of increments in dry mass (W), carbon, hydrogen, and nitrogen (collectively, CHN), following standard techniques (Anger and Harms 1990). Samples of larvae were briefly rinsed in distilled water, blotted on fluff-free Kleenex™ paper for optical use, transferred to pre-weighed tin cartridges, and stored frozen at –18°C. Later, the samples were freeze-dried in a Lyovac GT-2E vacuum apparatus, weighed to the nearest 0.1 µg on a Sartorius SC microbalance, and analysed with an Elementar Vario Micro CHN Analyser using acetanilid as a standard. Each set of measurements comprised n = 5 replicate determinations with 30 (zoea I) or 2 (zoea VIII) individuals each.

Dissections were made under a Wild MZ6 stereo microscope and drawings and measurements were carried out using a Zeiss Axioskop compound microscope equipped with a *camera lucida*. Semi-permanent mounts were made of whole larvae. All measurements were taken with an ocular micrometer. Drawings were based on 5-8 larvae, and size measurements on 10 larvae per stage. In zoeae, rostro-dorsal length (rdl) was measured from the tip of the rostral spine to the tip of the dorsal spine; cephalothorax length (cl) from the base of the rostrum to the posterior margin; cephalothorax width (cw) as the greatest distance across the cephalothorax in zoea I, and as the distance between the tips of lateral spines in zoea II-VIII. Furcal length (fl) was deduced from an imaginary line across the base of the outer seta in the posterior margin of the telson to the furcal tip; basal telson length (bt), from a line across the anterior margin to the posterior margin of the telson (base of the outer seta). In the megalopal stage, cephalothorax length (cl) was measured from the base of the rostrum to the posterior margin, and cephalothorax width (cw) as the maximum width.

Long aesthetascs of the antennules, the long natatory setae on the distal exopod segments of the first and second maxillipeds, and on the exopod of first and fourth pleopods, and uropod are drawn truncated. Description and figures are arranged according to the standards proposed by Clark *et al*. (1998).

Samples of larvae (zoea I to megalopae) of *Geograpsus lividus* were deposited at the Smithsonian Natural History Museum of Washington, under the catalog number ###### (pending).

RESULTS

Larval culture

Minimum duration of the complete zoeal phase (stages I-VIII combined) was 60 days. The duration of the successive stages increased from 6-7 days in stages I-V to 8, 9 and 11 days in stages VI, VII and VIII, respectively. All larvae died in the moult from the zoea VIII to the megalopa stage or within 2 days thereafter.

Size growth

Larval body size (measured as cephalothorax length, CL) increased exponentially both as a function of the number of larval instars and of the time of development (Fig. 1). From hatching to the onset of the zoea VIII stage, CL increased from 0.50±0.02 to 2.20±0.02 mm, i.e. by a factor of 4.4.

Biomass growth

During the two months of zoeal development from hatching (zoea I, 0 days) to the day of moulting of the zoea VIII stage to the megalopa, the larvae showed in all measures of biomass a substantial growth, with a 57 to 73-fold increase in total dry mass (W) and CHN (Table 1). It was highest in W, lowest in the N fraction, and intermediate in the C and H contents. When

CHN is considered in relation to total W, significantly decreasing percentage values occurred in all three measures of organic biomass, indicating an increasing proportion of inorganic constituents within W. Within the organic fraction, a relatively low growth factor in the N fraction and a significantly increasing C:N mass ratio (from 4.22 to 4.52) indicated a proportionally stronger accumulation of lipids in relation to the protein content.

Larval description

The first zoeal stage and megalopa of *Geograpsus lividus* is described completely. For the subsequent stages only the main differences from the first zoea are described. In Figures 7 and 8, maxillule of zoea III-VI and maxilla of zoea II-VI, respectively, are not shown, because they differ only in size and additional setae. Similarly, in Figures 10 and 11, first maxilliped and second maxilliped of the zoea II – VI, respectively, are not shown, because no differences in relation to the zoea I were found, they differed only in size. Megalopae reared did not present a complete development of pereiopods, with typical spinulation and setation not completely evaginated, therefore these appendages have not been describe them and illustrated since they cannot be considered a normal morphology for this stage.

Geograpsus lividus (A. Milne-Edwards, 1837)

Figures (2-18)

Zoea I

Pautsch (1965), figures 1-2; Cuesta and Schubart (1999), pp. 165-169, figures1-3; Guerao *et al*. (2001), p. 113, figure 5.

Dimensions: rdl: 0.67± 0.02 mm; cl: 0.50± 0.02 mm; cw: 0.36± 0.03 mm.

Cephalothorax (Fig. 2a): Globose, smooth and without tubercles. Dorsal and rostral spines short, stout and smooth; lateral spines minute, visible as rounded knob-like projections. Pair of dorsolateral simple setae present. Anterodorsal, posterior and ventral margin without setae. Eyes sessile.

Antennule (Fig. 5a): Uniramous. Endopod absent. Exopod unsegmented, with 3 aesthetascs (2 long and 1 think and shorter) and 1 simple seta.

Antenna (Fig. 6a): Protopod process well developed, slightly longer than rostral spine, with two rows of 5-6 spines increasing in size distally. Endopod absent. Exopod present as a small protuberance with 1 simple seta.

Mandible: Incisor and molar process present. Palp absent.

Maxillule (Fig. 7a): Coxal and basial endites with 6 plumose and 5 (3 plumodenticulate cuspidate, 2 plumodenticulate) setae respectively. Endopod 2-segmented, proximal segment with 1 plumodenticulate seta, distal segment with 1 medial, 2 subterminal and 2 terminal plumodenticulate setae. Exopodal seta absent.

Maxilla (Fig. 8a): Coxal endite bilobed with 5 (2 plumodenticulate, 3 plumose) + 4 (1 plumodenticulate, 3 plumose) setae. Basial endite bilobed with 5 (2 plumodenticulate, 3 plumose) + 4 (3 plumodenticulate, 1 plumose) setae. Endopod unsegmented, bilobed, with 2+2 long plumodenticulate setae. Scaphognathite with 4 marginal plumose setae and a long setose posterior process.

First maxilliped (Fig. 10a): Coxa with 1 simple seta. Basis with 8 simple setae arranged 2+2+2+2. Endopod 5-segmented with 1, 2, 1, 2, 5 (1 subterminal and 4 terminal) setae. Exopod incompletely segmented with 4 long terminal plumose natatory setae.

Second maxilliped (Fig. 11a): Coxa without setae. Basis with 4 simple setae arranged 1+1+1+1. Endopod 3-segmented with 0, 1, 5 setae. Exopod incompletely segmented with 4 long terminal plumose natatory setae.

Third Maxilliped. Absent.

Pereiopods. Absent.

Pleon (Figs. 14a, 16a): Five abdominal somites. Dorsolateral knobs on somites 2-4 (very small on somite 4); somites 2-5 with posterolateral processes and a pair of setae on posterodorsal margin. Pleopods absent.

Telson (Figs. 14a, 16a). Three pairs of stout serrulate setae on inner posterior margin. Two minute lateral spines at outer base of each furcal arm; distal part of furcal arms spinulated. bt/fl>1.

Zoea II

Dimensions: rdl= 1.37± 0.02 mm; cl= 0.62± 0.01 mm; cw = 0.80± 0.01 mm.

Cephalothorax (Fig. 2b): Rostral spine longer than antenna and with distal scale-like protuberances. Lateral spines well developed. Two pairs of anterodorsal setae, and a pair of simple setae on dorsal spine. Each ventral margin with one seta. Eyes stalked.

Antennule. Exopod with 4 terminal aesthetascs and 2 terminal minute setae.

Antenna. With two rows of 10-11 spines.

Maxillule (Fig. 7b). Basial endite with 7 setae. Exopodal seta present.

Maxilla. Scaphognathite with 8 plumose marginal setae.

First Maxilliped. Exopod with 6 long terminal plumose natatory setae.

Second Maxilliped. Exopod with 6 long terminal plumose natatory setae.

Pleon (Figs. 14b and 16b). Somite 1 with one mid-dorsal seta.

Telson (Figs. 14b and 16b). Lateral spines on furcal arms absent; bt/fl >1.

Zoea III

Dimensions: rdl= 1.9± 0.03 mm; cl= 0.67± 0.02 mm; cw = 1.05± 0.01 mm.

Cephalothorax (Fig. 2c): Lateral spines with small denticles. Three pairs of anterodorsal setae. Dorsal spine with 3-4 pairs of setae and orange-coloured and scaly surface distally. Each ventral margin with 2 setae.

Antennule. Exopod with 4 terminal aesthetascs.

Maxilla. Scaphognathite with 11 plumose marginal setae.

First Maxilliped. Exopod with 8 long terminal plumose natatory setae.

Second Maxilliped. Exopod with 8 long terminal plumose natatory setae.

Pleon (Figs. 14c,16c). Somite 1 with 2 mid-dorsal setae. Somite six now present, without setae.

Telson (Figs. 14c,16c). bt/fl<1.

Zoea IV

Dimensions: rdl= 2.5± 0.03 mm; cl= 0.87± 0.01 mm; cw = 1.25± 0.02 mm.

Cephalothorax (Fig. 2d): Four pairs of anterodorsal setae. Dorsal spine with 12 setae. Each ventral margin with 3 setae.

Antennule. Exopod with 4 terminal aesthetascs and one minute seta.

Maxillule. Coxal endite with 7 setae; basial endite with 9 setae.

Maxilla (Fig. 8b). Scaphognathite with 16 plumose marginal setae.

First Maxilliped. Endopod segment 5 with one additional seta. Exopod with 9 long terminal plumose natatory setae.

Second Maxilliped. Exopod with 10 long terminal plumose natatory setae.

Pleon (Figs. 14d, 16d). Somite 1 with 3 mid-dorsal setae.

Telson (Figs. 14d, 16d). Posterior margin with 3-4 (3+4 or 4+4) serrulate setae; length of the inner setae (in the case of 4 setae) less than half of the length of the proximal ones. bt/fl<1.

Zoea V

Dimensions: rdl= 3.7± 0.03 mm; cl= 1.10± 0.02 mm; cw = 1.55± 0.02 mm.

Cephalothorax (Fig. 2e). Dorsal spine with 20-21 setae; each ventral margin with 4 setae.

Antennule (Fig. 5b). Exopod with 5 terminal aesthetascs and one minute seta.

Maxillule (Fig. 7c). Epipod seta present. Basial endite with 10 setae; epipod seta present.

Maxilla. Coxal endite with 5-6+4 setae. Scaphognathite with 20 plumose marginal setae.

First Maxilliped. Endopod segment 5 with one additional seta. Exopod with 10 long terminal plumose natatory setae.

Second Maxilliped. Exopod with 12 long terminal plumose natatory setae.

Pleon (Figs. 15a, 17a). Somite 6 longer.

Telson (Figs. 15a, 17a). Posterior margin with 4 setae, length of the inner setae more than half of the other setae. bt/fl<1.

Zoea VI

Dimensions: rdl= 5.00± 0.02 mm; cl= 1.20± 0.02 mm; cw = 1.80± 0.01 mm.

Cephalothorax (Fig. 3a). Dorsal spine with 23-24 setae. Each ventral margin with 5 setae; each posterior margin with one simple seta.

Antennule (Fig. 5c). Exopod with 2 lateral minute setae, and with one subterminal and 6 terminal aesthetascs, and one terminal minute seta.

Antenna (Fig. 6c). Endopod bud present.

Maxillule. Coxal endite with 9 setae. Basial endite with 15 setae.

Maxilla. Coxal endite with 7-8+5 setae. Basial endite with 6+6 setae. Scaphognathite with 26-27 setae.

First maxilliped. Endopod distal segment with 8 setae. Exopod with 11-12 long plumose natatory setae on distal segment.

Second maxilliped. Exopod distal segment with 15 setae.

Third Maxilliped. Present as undifferentiated buds.

Pereiopods. Present as undifferentiated buds.

Pleon (Figs 15b, 17b). First somite with 5 long mid-dorsal setae.

Telson (Fig 15b). Posterior margin with 4-5 pairs of setae, inner setae (in the case of 5 setae) small and simple. bt/fl>1.

Zoea VII

Dimensions: rdl= 5.72± 0.02 mm; cl= 1.82± 0.02 mm; cw = 2.30± 0.01 mm.

Cephalothorax (Fig. 3b). Dorsal spine with 26 setae; 5 pairs of antero-dorsal setae each ventral margin with 6 setae. Each posterior margin with 2 simple setae.

Antennule (Fig. 5d). Endopod bud present. Exopod with 3 lateral minute seta, and with 6 subterminal and 6 terminal aesthetascs.

Antenna (Fig. 6d). Endopod elongated reaching the middle of the protopod process.

Maxillule. Coxal endite with 10 setae. Basial endite with 18 setae.

Maxilla. Coxal endite with 9+5 setae. Basial endite with 7+8 setae. Scaphognathite with 33-34 setae.

First maxilliped (Fig. 10b). Coxa with 2 setae. Endopod distal segment with 9 setae. Exopod with 14 long plumose natatory setae on distal segment.

Second maxilliped (Fig. 11b). Coxa with 1 seta. Exopod with 19 setae.

Third maxilliped (Fig 12a). Present, rudimentary and biramous.

Pereiopods (Fig. 13a). Unsegmented, elongated and chelipeds bilobed.

Pleon (Fig. 15d, 17d). First somite with 7 long mid-dorsal setae. Somite 6 with a pair of postero-dorsal setae. Pleopods presents as buds.

Telson (Fig. 15d). Posterior margin with 5-6 pairs of setae. bt/fl>1.

Zoea VIII

Dimensions: rdl= 7.10± 0.03 mm; cl= 2.20± 0.02 mm; cw = 2.65± 0.02 mm.

Cephalothorax (Fig. 3c). Dorsal spine with 30-32 setae. Rostral spine with strong spines on distal part. Eight pairs of antero-dorsal setae. Each ventral margin with 7 setae, and each posterior margin with 12 simple setae.

Antennule (Fig. 5e). Biramous, endopod unsegmented. Exopod with 6 lateral plumose setae, and with 12 subterminal and 6 terminal aesthetascs.

Antenna (Fig. 6e). Endopod 2-segmented and longer than protopod (spinous process).

Mandible (Fig. 4c). Unsegmented palp bud present, without setae.

Maxillule (Fig. 7d). Coxal endite with 14 setae. Basial endite with 23-24 setae.

Maxilla (Fig. 8c). Coxal endite with 11+5 setae. Basial endite with 9+10; scaphognathite with 40-44 setae.

First maxilliped (Fig. 10c). Coxa with 3-5 setae. Basis with 10 setae arranged 2+2+3+3 (in some cases 2+2+4+3, 2+2+3+4 and 2+2+4+4). Endopod distal segment with 9-10 setae. Exopod with 18 (4 subterminal and 14 terminal) long plumose natatory setae on distal segment.

Second maxilliped (Fig. 11c). Endopod with 0,1,5 setae (some cases with setation 1,1,5; 0,1,6, or 5-segmented: 0,1,0,1,5). Exopod with 19-22 plumose setae.

Third maxilliped (Fig. 12b). Epipodite present, with 0-3 setae. Endopod unsegmented with 2 simple setae. Exopod unsegmented with one simple terminal setae.

Pereiopods (Fig. 13b). Chelipeds and pereiopods 2-5 incompletly segmented.

Pleon (Fig. 15d, 17d). First somite with 10 long mid-dorsal and 2 postero-dorsal setae. Somites 2 and 3 with a pair of dorso-medial setae. Somites 4 and 5 with 2 pairs of dorso-medial setae. Pleopods buds elongated, endopod buds present.

Telson (Fig. 15d). Posterior margin with 6 pairs of setae, inner setae small and simple. One pair of dorso-medial setae. bt/fl>1.

Megalopa

Dimensions: cl= 2.70± 0.03 mm; cw = 2.25± 0.02 mm.

Cephalothorax (Fig. 4a). Longer than broad, narrowing anteriorly and without spines. Dorsal surface smooth. Rostrum strongly deflected ventrally. Setation as illustrated.

Antennule (Fig. 5f). Peduncle 3-segmented, with 13,5,1 setae, respectively. Endopod 2-segmented with one subterminal and 3 terminal setae on distal segment. Exopod 4-segmented, with 0,13,10,5 aesthetascs and 0,1,2,2 setae, respectively.

Antenna (Fig. 6f). Peduncle 3-segmented, with 4,4,3 setae, respectively. Flagellum 8-segmented, with 0,0,4,2,5,2,3,4 setae, respectively.

Mandible (Fig. 4d). Palp 2-segmented, with 11 terminal setae on distal segment.

Maxillule (Fig. 9a). Coxal endite with 19 setae. Basial endite with 30-31 setae. Endopod unsegmented with 5 setae.

Maxilla (Fig. 9b). Coxal endite bilobed, with 16+7 setae. Basial endite bilobed with 11+16 setae. Endopod unsegmented, with 3 basal plumose setae. Scaphognathite with 75-77 plumose marginal setae and 4 lateral setae.

First maxilliped (Fig. 10d). Epipod with 20-22 long setae. Coxal endite with 24 setae. Basial endite with 17 setae. Endopod unsegmented with 4 setae. Exopod 3-segmented, proximal segment with 3 distal plumose setae, distal segment with 5 long terminal plumose setae.

Second maxilliped (Fig. 11d). Epipod with 10 long setae. Coxa and basis not differentiated, without setae. Endopod 4-segmented with 2,1,7,12 setae, respectively. Exopod 2-segmented, proximal segment with 4 setae, distal segment with 5 terminal plumose setae.

Third maxilliped (Fig. 12c). Epipod elongated, with 39-40 setae. Coxa and basis not differentiated, with 18 setae. Endopod 5-segmented, ischium, merus, carpus, propodus and dactylus with 16, 12, 10, 12, 15 setae, respectively. Exopod 2-segmented, proximal segment with 4 setae and distal segment with 4 long terminal plumose natatory setae.

Sternum (Fig. 4b). Setation as shown.

Pleon (Fig. 18a,b). Somites 2-5 each with pair of well developed biramous pleopods. Setation as shown.

Pleopods (Fig. 18d,e). Endopod unsegmented, with 3, 3-4, 3-4, 3-4 terminal cincinuli. Exopod unsegmented with 29, 32, 29, 25 long marginal plumose natatory setae, respectively.

Uropods (Fig. 18f). Two-segmented, proximal segment with 2-3, and distal segment with 17 long plumose setae, respectively.

Telson (Fig. 18c). Dorsal surface with 12 setae, posterior margin with one seta, and ventral surface with 2 setae.

Discussion

The exponential increase in larval size during its development through successive zoeal stages (Fig. 1) is consistent with the general patterns of larval growth known from most other decapod crustaceans (see Anger 1998, 2001). Since the increase in biomass during the course of larval development depends strongly on the number of zoeal stages of a species (Anger 1998, 2001), it may not be surprising that *Geograpsus lividus* shows unusually high accumulation rates in total dry mass (W) and organic constituents (measured as CHN; see

Table 1.). Growth factors of 57-73 (i.e. increments of 5600-7200% compared to the initial biomass at hatching) are substantially higher than in all other species, for which larval biomass growth has been determined. The portunid crab *Liocarcinus holsatus,* for instance, which passes through five zoeal stages, shows cumulative zoeal growth factors of only about 19-23 (see Harms 1990). The only other species, where comparably high zoeal biomass growth as in *G. lividus* has been observed, is the Chinese mitten crab, *Eriocheir sinensis*. This varunid crab also has five (occasionally six) zoeal stages (Montu *et al*., 1996), which grow by factors from 50-57 (Anger and Mataliotaki, unpubl. data; see Anger 2001). Very high rates of biomass accumulation generally indicate that the larvae of a given species strongly depend on planktonic food, while low rates in species with a comparable number of zoeal stages show a higher endotrophic potential, which may approach facultative lecithotrophy (Anger 1998, 2001). In *G. lividus*, an unusually long pelagic larval period (2 months at 24°C) is thus associated with an effective exploitation of planktonic food sources, allowing for substantial growth and a wide range of dispersal and connectivity between populations.

Also, our biomass data indicate that the larvae grew very well in our rearing experiments, gaining not only in protein (57-fold increase in N), but also accumulating great amounts of lipid reserves (increasing C:N ratio). Hence, an inappropriate nutrition can be excluded as a potential cause of the sudden and complete mortality that occurred at the transition from the last zoeal stage to the megalopa. This suggests that another unfavourable factor, most likely a lethal microbial or viral infection, killed the larvae during and shortly after this moult, caused megalopal incomplete molt, and prevented metamorphosis to the first juvenile crab instar.

For the Grapsidae, larval morphology is poorly documented with the exception of the genus *Metopograpsus*. In Table 2 a list of the known larval descriptions for this family is given; including plankton collected material tentatively identified as belonging to grapsid larvae. There are no data for the genus *Leptograpsodes*, whereas for the genera *Grapsus*, *Leptograpsus*, *Planes* and *Geograpsus* only descriptions of the first zoeal stage, and in *Goniopsis* the zoea I and II of one species have been described. In the genus *Pachygrapsus* there are several descriptions of the zoeal phase, including the complete zoeal development of *P. marmoratus* (see Cuesta and Rodríguez 2000), but for none of the above mentioned genera except for *Metopograpsus* the laboratory rearing was successfully carried through the megalopa stage, which has now been achieved with the present obtainment of the complete larval development of *Geograpsus lividus*, including eight zoeal and the megalopa stage (see Table 2). From a larval point of view *Metopograpsus* is an anomalous genus within Grapsidae, with clear differences in the number of zoeal stages (only 5) as well as distinctive morphological characters that allow separation from the rest of Grapsidae.

The first remarkable feature of the larval development of *Geograpsus lividus* is the high number of zoeal stages, representing with eight moulting stages the longest recorded developmental pathway for any brachyuran. In Grapsidae, six zoeal stages appeared to be the maximum number of zoeal stages, as described for *P. marmoratus* (see Cuesta and Rodríguez 2000) and also deduced for *P. crassipes* based on the larval morphology of its zoea V (reared in the laboratory by Schlotterbeck 1976) and the sixth zoeal stage later confirmed by Di Bacco (unpublished data). Therefore, the expected number of stages for the zoeal phase of *Pachygrapsus* had been 6 stages. There are descriptions of 13 and 7 zoeal stages for *P. gracilis* and *P. transversus* reared in the laboratory (Brossi-Garcia and Domingues Rodrigues 1993, 1997, respectively) but the corresponding illustrations clearly represent early zoeal stages, probably zoea V or VI, and do not show morphological characters defining terminal zoeal stages. Although long developments had been suggested for some species, based on specimens collected from the plankton, these were never confirmed by laboratory culture. There are two cases, *Callinectes sapidus* and *C. similis* (described by Costlow and Bookhout

1959 and Bookhout and Costlow 1977, respectively), where eight zoeal stages have been obtained by larval cultures, but with additional "extra" stages, since some zoea VII stage moulted to a megalopa, while none of the "extra" zoeae VIII did. In the case of *G. lividus* the zoeal VIII stage cannot be considered an "extra" stage, because in this species no zoea VII moulted directly to a megalopa.

The larvae of *G. lividus* share most characters established for the family Grapsidae (Cuesta *et al.* 1997; Cuesta and Schubart 1999; Cuesta *et al*. 2006), thereby confirming that there is a set of features that allows characterizing grapsid zoeae and megalopae. However, the two last zoeal stages show some new features, which do not correspond to the typical setation pattern known from grapsid species with 5 or 6 zoeal stages (see Table 3). These characters are: the setation of the basis and terminal segment of the endopod of the first maxilliped, the number of natatory setae on the exopod of maxillipeds, and the number of terminal processes on the telson. A similar case of an aberrant last stage has been reported in other species with an extended mode of larval development: the gecarcinid *Cardisoma armatum* presents 6 zoeal stages (instead of the five observed in the other species of this genus) of which the last stage also shows an unusual setation pattern that breaks the expected rule (basis of first maxilliped setation 2,2,4,4 and endopod of the second maxilliped 1,1,7 instead of the expected 2,2,3,3 and 1,1,6 respectively) (see Cuesta and Anger 2005). The knowledge of this change in the setation pattern in later stages of expanded developments is especially interesting for the identification of larval stages collected in the plankton. Now, in the light of these data we can correctly assign the larvae ASM30 and ASM31 (see Table 3) described by Rice and Williamson (1977) as "Grapsidae sp." to the genus *Planes* and, taking into account the locality of samples and distribution of the species of this genus, to the species *Planes minutus*. Comparison with setation patterns of zoeal stages from *P. marmoratus* and *G. lividus* suggests that ASM31 must be considered the stage zoea VII instead of the zoea VI as Rice and Williamson (1977) suggested (see Table 3). The fact of finding these same features in later stages of plankton-collected larvae corroborates that these changes in the setation pattern are normal when reaching later stages and not artefacts due to laboratory conditions of cultures, even if they break the commonly accepted rule that certain setation patterns of mouthparts are constant throughout zoeal development (Clark 2000).

One feature shown by zoeae of *Geograpsus lividus* is presently not considered typical for Grapsidae, but was also described for *Pachygrapsus marmoratus* and *Planes minutus* (as ASM30-31), so at this point it could be proposed as a grapsid characteristic, although pending confirmation, when morphologies of zoea III and subsequent stages of *Goniopsis*, *Grapsus* and *Leptograpsus* are described. The feature is a scaly texture, and coloured (pink to orange) area, on the distal part of dorsal cephalotoracic spines (sometimes on rostral one) (see fig. 2c, and fig. 19). This feature had never been observed in zoeae of *Metopograpsus,* but as mentioned above, this genus presents other morphological characters (especially antennal and abdominal types) that clearly separate it from the rest of Grapsidae.

Moreover, zoeae III-VIII of *G. lividus* present a spinulation on the lateral and rostral spines of the cephalotorax (Figs. 2c-e, 3). This character is recorded for the first time in grapsid crabs. The megalopal morphology of Grapsidae is poorly documented; it has only been described for *Metopograpsus*, *Pachygrapsus* and *Planes*. The general morphology of the megalopa of *Geograpsus lividus* (Fig. 4a) agrees with those proposed as distinctive for grapsid megalopae (Cuesta *et al*. 2006). In the present study, the sternal plate of a grapsid megalopa is described and illustrated for the first time (Fig. 4b), presenting an elevated number of setae compared to other Thoracotremata.

The zoea I of *G. lividus* was previously described from the Pacific coast of Panama and the Gulf of Mexico (by Cuesta and Schubart 1999 and Guerao *et al*. 2001, respectively). The comparison of these zoea I with the present one from Jamaica show first differences in size, with the Jamaican larvae being the smallest (rdl: 0.67± 0.02 mm), the ones from the Pacific coast of Panama intermediate (rdl: 0.75± 0.03 mm) and the largest ones being those from the Gulf of Mexico (rdl: 0.81 ± 0.02 mm). This may follow a temperature gradient rather than indicate geographic separation as similarly documented for larvae of *Pachygrapsus transversus* and *P. socius* (see Cuesta and Schubart 1998; Schubart *et al*. 2005). According to Guerao *et al*. (2001), the zoea I stage of *G. lividus* from the Pacific coast of Panama and those from the Gulf of Mexico could be distinguished from each other by the antennal and abdominal morphology supporting molecular data that suggest they may belong to two different species (Schubart, unpublished data). Now, taking into account that the morphology of the antennal and abdominal characters in zoeae I from Jamaica are more similar to those from the Pacific coast of Panama than to those from the Gulf of Mexico, these structures must be carefully considered for separation at interspecific level. This was previously indicated for the antennal morphology of *Pachygrapsus transversus* and *P. socius* (see Schubart *et al*. 2005), which varies between populations but does not follow a species-specific pattern.

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References

Aikawa, H. 1937. Further notes on brachyuran larvae. **-** *Records of Oceanographic Works of Japan* **9**: 87-162.

Al-Khayat, J. A. and Jones, D. A. 1996. Two new genera, *Manningis* and *Leptochryseus* (Decapoda: Camptandriinae), and description of the first zoea of six brachyurans from the Arabian Gulf. – *Journal of Crustacean Biology* **16**: 797-813.

Anger, K. 1998. Patterns of growth and chemical composition in decapod crustacean larvae. – *Invertebrate Reproduction & Development* **33**: 159-176.

Anger, K. 2001. *The biology of decapod crustacean larvae*. Crustacean Issues Vol. **14**. A. A. Balkema, Lisse, The Netherlands, 420 pp.

Anger, K. and Harms, J. 1990. Elemental (CHN) and proximate biochemical composition of decapod crustacean larvae. – *Comparative Biochemistry and Physiology* **97B**: 69-80.

Bookhout, C. G. and Costlow, J.D. Jr. 1977. Larval development of *Callinectes similis* reared in the laboratory. – *Bulletin of Marine Science* **27**: 704-728.

Bourdillón-Casanova, L. 1960. Le méroplancton du Golfe de Marseille: les larves de Crustaces décapodes. – *Recuéil des Travaux de la Station Marine d´Endoume (Marseille)* **30**: 1-286.

Brossi-Garcia, A. L. and Domingues Rodrigues, M. 1993. Zoeal morphology of *Pachygrapsus gracilis* (Saussure, 1858)(Decapoda, Grapsidae) reared in the laboratory. – *Invertebrate Reproduction and Development* **24**: 197-204.

Brossi-Garcia, A. L. and Domingues Rodrigues, M. 1997. Zoeal morphology of *Pachygrapsus transversus* (Gibbes) (Decapoda, Grapsidae) reared in the laboratory. – *Revista brasileira de Zoologia* **14**: 803-819.

Cano, G. 1892. Sviluppo postembrionale dei Dorippidei, Leucosiadi, Corystoidei e Grapsidi. – *Memorie della Società Italiana di Scienze Naturali* 8, III **4**: 1-14.

Cházaro-Olvera, S. and Rocha-Ramírez, A. 2007. Morphology of the *Pachygrapsus gracilis* (De Saussure, 1858) megalopa (Brachyura, Grapsidae) reared in the laboratory. – *Crustaceana* **80**: 19-30.

Chhapgar, B. F. 1956. On the breeding habits and larval stages of some crabs of Bombay. – *Rec. Indian Museum* **54**: 33-52.

Clark, P. F., Calazans, D. K. and Pohle, G. W. 1998. Accuracy and standardization of brachyuran larval descriptions. – *Invertebrate Reproduction and Development* **33**:127-144.

Clark, P. F. 2000. Interpreting patterns in chaetotaxy and segmentation associated with abbreviated brachyuran zoeal development. – *Invertebrate Reproduction and Development* **38**: 171-181.

Costlow, J. D. Jr. and Bookhout, C. G. 1959. The larval development of *Callinectes sapidus* Rathbun reared in the laboratory. – *The Biological Bulletin* **116**: 373-396.

Cuesta, J. A. and Anger, K. 2005. Morphology and salinity tolerance of the larval stages of *Cardisoma armatum* (Brachyura: Grapsoidea: Gecarcinidae) reared in the laboratory. – *Journal of Crustacean Biology* **25**: 640-654.

Cuesta, J. A., González-Gordillo, J. I. and Rodríguez, A. 1997. First zoeal stages of *Grapsus adscensionis* (Osbeck) and *Planes minutus* (Linnaeus) (Brachyura: Grapsidae) described from laboratory hatched material, with notes on larval characters of the Grapsinae. – *Journal of Natural History* **31**: 887-900.

Cuesta, J. A., Guerao, G., Liu, H-C. and Schubart, C. D. 2006. Morphology of the first zoeal stages of eleven Sesarmidae (Crustacea, Brachyura, Thoracotremata) from the Indo-West Pacific, with a summary of familial larval characters. – *Invertebrate Reproduction and Developmen*. **49**: 151-173.

Cuesta, J. A. and Rodríguez, A. 1994. Early zoeal stages of *Pachygrapsus marmoratus* (Fabricius), *P. transversus* (Gibbes) and *P. maurus* (Lucas) (Decapoda, Brachyura, Grapsidae) reared in the laboratory. – *Scientia Marina* **58**: 323-327.

Cuesta, J. A. and Rodríguez, A. 2000. Zoeal stages of the intertidal crab *Pachygrapus marmoratus* (Fabricius, 1787) (Brachyura: Grapsidae) reared in the laboratory. – *Hydrobiologia* **436**: 119-130.

Cuesta, J. A. and Schubart, C. D. 1998. Morphological and molecular differentiation between three allopatric populations of the littoral crab *Pachygrapsus transversus* (Gibbes, 1850) (Brachyura: Grapsidae). – *Journal of Natural History* **32**: 1499-1507.

Cuesta, J. A. and Schubart, C. D. 1999. First zoeal stages of *Geograpsus lividus* and *Goniopsis pulchra* from Panama confirm consistent larval characters for the subfamily Grapsinae. – *Ophelia* **51**: 163-176.

Fielder, D. R. and Greenwood, J. G. 1983. The complete larval development of *Metopograpsus frontalis* Miers (Decapoda, Grapsidae), reared in the laboratory. – *Proceedings of the Royal Society of Queensland* **94**: 51-60.

Flores, A. A. V., Negreiros-Fransozo, M. L. and Fransozo, A. 1998. The megalopa and juvenile development of *Pachygrapsus transversus* (Gibbes, 1850) (Decapoda, Brachyura) compared with other Grapsid crabs. – *Crustaceana* **71**: 198-222.

Flores, A. A. V., Paula, J. and Dray, T. 2003. First zoeal stages of grapsoid crabs (Crustacea: Brachyura) from the East African coast. – *Zoological Journal of the Linnean Society* **137**: 355-383.

Fransozo, A., Cuesta, J. A. and Negreiros-Fransozo, M. L. 1998. The first zoeal stage of two species of Grapsidae (Decapoda, Brachyura) and a key to such larvae from the Brazilian coast. – *Crustaceana* **71**: 331-343.

Gohar, H. A. F. and Al-Kholy, A. A. 1957. The larvae of some brachyuran Crustacea. – *Publications of the Marine Biological Station, Gardaqa* **9**: 145-176.

Guerao, G., Abelló, P. and Cuesta, J. A. 1997. Morphology of the megalopa and first crab stage of the mediolitoral crab *Pachygrapsus marmoratus* (Brachyura, Grapsidae, Grapsinae). – *Zoosystema* **19**: 439-449.

Guerao, G., Schubart, C. D. and Cuesta, J. A. 2001. The first zoeal stages of *Grapsus grapsus* (Linnaeus) and *Geograpsus lividus* (H. Milne Edwards) (Decapoda, Brachyura, Grapsidae) from the western Atlantic. – *Nauplius* **9**: 111-121.

Harms, J. 1990. Accumulation and loss of biomass in *Liocarcinus holsatus* larvae during growth and exuviation. – *Marine Biology* **104**: 183-190.

Hashmi, S. L. 1971. Studies on the larvae of Grapsidae Metopograpsus, Sesarma and Metaplax reared in the laboratory (Decapod: Crustacea). – *Pakistan Journal of Scientific Research* **23**: 105-113.

Hyman, O. W. 1924. Studies on larvae of crabs of the family Grapsidae. – *Procceding of the United States National Museum* **65**: 1-8.

Ingle, R. W. 1987. The first zoea of three *Pachygrapsus* species and of *Cataleptodius floridanus* (Gibbes) from Bermuda and Mediterranean (Crustacea: Decapoda: Brachyura). – *Bulletin of the British Museum (Natural History), Zoology* **52**: 31-41.

Kakati, V. S. 1982. Larval development of the Indian Grapsid crab, *Metopograpsus latifrons* H. Milne Edwards in vitro. – *Indian Journal of Marine Science, New Delhi* **2**: 311-316.

Konishi, K. and Minagawa, M. 1990. The first zoeal larva of the Gulfweed crab *Planes cyaneus* Dana, 1851 (Crustacea: Brachyura: Grapsidae). – *Procedings of the Japanese Society of Systematic Zoology* **42**: 14-20.

Lebour, M. V. 1944. Larval crabs from Bermuda. – *Zoologica* **29**:113-128.

Montú, M., Anger, K., Bakker, S. de. 1990. Variability in the larval development of *Metasesarma rubripes* (Decapoda, Grapsidae) reared in the laboratory. *Neritica* **5**: 113-128.

Montu, M., Anger, K., Bakker, S. de. 1996. Larval development of the Chinese mitten crab *Eriocheir sinensis* H. Milne-Edwards (Decapoda: Grapsidae) reared in the laboratory. – *Helgoländer Meeresuntersuchungen* **50**: 223-252.

Muraoka, K. 1973. On the characters of the larva and the seasonal change of ocurrence of the *Sargassum* crab, *Planes cyaneus*. – *Bulletin of the Kanagawa Prefectural Museum* **6**: 45-53.

Ng, P. K. L., Guinot, D. and Davie, P.J.F. 2008. Systema Brachyurorum: Part I. An annotated checklist of extant brachyuran crabs of the world. – *Raffles Bulletin of Zoology* **17**: 1-286.

Pasupathi, K. and Kannupandi, T. 1986. Laboratory reared larval stages of the mangrove grapsid crab, *Metopograpsus maculatus* H. Milne-Edwards. – *Mahasagar* **19**: 233-244.

Paula, J. 1985. The first zoeal stages of *Polybius henslowi* Leach, *Maja squinado* (Herbst), *Pachygrapsus marmoratus* (Fabricius) and *Uca tangeri* (Eydoux) (Crustacea, Decapoda, Brachyura). – *Arquives do Museo Bocage, B(II)* **17**: 137-147.

Pautsch, F. 1965. System of chromatophores and their behaviour in the larva of the crab, *Geograpsus lividus* (Milne Edwards). – *Acta Biologica et Medica (Gdansk)* **9**: 15-24.

Rajabai, K. G. 1961. Studies on the larval development of Brachyura. VII. Early development of *Metopograpsus messor* (Forskal), *Plagusia depressa squamosa* (Herbst), *Metasesarma rousseauxi* A. M. Edwards and *Sesarma tetragonum* (Fabricius) of the family Grapsidae. – *Journal of the Zoological Society of India* **13**: 153-165.

Rathbun, M. 1923. The Brachyuran crabs collected by the U.S. Fisheries Steamor "Albatros" in 1911, chiefly on the West Coast of Mexico. – *Bulletin of the American Museum of Natural History* **48**: 619-637.

Rice A. L. and Williamson, D. I. 1977. Planktonic stages of Crustacea Malacostraca from Atlantic Seamounts. – *Meteor Forschungsergebnisse (Berlin & Stuttgart)* **26**: 28-64.

Rieger, P. J. 1998. Desenvolvimento larval de *Uca* (*Minuca*) *burgersi* Holthuis (Crustacea, Decapoda, Ocypodidae), em laboratorio. – *Revista Brasileira de Zoologia* **15**: 727-756.

Rossignol, M. 1957. II. Crustacés Décapodes Marines de la Region de Pointe-Noire. In J. Collignon, M. Rossignol and Ch. Roux (Eds): *Mollusques, Crustacés, Poissons Marines des côtes d'A.E.F.*, pp. 71-136. Collection au Centre d'Oceanographie de l'Institut d'Etudes Centrafricaines de Pointe-Noire. – Ministère de la France d'Outre-Mer.

Schlotterbeck, R. E. 1976. The larval development of the lined shore crab, *Pachygrapsus crassipes* Randall, 1840 (Decapoda, Brachyura, Grapsidae) reared in the laboratory. – *Crustaceana* **30**: 184-200.

Schubart, C. D., Cuesta, J. A. and Felder, D. L. 2005. Phylogeography of *Pachygrapsus transversus* (Gibbes, 1850): The effect of the American continent and the Atlantic Ocean as gene flow barriers and recognition of *Pachygrapsus socius* Stimpson, 1871 as a valid species. – *Nauplius* **13**: 99-113.

Seridji, R. 1971. Contribution à l'étude des larves de Crustacés Décapodes en Baie d'Alger. – *Bulletin de L'Institut Oceanographique D'Alger* **III**: 1-105.

Spivak, E. D. and Cuesta, J. A. 2009. The effect of salinity on larval development of *Uca tangeri* (Eydoux, 1835) (Brachyura: Ocypodidae) and new findings of the zoeal morphology. – *Scientia Marina* **73**: 297-305.

Villalobos, C. R. 1971. First zoeal stage of *Pachygrapsus crassipes* Randall. – *Revista de Biología Tropical* **18**: 107-113.

Wear, R. G. 1970. Life-history studies on New Zealand Brachyura. 4. Zoea larvae hatched from crabs of the family Grapsidae. – *New Zealand Journal of the Marine and Freshwater Research* **4**: 3-35.

Figure Captions

Figure 1. *Geograpsus lividus* (A. Milne-Edwards, 1837). Larval growth (cephalothorax length, CL) during the development from hatching through eight successive zoeal stages; regression equations describing an exponential increase in CL with (a) the number of stages, (b) time of development from hatching; r^2, coefficient of determination for regression coefficient.

Figure 2. *Geograpsus lividus* (A. Milne-Edwards, 1837). Cephalothorax, lateral view. a, zoea I; b, zoea II; c, zoea III (detail of the scaly surface of dorsal spine); d, zoea IV; e, zoea V (detail of spinulation on lateral spine). Scale bars = 0.3 mm.

Figure 3. *Geograpsus lividus* (A. Milne-Edwards, 1837). Cephalothorax, lateral view. a, zoea VI; b,zoea VII; c, zoea VIII (detail of spinulation on lateral spine). Scale bars = 1 mm.

Figure 4. *Geograpsus lividus* (A. Milne-Edwards, 1837). a, cephalothrorax of the megalopa, dorsal view; c, sternum of the megalopa; c, mandible of the zoea VIII; d, mandible of the megalopa. Scale bars: a = 1 mm; b = 0.5 mm; c-d = 0.1mm.

Figure 5. *Geograpsus lividus* (A. Milne-Edwards, 1837). Antennule. a, zoea I; b, zoea V; c, zoea VI; d, zoea VII; e, zoea VIII; f, megalopa. Scale bars = 0.1 mm.

Figure 6. *Geograpsus lividus* (A. Milne-Edwards, 1837). Antenna. a, zoea I; b, zoea V; c, zoea VI; d, zoea VII; e, zoea VIII; f, megalopa. Scale bars =0.1 mm.

Figure 7. *Geograpsus lividus* (A. Milne-Edwards, 1837). Maxillule. a, zoea I; b, zoea II; c, zoea V; d, zoea VIII. Scale bars = 0.1 mm.

Figure 8. *Geograpsus lividus* (A. Milne-Edwards, 1837). Maxilla. a, zoea I; b, zoea IV; c, zoea VIII. Scale bar = 0.1 mm.

Figure 9. *Geograpsus lividus* (A. Milne-Edwards, 1837). Megalopa. a, maxillule; b, maxilla. Scale bar = 0.1 mm.

Figure 10. *Geograpsus lividus* (A. Milne-Edwards, 1837). First maxilliped. a, zoea I; b, zoea VII; c, zoea VIII; d, megalopa. Scale bars = 0.1 mm.

Figure 11. *Geograpsus lividus* (A. Milne-Edwards, 1837). Second maxilliped. a, zoea I; b, zoea VII; c, zoea VIII, with a detail of rare endopod; d, megalopa. Scale bars = 0.1 mm.

Figure 12. *Geograpsus lividus* (A. Milne-Edwards, 1837). Third maxilliped. a, zoea VII; b, zoea VIII; c, megalopa. Scale bars = 0.1 mm.

Figure 13. *Geograpsus lividus* (A. Milne-Edwards, 1837). Pereiopods. a, zoea VII, b zoea VIII. Scale bars: a = 0.2 mm; b = 0.5 mm.

Figure 14. *Geograpsus lividus* (A. Milne-Edwards, 1837). Pleon, dorsal view. a, zoea I; b, zoea II; c, zoea III; d, zoea IV. Scale bars = 0.3 mm.

Figure 15. *Geograpsus lividus* (A. Milne-Edwards, 1837). Pleon, dorsal view. a, zoea V; b, zoea VI; c, zoea VII; d, zoea VIII. Scale bars = 0.3 mm.

Figure 16. *Geograpsus lividus* (A. Milne-Edwards, 1837). Pleon, lateral view. a, zoea I; b, zoea II; c, zoea III; d, zoea IV. Scale bars = 0.3 mm.

Figure 17. *Geograpsus lividus* (A. Milne-Edwards, 1837). Pleon, lateral l view. a, zoea V; b, zoea VI; c, zoea VII; d, zoea VIII. Scale bars = 0.3 mm.

Figure 18. *Geograpsus lividus* (A. Milne-Edwards, 1837). Megalopa. a, pleon, dorsal view; b, pleon, lateral view; c, telson; d, pleopod 1; e, pleopod 4; f, uropod. Scale bars = 0.3 mm.

Figure 19. Lateral view of the last zoeal stage of *Planes minutus* (Linnaeus, 1758) zoea VII? and *Pachygrapsus marmoratus* (Fabricius, 1787) zoea VI showing details of the scaly and coloured area on the distal part of dorsal spine (modified from Rice and Williamson 1977 and Cuesta and Rodriguez 2000, respectively).

Table 1. *Geograpsus lividus*. Larval biomass (measured as dry mass, W; carbon, nitrogen and hydrogen contents, in µg per individual and % of W; C:N mass ratio) at hatching (zoea I, day 0) and at the end of the zoeal phase (zoea VIII, 60 days after hatching); growth factor: increment factor in relation to the initial larval biomass at hatching

		Zoea I (0d)	**Zoea VIII (60d)**	**Growth Factor**
W (µg/ind)	x ± SD	11.3 ± 1.1	824 ± 85	73
C (µg/ind)	x ± SD	4.50 ± 0.2	277 ± 40	62
N (µg/ind)	x ± SD	1.07 ± 0.01	61.5 ± 9.5	57
H (µg/ind)	x ± SD	0.65 ± 0.03	39.6 ± 5.8	61
C (%W)	x ± SD	40.2 ± 2.0	33.6 ± 1.8	
N (%W)	x ± SD	9.55 ± 0.85	7.44 ± 0.47	
H (%W)	x ± SD	5.80 ± 0.31	4.79± 0.26	
C:N ratio	x ± SD	4.22 ± 0.15	4.52 ± 0.05	

Table 2. Descriptions of larval stages of the family Grapsidae. Abbrevitions: Z, zoeal stage; M, megalopa stage; (CLD), complete larval development; (L) laboratory reared or hatched at the laboratory; (P) plankton collected material; (-), no data.

Species	**Described stages**	**Author/year**
Geograpsus lividus	ZI (L)	Pautsch (1965)
Geograpsus lividus	ZI (L)	Cuesta and Schubart (1999)
Geograpsus lividus	ZI (L)	Guerao *et al*. (2001)
Geograpsus lividus	ZI-VIII (L), M (L) **(CLD)**	Present study
Goniopsis cruentata	ZI-II (L)	Fransozo *et al*. (1998)
Gonopsis pulchra	ZI (L)	Cuesta and Schubart (1999)
Grapsus adscensionis	Z1(L)	Cuesta *et al*. (1997)
Grapsus fourmanoiri	ZI (L)	Flores *et al.* (2003)
Grapsus grapsus	ZI (L)	Guerao *et al*. (2001)
Grapsus tenuicrustatus	ZI (P)	Aikawa (1937)
Grapsus tenuicrustatus	ZI (L)	Flores *et al.* (2003)
Grapsus strigosus	ZI-V (P)	Gohar and Al-Kholy (1957)
Leptograpsus variegatus	ZI (L)	Wear (1970)
Metopograpsus frontalis	ZI-V/VI (L) M(L) **(CLD)**	Fielder and Greenwood (1983)
Metopograpsus latifrons	ZI-V (L) M(L) **(CLD)**	Kakati (1982)
Metopograpsus maculatus	ZI-V (L) M(L) **(CLD)**	Pasupathi and Kannupandi

		(1986)
Metopograpsus messor	ZI (P)	Chhapgar (1956)
Metopograpsus messor	ZI (L)	Rajabai (1961)
Metopograpsus messor	ZI (L)	Hashmi (1971)
Metopograpsus messor	ZI (L)	Al-Khayat and Jones (1996)
Metopograpsus messor	ZI (L)	Flores *et al.* (2003)
Pachygrapsus crassipes	ZI (L)	Villalobos (1971)
Pachygrapsus crassipes	M (P)	Rathbun (1923)
Pachygrapsus crassipes	ZI-V (L)	Schlotterbeck (1976)
Pachygrapsus crassipes	ZI-VI (L)	Di Bacco *et al*. (unpublished)
Pachygrapsus gracilis	ZI (L)	Ingle (1987)
Pachygrapsus gracilis	ZI-XIII (L)	Brossi-García and Domingues Rodrigues (1993)
Pachygrapsus gracilis	M (P)	Chazaro-Olvera and Rocha-Ramirez (2007)
Pachygrapsus marmoratus	Z I (L), ZIII-V (P), MI-II (P)	Cano (1892)
Pachygrapsus marmoratus	Z I (L), ZIII-V (P), MI-II (P)	Hyman (1924)
Pachygrapsus marmoratus	ZI (L)	Bourdillon-Casanova (1960)
Pachygrapsus marmoratus	ZI (L)	Paula (1985)
Pachygrapsus marmoratus	ZI (L)	Ingle (1987)
Pachygrapsus marmoratus	ZI-II (L)	Cuesta and Rodriguez (1994)
Pachygrapsus marmoratus	M (P)	Guerao *et al*. (1997)
Pachygrapsus marmoratus	ZI-ZVI (L)	Cuesta and Rodriguez (2000)
Pachygrapsus maurus	ZI-II (L)	Cuesta and Rodriguez (1994)

Pachygrapsus minutus	ZI (L)	Flores *et al.* (2003)
Pachygrapsus plicatus	ZI (L)	Flores *et al.* (2003)
Pachygrapsus transversus	ZI (L)	Lebour (1944)
Pachygrapsus transversus	ZI (L)	Ingle (1987)
Pachygrapsus transversus	ZI-II (L)	Cuesta and Rodriguez (1994)
Pachygrapsus transversus	M (P)	Rossignol (1957)
Pachygrapsus transversus	M (P)	Flores *et al.* (1998)
Pachygrapsus socius	ZI (L)	Schubart *et al*. (2005)
Planes major	M (P)	Muraoka (1973)
Planes major	ZI (L)	Konishi and Minagawa (1990)
Planes marinus	ZI (L)	Wear (1970)
Planes minutus	ZI (P), Ib?(P), V?(P), M(P)	Cano (1892)
Planes minutus	ZI (L)	Hyman (1924)
Planes minutus	M (P)	Lebour (1944)
Planes minutus	ZI (L)	Cuesta *et al*. (1997)
Grapsinae ASM30	ZIII (P)	Rice and Williamson (1977)
Grapsinae ASM31	ZVI? (P)	Rice and Williamson (1977)
Grapsidae undetermined	ZI (P)	Seridji (1971)

Table 3. Changes in setation patterns of selected appendages through the zoeal phase of grapsoid genera. Abbreviation: (-), no data.

Appendages setation	Genera/Species	Zoea I	Zoea II	Zoea III	Zoea IV	Zoea V	Zoea VI	Zoea VII	Zoea VIII
Basis of first maxilliped	*Metopograpsus*	2,2,2,2							
	Pachygrapsus marmoratus	2,2,2,2	2,2,2,2	2,2,2,2	2,2,2,2	2,2,2,2	2,2,2,2		
	Planes sp. (ASM30-31)	-	-	2,2,2,2	-	-	2,2,**3**,**3**		
	Geograpsus lividus	2,2,2,2	2,2,2,2	2,2,2,2	2,2,2,2	2,2,2,2	2,2,2,2	2,2,2,2	2,2,**3**,**3**
Terminal segment of the endopod of first maxilliped	*Metopograpsus*	5	5	5	6-7	8			
	Pachygrapsus marmoratus	5	5	6	7	8	9		
	Planes sp. (ASM30-31)	-	-	5	-	-	9		
	Geograpsus lividus	5	5	5	6	7	8	**9**	**9-10**
Exopod of first and second maxillipeds	*Metopograpsus*	4/4	6/6	8/8	10/10	12/12			
	Pachygrapsus marmoratus	4/4	6/6	8/8	10/10	12+**2**/12+**2**	14+**6**/14+**4**		
	Planes sp. (ASM30-31)	-	-	7/8	-	-	14/19		
	Geograpsus lividus	4/4	6/6	8/8	9/10	10/12	11-12/15	14/19	**18/19**
Terminal processes on telson	*Metopograpsus*	3+3	3+3	3+3	3+3	3+3			
	Pachygrapsus marmoratus	3+3	3+3	3+3	4+4	4+4	4+4		
	Planes sp. (ASM30-31)	-	-	3+3	-	-	4+4		
	Geograpsus lividus	3+3	3+3	3+3	4+4	4+4	4+4	**5+5**	**6+6**