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Postlarval development of *Halicarcinus planatus* females (Crustacea: Decapoda: Hymenosomatidae) in the estuary of the Deseado River, Argentina

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SUMMARY: This study analyses morphology and morphometric growth changes of *Halicarcinus planatus* females until their terminal moult, and characterises new juvenile stages. Monthly samples were collected in the estuary of the Deseado River, Santa Cruz Province, Argentina. Crabs were sampled between the mid-intertidal and upper subtidal levels. Intermoult stages were analysed in sub-samples of adolescents and adults, and the presence of epizoic organisms was registered. Juveniles and adults were reared at the laboratory and examined for moult changes. All 3376 crabs caught were females, indicating a clear spatial segregation between sexes. Five juvenile stages (immature 1, 2, 3, 4 and adolescent) and a mature one were recognised on the basis of morphology and morphometry. All immature stages differed in cephalothorax width (CW) and abdomen width (AW). Positive allometry was observed in some juvenile stages and isometry in an immature stage and in mature females. Adolescents and adults encompassed a wide range of sizes, and the considerable size overlap between them suggests an anomalous growth process. Moult staging analysis indicated that adolescents have a high incidence of pre-moult stages in winter, when the terminal moult occurs. The measurements performed in laboratory-reared females indicated no abnormal increases during the moult. The terminal moult occurs within a wide size range, perhaps in association with mating.

Keywords: morphology, morphometry, relative growth, juvenile stages, females, *Halicarcinus planatus*.

RESUMEN: Desarrollo postlarval de las hembras de *Halicarcinus planatus* (Crustacea, Decapoda, Hymenosomatidae) en el estuario del río Deseado, Argentina. – Se analizan los cambios morfológicos y morfométricos de las hembras de *Halicarcinus planatus* hasta su muda terminal, caracterizando sus estadios juveniles. Se realizaron muestreos mensuales en el intermareal inferior y submareal, principalmente. Se estudiaron los estadios de intermuda y se registraron los organismos epizoicos, analizándose también los cambios que ocurren en las mudas en cangrejos criados en laboratorio. Todos los animales capturados fueron hembras, lo que indica una neta segregación espacial entre los sexos. Se reconocieron cinco estadios juveniles, cuatro etapas de inmadurez progresivas, una etapa de adolescencia y una última de madurez o adultez. Las etapas de inmadurez difieren en la talla del caparazón y del abdomen. Se observó alometría positiva en tres de las etapas juveniles e isometría en una etapa juvenil y en las adultas. Las adolescentes presentan una elevada frecuencia de estadios premuda durante el invierno, cuando ocurre la muda terminal. No existen incrementos de talla anormales durante las mudas. Adolescentes y adultas presentan un intervalo de tallas muy similar, lo que sugiere un proceso de crecimiento anómalo, relacionado probablemente con la cópula e impregnación.

Palabras clave: morfología, morfometría, crecimiento relativo, estadios juveniles, hembras, *Halicarcinus planatus.*

INTRODUCTION

The family Hymenosomatidae is a group of small spider crabs mainly distributed in the Indo-West Pacific region. Within this family, the genus *Halicarcinus* comprises 17 species mostly found in the southwestern Pacific Ocean, and less commonly in Japanese waters (Melrose, 1975; Lucas, 1980). *Halicarci-*

nus planatus (Fabricius, 1775) is the only species of the family occurring at the southern tip of America and in circumpolar, cold-temperate waters. This crab is larger than almost all other hymenosomatids and can reach up to 19.5 mm in cephalothorax width in the Kerguelen Islands (Richer de Forges, 1977). The species lives mainly in shallow marine waters, and is the dominant brachyuran in subtidal rocky coasts. It is usually abundant in protected areas such as bays and inlets, although it has also been found along exposed rocky coasts of Patagonia, in lower densities. Information on the biology of *H. planatus* is scarce and limited to the following locations: Mar del Plata (Boschi *et al.*, 1969) and Kerguelen Islands (Richer de Forges, 1977). The *H. planatus* population inhabiting the estuary of the Deseado River differs from those of other places. Individuals are spatially segregated by sex, as indicated by the absence of males in samples from the intertidal and upper subtidal zones all year round (Vinuesa *et al*., 2005).

Halicarcinus planatus, like other species of the genus, is characterised by determinate growth with a terminal (or pubertal) moult (Lucas and Hodgkin, 1970; Richer de Forges, 1977; Lucas, 1980). As a result, this little spider crab has two main post-larval phases: a juvenile or growth phase and an adult or reproductive phase. A similar development pattern has been described for some Majidae crabs (Teissier, 1935; Vernet-Cornubert, 1958; Sainte-Marie *et al*., 1995; Sampedro *et al.*, 1999). At the terminal moult, crabs undergo pronounced morphological changes that make it possible to differentiate between adults and juveniles (Hartnoll, 1965; Lucas, 1968; Lucas and Hodgkin, 1970; Sampedro *et al*., 1999). In the genus *Halicarcinus*, a decrease in the size of the chelae during the terminal moult of females was observed in *H. australis* (Lucas and Hodgkin, 1970) and in *H. planatus* from the Kerguelen Islands (Richer de Forges, 1977).

The objective of this study was to analyse morphologic and morphometric growth changes of *H. planatus* females in the estuary of the Deseado River until their terminal moult, and to redefine the juvenile stages.

MATERIALS AND METHODS

The study was conducted in the estuary of the Deseado River (47°45'S, 65°55'W), Santa Cruz Province, Argentina. This area is influenced by the cold-temperate waters of the Patagonian current, which has low salinity and flows from the Strait of Magellan in the south to the Patagonian coasts in the north (Brandhorst and Castello, 1971). Annual sea surface temperatures in the estuary ranged during samplings between 5.8 and 16.6°C.

Crab samples were taken under rocks at three tidal levels: mid- and low intertidal and upper subtidal zones of rocky shores, located along the northern margin near the mouth of the estuary. Sampling was carried out monthly between March 2002 and May 2003 during spring tides (N= 3153). Other samples (N= 223) were also collected in 2004 and 2005 from subtidal bottoms and *Macrocystis pyrifera* holdfasts, to search for the presence of males.

Females were classified as juveniles, comprising the immature (IMM), and adolescent (ADO) stages, and adults or the mature stage (MAT) according to Sampedro *et al*. (1999). After examining the abdomen morphology and separating some ADO and MAT for recognising intermoult stages, representative sub-samples of the different juvenile stages were fixed in 7% formalin-seawater solution. Maximum cephalothorax width at the level of the two posterior spines (CW) and maximum abdomen width (AW) at the level of the sixth segment were measured in specimens from the monthly sub-samples (N=448). Dimensions up to 4 mm were measured with the aid of a zoom stereomicroscope provided with a micrometric eyepiece, and a digital caliper was used for larger dimensions. All measurements were taken to the nearest 0.1 mm. Different stages were assigned to each growth phase on the basis of abdomen shape and a morphometric index (CW/AW). Statistical differences for CW and AW among stages were tested using one-way ANOVA followed by Tukey's multiple comparison test, after verification of the assumption of normal distribution and homoscedasticity of data (Zar, 1999).

Relative growth was examined based on the hypothesis that there are different stages of postlarval growth in *Halicarcinus planatus.* Allometric relationships were established for abdomen width (AW) and carapace width (CW) for each morphological stage. The logarithmic transformation $\log y = \log a + b.\log x$, linearised from the traditional equation $y = a.x^b$, provides the best empirical description of patterns of relative growth (see Hartnoll, 1978, 1982). The derived slope of each regression line was tested for allometric status against the isometric slope of 1 using Student's test.

The moulting stages were determined according to the method described by Drach and Tchernigovtzeff (1967) for slightly calcified species. In this method, which was also used by Richer de Forges (1977), the branchial epipod of the third maxilliped is mounted in glycerin-gelatin on a slide soon after dissection, a coverslip is placed on top, and then the slide is sealed. The tip of the epipod was examined under a compound microscope for signs of epidermal retraction or presence of developing setae. This technique was applied to sub-samples of 261 ADO females. The incidence and size of epizoic organisms on the cephalothorax and appendages was used as a tool to help in the estimation of the intermoult stage.

In order to study moult increment, juvenile (54 IMM and 116 ADO) females were reared from July to December 2002 under conditions of controlled increase in temperature (7-9 ± 1ºC) and salinity (33-34 ± 1 psu). Groups of 10-30 individuals were kept in 1000 cm³ plastic containers with seawater and fed open mussels (*Perumytilus purpuratus)* and pieces of isopods (*Exosphaeroma sp)*. Seawater was changed weekly. Crabs were not individually tagged for identification, but the shape of abdomen, colour change and the size of discarded exuviae indicated which animal had moulted. Crabs were checked twice a day for moulting and the moult increment was recorded two or three times after ecdisis (1-7 days). The CW–moult increment relationship was estimated in terms of percentage of increment to assess the possible occurrence of abnormal increments in the moult of juvenile females.

RESULTS

In the studied population of *H. planatus*, all 3376 crabs collected were females ranging from 1.7 to 14.2 mm in CW. Juveniles were observed to pass through several immature stages before attaining the ADO stage. The developmental stages are as follows:

Immature 1 (IMM1: Fig 1a): very small crabs (between 1.7 and 2.7 mm CW), with an almost triangular abdomen and a triangular terminal article. Only five specimens of this morphotype were registered, and they were assumed to be females, because none of the collected individuals possessed a constriction between abdominal segments 4 and 5 typical of males, and because no males were found during the whole study period.

Immature 2 (IMM 2: Fig. 1b): small crabs (between 2.4 and 4.7 mm CW). The first abdominal segment is the largest and the last abdominal segment is triangular in shape. Interposed abdominal segments are of the same size. The CW/AW ratio ranges from 2.71 to 3.88. All the specimens were females because abdomen differentiation in males occurs in smaller

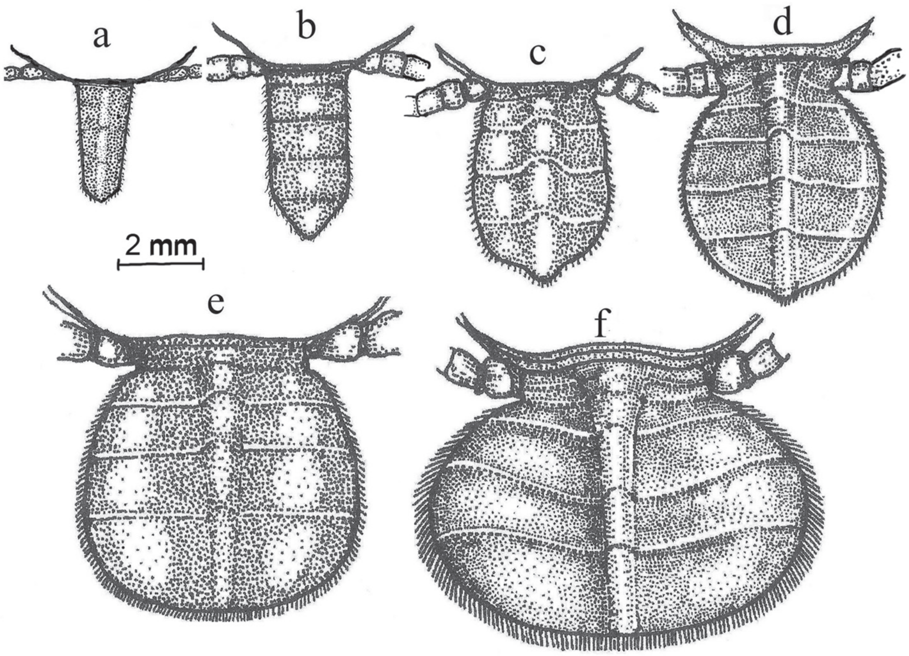

FIG. 1. – Abdominal morphology of the different stages described. a: first immature stage (IMM 1); b: IMM 2; c: IMM 3; d, IMM 4; e: adolescent (ADO); f: adult or mature (MAT).

individuals, as was observed in the Beagle Channel (Vinuesa, unpublished data). IMM2 crabs cultured in the laboratory moulted to the IMM3 stage.

Immature 3 (IMM 3: Fig. 1c): Crabs between 3.7 and 6.2 mm CW. There is an enlargement of the abdomen at the level of the three last segments. The pleon is flattened. The CW/AW ratio ranges from 2 to 2.72.

Immature 4 (IMM 4: Fig. 1d): Crabs between 4.4 and 6.7 mm CW. The pleon is oval in shape and the third, fourth and fifth segments are more expanded. It is flattened and does not cover the sternal plates. The CW/AW ratio ranges from 1.71 to 2.58.

Adolescents (ADO: Fig. 1e): Crabs between 4.9 and 14.2 mm CW. The posterior end of the pleon is approximately quadrangular in shape because the last three segments are almost identical, and has rounded edges. It is flattened and does not cover the sternal plates. The CW/AW ratio ranges from 1.22 to 2.09. The abdomen of crabs looks darker before the terminal moult.

Mature or Adult females (MAT: Fig. 1f): Crabs between 5.5 and 13.8 mm CW in our samples. The abdomen is remarkably enlarged and completely covers the sternal plates. It has a very pronounced curvature that forms a large cavity for egg incubation. In addition, female pleopods increase in size and bear numerous setae on both branches; setae on the border of the abdomen also become enlarged. The CW/AW ratio ranges from 0.93 to 1.06. MAT includes three different phases: a) ovigerous females (carrying eggs), b), post-ovigerous females (with egg remnants and/or empty egg cases), and c) older post-ovigerous females (without signs of carrying eggs). Post-ovigerous females were observed only among females with recent larval hatching and in laboratory-reared crabs.

There were significant differences in size among the five stages (p<0.01) for AW ($F_{4, 443}$ = 868.34) and CW ($F_{4, 443}$ = 468.32), except for CW between ADO and MAT females because of the considerable overlap in the values (Fig. 2).

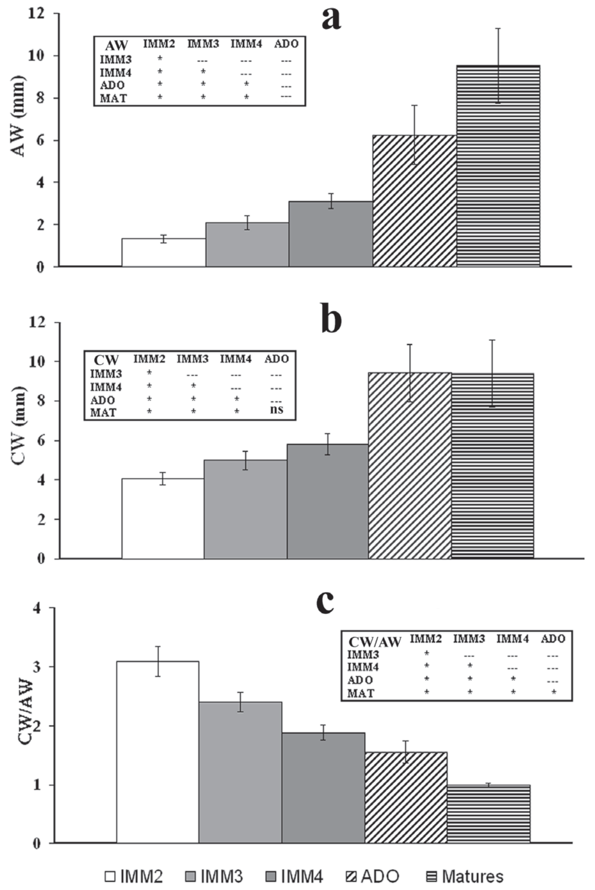

Fig. 2. – Mean ± SD for AW (a), CW (b) and CW/AW index (c) for each morphotype considered. IMM2 (n= 82), IMM3 (n= 103), IMM4 (n= 47), ADO (n= 87), MAT (n= 103). Corresponding matrix of Tukey's comparisons is included in the histogram area. *: statistically significant (p ≤0.05); ns: non-significant.

Relative growth of the abdomen in relation to CW for each morphological stage are included in Table 1, together with the allometric status. IMM2, IMM3 and ADO demonstrated a positive allometric growth, whereas IMM4 and MAT crabs showed isometric growth.

In ADO females, the "C" stage—which is equivalent to a period of tegument stability or intermoult—and some premoult stages (i.e. D0 and D1) were detected between November and February, while all

Table 1. – Allometric growth equations of juvenile stages (IMM2, IMM3, IMM4 and ADO) and adult females (MAT), using abdomen width as a reference variable. AW= Abdomen width. CW = Cefalothorax width. The number of crabs and their standard error are shown. P<0.00001 in all cases. Allometric status is added ($t_{0.05}$)

AW	Growth equation	R²	N	F	b(SE)	Allometry
IMM2	log AW = -1.9604 + 1.5956 log CW	0.7795	82	282.9185	0.0302	+
IMM3	log AW = -1.6201 + 1.4668 log CW	0.8712	103	683.3305	0.0561	+
IMM4	log AW = -0.7136 + 1.0484 log CW	0.7042	47	107.1101	0.1013	Isometry
ADO	log AW = -1.3061 + 1.3938 log CW	0.8421	113	591.9861	0.0573	+
MAT	log AW = -0.0446 + 1.0262 log CW	0.9763	103	4156.2790	0.0159	Isometry

of them were in the premoult stages D1 and D2 between May and August.

The epizoic macrofauna on MAT showed a higher incidence in older post-ovigerous (74%) than in ovigerous females (28%), and was represented by several species of Bryozoa (*Celleporella yagana*, *Celleporella hyalina*, *Celleporella* sp., *Alcyonidium* sp., *Walkeria atlantica* and a Tubuliporidae) and two species of spirorbid polychaetes (*Paralaeospira levinseni* and *Romanchella perrieri*). The same epizoic species were found on ADO females, but with smaller size and lower frequency.

A total of 129 moults occurred during rearing of crabs. Moult increment varied from 0.2 mm in a crab of 3.2 mm CW to 1.1 mm in a crab of 9.1 mm CW. After moult, CW increased from 0.2 to 0.5 mm for IMM2; from 0.2 to 0.4 mm for IMM3; from 0.4 to 0.7 for IMM4, and from 0.3 to 1.4 for ADO females. The percentage size increment showed a decreasing tendency, with 9.17% for IMM2 and 7.73% for ADO. However, there were pronounced variations even within the same developmental stage; for example, during the experiments it varied between 4.6 and 15.0% for ADO. Almost 95% of the ADO females laid eggs after their moult. Except for some ADO females, all moulting crabs reached the following stage of development.

DISCUSSION

Hymenosomatids studied with free larval stages pass through three planktonic zoeal stages, and the last zoea moults to the first juvenile instar; there is no intermediate megalopa larva (Lucas, 1980).

In the study area, the mean cephalothorax length of the third zoea found in plankton samples was 0.91 mm. Taking into account the relationship between the sizes of third zoea larvae and first juvenile instar crabs from Mar del Plata (Boschi *et al*., 1969) and the Kerguelen Islands (Richer de Forges, 1977), the first juvenile instar (IMM 0) from the Deseado estuary would range between 1.1 and 1.3 mm CW. However, crabs of such small sizes were never found in the intertidal zone during this study, and the smallest juvenile crabs (IMM1) were found only on kelp holdfasts. Therefore, settlement of third zoea and recruitment undoubtedly take place at subtidal levels. Juvenile females remain there until reaching larger sizes, and then move to upper levels as IMM2, IMM3, IMM4, or even as ADO.

The immature stages of the Deseado estuary crabs have well-defined characteristics and intermediate forms are rare. The fact that no moults were recorded for any cultured immature crab between early July and late August—almost 60 days—suggests long intermoult periods at these stages. In crabs from the Kerguelen Islands kept under culture conditions, intermoult durations of successive juvenile stages vary between 30 and 127 days (Richer de Forges, 1977).

The monitoring of the abdomen shape during the juvenile phase of *H. planatus* showed a general pattern of changes in the abdomen (see Figs. 1 and 2). A terminal (pubertal) moult took place after this series of immature crab instars. In the estuary of the Deseado River, ADO females underwent their terminal moult between May and August at intertidal or upper subtidal levels; as a result, the abdomen of females showed the most pronounced changes in morphology.

In crab species with determinate growth, the most striking morphological changes take place during the terminal moult. For example, in family Majidae, males show an increase in the size of the chelipeds, and females undergo changes in morphology and in the allometry of the abdomen width (Teissier, 1935; Vernet-Coubert, 1958; Hartnoll, 1978; Sainte-Marie *et al*., 1995; Sampedro *et al*., 1999; Corgo and Freire, 2006). Significant differences in relative growth of the abdomen were found in some juvenile stages of *H. planatus*: IMM2, IMM3 and ADO showed a positive abdomen allometry. In other crabs, few phases of immature growth have been described—only two in *Maja squinado*, with a pre-puberty molt between them (Hartnoll, 1982). Morphological changes associated with the pre-puberty moult have also been described in males of *Pisa tetraodon* (Vernet-Cornubert, 1958). In *H. planatus* females, a pre-puberty moult took place between IMM4 and ADO. Similar results have been obtained for other Brachyura with indeterminate moult, in which the adult condition is be achieved following a gradual abdominal development (Chu, 1999; Flores and Negreiros-Fransozo, 1999).

The absence of males in the area is puzzling. Ferrari (unpublished) reported the capture of two *H. planatus* males in a study conducted between 1980 and 1982 in the area (N= 1355), and another two males were recently collected in Punta Cascajo (about 1 km from the study area) on kelp holdfasts. The presence of *H. planatus* males was also detected in the Malvinas Islands (51°42'S; 57°51'W), and near

Puerto Madryn (42°46'S; 65°02'W), with a male-female ratio of 1:1.83 and 1:1.78, respectively (Ferrari, unpublished). In the Kerguelen Islands (Pointe Guite), the average male:female ratio was 1.37:1 (N = 2088 crabs) (Richer de Forges, 1977). Males are common in other *H. planatus* populations, but they were not found during the samplings in the estuary of the Deseado River. The absence of males would account for the particular developmental features observed in the studied population. Here, cephalothorax width cannot be used as an age criterion or growth parameter because of the almost total overlap of values between ADO and MAT (see Fig. 3). In fact, the largest specimen captured was an ADO female (CW = 14.2 mm). Interestingly, in the *H. planatus* population of the Kerguelen Islands, the ADO females are generally smaller than 12 mm CW and the MAT females larger than 14 mm, with sizes exceeding 19 mm CW (Richer de Forges, 1977). Therefore, the growth process is to all appearances quite different in the two populations. The most plausible hypothesis is that mating and impregnation triggers the terminal or pubertal moult. Therefore, impregnated ADO females moult to MAT and thus begin the reproductive phase, whereas non-impregnated ADO females also undergo moulting, but to a larger size.

Results from the laboratory-reared females revealed that postmoult sizes are premoult-size-dependant, and that there are no abnormal increments during moult. This information, together with the almost complete overlap of CW values for ADO and MAT females, and the large proportion of laboratory-reared ADO females that laid eggs after moulting without the presence of males, leads us to infer that the terminal moult occurs within a wide size range, in association with gonadal maturation, mating and oviposition.

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