

Moult cycle and growth of the crab *Halicarcinus planatus* (Brachyura, Hymenosomatidae) in the Beagle Channel, southern tip of South America

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Abstract The crab *Halicarcinus planatus* is the only hymenosomatid crab that inhabits the southern tip of South America and is the only decapod species that reproduces twice a year in the Beagle Channel. In this article, we study the moult cycle in the field (moult frequency, analysis of size frequency distribution) and linked it with growth studied in the laboratory (absolute and per cent growth increment, Hiatt function). Hiatt functions were similar for males and females. Moult frequency was seasonal: in early austral spring and in austral summer. In females, the pubertal moult is the terminal moult, whereas males continue moulting after attaining the size of morphometric maturity. Moult increment was highly variable. The relationship between absolute moult increment and crab size was described by a quadratic function. Per cent growth increment decreased with size, and relationships were different for each sex: linear for females and quadratic for males. Seven and eight modal groups explained the size frequency distributions for females and males from the field, respectively, and revealed the existence of two cohorts of recruits per year. Further modal analysis was mainly hampered by the high variability of size increment that could make any moulting individual fall in its own or one of two following modal groups. The antagonism between growth and reproduction was evident in small males. We hypothesize that the terminal pubertal moult is an advantageous feature that allows females to maximize

their investment in reproduction after their terminal moult, which allows this species to have two spawnings per year.

Keywords Ecdysis · Decapoda · Sub-Antarctic · SW Atlantic · Terminal moult

Introduction

Growth in crustaceans is a discontinuous process, in which the exoskeleton is periodically replaced during successive moults or ecdyses (Hartnoll 1985). In decapods with determinate growth, this moult may coincide with the last one of the growth process, defined as the terminal pubertal moult (Sampedro et al. 1999, 2003; Corgos and Freire 2006; Vinuesa and Ferrari 2008). This moult marks the complete development of secondary traits, such as the differentiation of chelae in males and abdomen in females, thereby fixing their allometric growth pattern (Sampedro et al. 1999).

In crustacean decapods, the study of growth considers both relative and absolute growth (Hartnoll 1978; Gonzalez-Gurriaran et al. 1995; Carmona-Suárez 2003; Luppi et al. 2004; Biagi and Mantelatto 2006; Protopapas et al. 2007). Particularly in crabs, many studies are based on moult increment and duration of intermoult period in animals maintained in captivity. In species with commercial interest, the absolute growth of different species in their natural habitat has been estimated in an indirect way through the analysis of size frequency distributions, or specially with capture–recapture methods (Le Vay et al. 2007; Diele and Koch 2010). In crabs of the family Hymenosomatidae, the information on growth is very limited. Studies on relative growth have been done in some species (e.g. *Rhyncoplax coralicola*, *Halicarcinus cooki*,

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Hymenosoma orbiculare, *Halicarcinus innominatus*) (Gao et al. 1994; Dunnington 1999; van den Brink 2006; McLay and Van den Brink 2009).

Halicarcinus planatus (Fabricius, 1775) is the only hymenosomatid inhabiting the southern tip of South America, with a sub-Antarctic distribution including the peri-Antarctic islands (Boschi et al. 1969; Richer de Forges 1977; Lucas 1980). It occurs along the south-western Atlantic coast from Mar del Plata (38°S) to the archipelago of Tierra del Fuego (54°S) (Boschi et al. 1992; Spivak 1997). *H. planatus* is the crab most abundant in the intertidal zone of the Beagle Channel (Diez et al. 2011) and the only decapod crustacean that reproduces twice a year in this sub-Antarctic region (Diez and Lovrich 2010).

The aim of this study is to determine different aspects of the moult cycle of *H. planatus* in its natural environment in the intertidal zone of the Beagle Channel. These results are linked with the information about growth in the laboratory of crabs sampled in the same study area.

Materials and methods

Study area

The study was carried out in the intertidal zone of Bahía Brown, Beagle Channel (54°51'S, 67°30'W). The Beagle Channel is located at the southern tip of South America and is a sub-Antarctic coastal marine-estuarine environment (Isla et al. 1999; Aguirre et al. 2012). The environmental conditions are markedly seasonal: sea surface temperature in the lower intertidal zone ranges from 5.2 °C in August to 9.5 °C in January (Laboratorio Biología de Crustáceos, CADIC, unpublished data). Bahía Brown is a bay with rocky beaches, which are composed of boulders of ca. 25 cm diameter sitting on cobbles and shells, providing a lot of interstitial spaces for shelter, where *H. planatus* thrives.

Moult frequency

To identify periods with moult activity in both sexes of *H. planatus*, monthly samples were collected from February 2007 to January 2008 during spring tides in the intertidal zone of Bahía Brown. Individuals were transported to the CADIC laboratory and transferred to 25-l tanks with aerated seawater kept at 8 ± 0.5 °C, 30 PSU, until their dissection, within 2–3 days after capture. At each monthly sampling, sexes were determined and crabs were measured. The carapace width (CW), as a standard measure of body size, was determined at the level of the second posterior spines using an eyepiece mounted on a stereomicroscope. Later, crabs were dissected and the left branchial epipodite

from the third pair of maxillipeds was extracted and mounted on a slide with filtered seawater.

The epipodite was observed under microscope to detect different moult stages, C (intermoult, period of stability teguments), D0 (early pre-moult, beginning of the separation between old and new cuticle), D1 (late pre-moult, the new setae begin to appear inside the old ones) and D2 (moult, crabs which are likely to moult within a few days or hours), according to Richer de Forges (1977). To detect temporal variations in moult stages, both sexes were pooled into three size classes according to size of sexual maturity (Diez and Lovrich 2010). Males were grouped according to the following size intervals: 2.50–6.99, 7.00–11.49 and ≥ 11.50 mm CW. Females were pooled according to the following intervals: 2.5–6.99 mm; immature females ≥ 7.00 mm CW and mature females ≥ 7.00 mm CW. The limit of 7.00 mm CW is the approximate size of the smallest ovigerous female and the smallest male exhibiting allometric change of the right chela, whereas the limit of 11.5 mm CW is the approximate size of a second allometric change in male right chela (Diez and Lovrich 2010). Then, within each month, sex and size class, the proportion of crabs for each moult stage was estimated. A test of difference of proportions (Di Rienzo et al. 2009) was used to evaluate moult frequencies of the different moult stages between males and females within the study period.

Moult increment

In December 2007 and January 2011, crabs were captured in the intertidal zone of Bahía Brown and transported alive to the laboratory with the objective of determining the moult increment of *H. planatus* and its relationship with size. Animals < 6 mm CW were kept individually in plastic flasks (300 ml) at 8 ± 0.5 °C with an artificial photoperiod 12:12 h (light/darkness) and salinity 30 PSU. Every second day, water was changed and Tetra Color granules were supplied as food, ad libitum. Animals > 6 mm CW were kept individually in a seawater re-circulation system. They were placed into PVC cylinders with the bottom covered by a 1-mm mesh, floating in 25-l tanks in the flow-through system, 10 crabs per tank. In both cases, the presence of exuviae was recorded daily. Before and after moult, crabs were measured (CW) using an eyepiece mounted on a stereomicroscope. Post-moult size was recorded 4 days after moult to ensure sufficient time for hardening of the exoskeleton.

The moult increment was expressed as follows:

Hiatt model (Hiatt 1948): $L_{t+1} = aL_t + b$

where, L_t is the pre-moult CW at stage t , L_{t+1} is post-moult CW at the following stage, a is the slope and b is the y-intercept of the regression line.

Table 1 Growth of *H. planatus* expressed as Hiatt functions for males and females, and also for both sexes per time elapsed in captivity before moulting

	Equation of regression	<i>n</i>	<i>r</i> ²	<i>F</i>	<i>P</i>
Both sexes	Post-moult CW = 1.04 pre-moult CW + 0.67	173	0.97	69.83	<0.0001
Females	Post-moult CW = 1.03 pre-moult CW + 0.76	73	0.96	1744.25	<0.0001
Males	Post-moult CW = 1.05 pre-moult CW + 0.6	100	0.97	3165.31	<0.0001
Ho equal slopes				0.72	0.39
Ho equal ordinates				0.13	0.72
Month 0	Post-moult CW = 1.06 pre-moult CW + 0.61	49	0.97	1398.69	<0.0001
Month 1	Post-moult CW = 1.02 pre-moult CW + 0.79	59	0.96	1448.98	<0.0001
Month 2	Post-moult CW = 1.07 pre-moult CW + 0.36	40	0.96	986.76	<0.0001
Month 3	Post-moult CW = 1.00 pre-moult CW + 0.96	25	0.98	1068.22	<0.0001
Ho equal slopes				1.5	0.2
Ho equal ordinates				2.62	0.06

n sample size, *r*² coefficient of determination, *F* statistic *P* probability that the slope equals to zero

Size increment: post-moult CW – pre-moult CW

Percentage increment: (post-moult CW – pre-moult CW) · pre-moult CW⁻¹ · 100

To evaluate differences between sexes in the Hiatt model, an analysis of covariance (ANCOVA) was conducted following Sokal and Rohlf (1995). No differences were found (Table 1), so sexes were pooled and an ANCOVA was used to evaluate the effect of captivity time on growth. Homogeneity of slopes among groups of data was checked prior to the ANCOVA.

Analysis of size frequency distributions

Size frequency distributions were analysed from monthly samples collected in the intertidal of Bahía Brown between November 2006 and October 2007. Each month, five replicates were randomly taken with a 0.25 m⁻² quadrat along a transect 0.20–0.25 m above the chart datum. In each quadrat, crabs at the surface were manually collected and sediment up to 5 cm deep was sifted through a 1-mm sieve and fixed in a solution of 6 % buffered formaldehyde in seawater. All crabs were measured using an eyepiece mounted on a stereomicroscope. Size frequency distributions were made using two different intervals, because the software is limited to process less than 24 size classes. For CW < 10 mm CW, size classes were 0.5 mm, whereas for CW > 10 mm, CW interval values were 0.75 mm CW. Observed size frequency distributions were fitted to the expected values assuming a mixture of normal distributions by the least squares method, through a modification of the procedure proposed by MacDonald and Pitcher (1979) (MIX) described by Bas et al. (2005). Mathematically, the mixed normal probability density function *g* is a weighted sum of *k* components densities, where *k* is assumed to be known.

$$g\left(\frac{x}{\pi, \mu, \sigma}\right) = \mu_1 f\left(\frac{x}{\mu_1, \sigma_1}\right) + K + \pi_k f\left(\frac{x}{\mu_k, \sigma_k}\right)$$

Parameters π , μ and σ represent the proportion, the mean and the standard deviation, respectively, of the *k* component normal distributions. Parameter values were obtained by a fitting procedure implemented in Visual Basic for Excel® 2007 (Microsoft Corp., Redmond, WA) by minimizing the sum of squared differences between the observed and expected values with Solver®, a non-linear optimization utility for Excel®. The goodness of fit was assessed by the χ^2 statistic at $\alpha = 0.05$. Previous to the analysis with MIX, for each sex, size frequency distributions of all sampling dates were pooled and the number of modal stages was determined using the Bhattacharya (1967) method with FISAT II software (v 12.2).

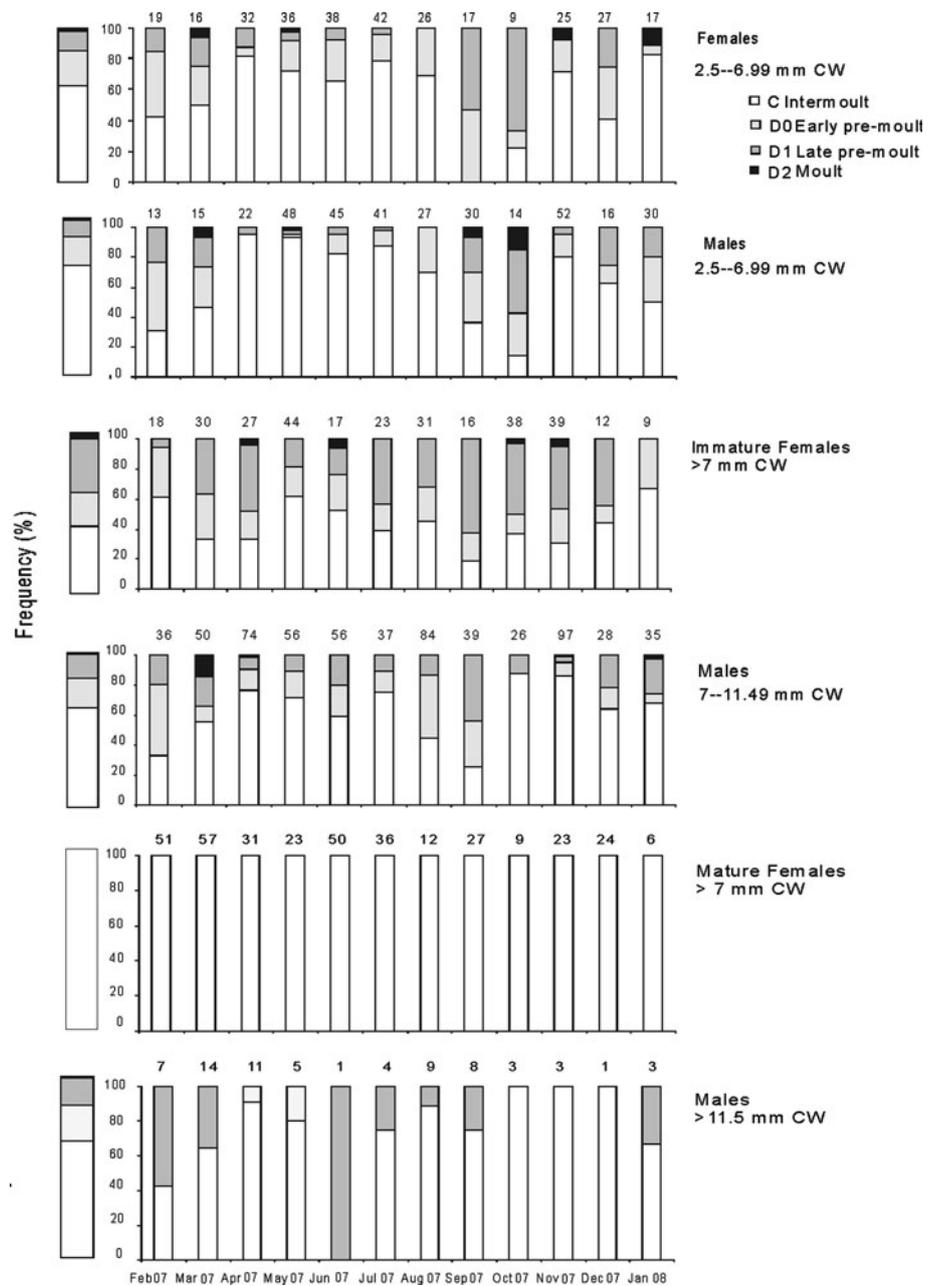
The number of modal groups present in each size frequency distribution (*k* value) was established at first visually from each graph. The modes were added or removed when goodness of fit was poor, standard deviations were high (more than 15 % of the value of the corresponding mean) or too low (lower than 5 %), or when differences between successive modes were completely out of the range of observed increment per moult. Hereafter, the products of the analysis of size frequency distributions are called modal groups, instead of instars or cohorts.

Results

Moult frequency

The temporal variation in the morphology of the branchial epipodite of *H. planatus* revealed high frequencies of D0, D1 and D2, which are indicative of imminent moult. These stages were present in crabs 2.5–6.99 mm CW of both

Fig. 1 Proportions of individuals of *H. planatus* in different moult stages according to state of the branquial epipodite of the third pair of maxillipeds. Bars on the left indicate the overall annual percentage. Numbers above bars are sample sizes



sexes during two different periods: summer (February–March) and early spring (September–October) (Fig. 1). During summer, there were no differences between sexes in the proportion of individuals with evidence of moult activity (difference of proportions, $p = 0.62$). In contrast, during spring, the proportion of females with moult activity was higher than males (difference of proportions, $p = 0.03$) (Fig. 1).

Over the year, in immature females ≥ 7 mm CW, branchial epipodites in D0, D1 and D2 stages were present in higher proportions during July–December and March–April (Fig. 1). Within this size range throughout all the

year, females showed higher moult activity than males 7–11.49 mm (differences of proportions $p < 0.001$).

Mature females show no moulting activity at all during the study period. Contrastingly, males ≥ 11.5 mm CW showed evidence of moulting throughout the year though the proportion was lower than for males 2.5–6.99 mm CW (Fig. 1).

Moult increment

The relationship between pre- and post-moult sizes was similar in both sexes of *H. planatus* (Fig. 2). The slopes of

Hiatt lines for males and females were significantly >1 (Fig. 2), and no differences between sexes were observed (Table 1). On the other hand, the Hiatt relationship between pre-moult and post-moult size was not affected by time in captivity (Table 1). Therefore, to further analyse both size and per cent increment at moult, all individuals were pooled (Fig. 2).

The size increment at moult of *H. planatus* differed with sex and size. Size increment was very variable in both sexes (range: 0.2–1.8 mm CW; Fig. 3; Table 2). The best fit to the relationship between pre-moult size and size

increment was obtained with quadratic equations (Fig. 3; Table 2). Females showed a variable size increment (range: 0.3–1.8 mm) for the same size range of 5–8 mm CW (Fig. 3), yet decreased (range: 0.6–1 mm) towards larger sizes >8 mm CW (Fig. 3). Males showed a less variable size increment than females in small sizes (range: 0.49–1.27 and 0.3–1.7 mm for males and females of 4–4.5 mm CW, respectively) yet was higher in crabs of medium sizes ca. 5 mm CW.

As the size increases, the per cent increment differed with sex and pre-moult size. The relationship between pre-moult size and per cent increment was described with quadratic and linear equations for males and females, respectively (Table 2; Fig. 3). The greatest variability in the per cent increment of *H. planatus* was observed in small and medium sizes, for females and males, respectively (Fig. 3).

Analysis of size frequency distributions

The analysis of monthly size frequency distributions of *H. planatus* showed a polymodal distribution (Figs. 4 and 5), and the fitted modal groups explained the distribution with a good fit ($0.98 < p \leq 1$, Tables 3, 4). During the studied period, 7 and 8 fitted modal groups explained the size frequency distributions for females and males from the field, respectively. To define the products of this analysis, we prefer to use a cautionary approach by using the term “modal group” instead of cohort or instars, mainly because these groups could be composed of individuals of different ages and instar stages (see “Discussion” for a detailed explanation). The modal group 0 was observed only for males during December and in a low proportion (Fig. 4; Table 3). This modal group showed the lowest mean size

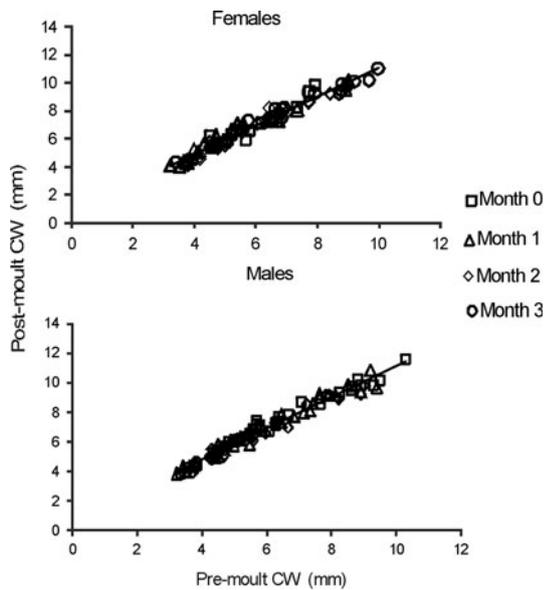


Fig. 2 Growth of both sexes of *H. planatus* provided as Hiatt function. Number of months indicates the elapsed time in captivity before moulting

Fig. 3 Growth of both sexes of *H. planatus* provided as size increment and per cent increment on crab pre-moult size

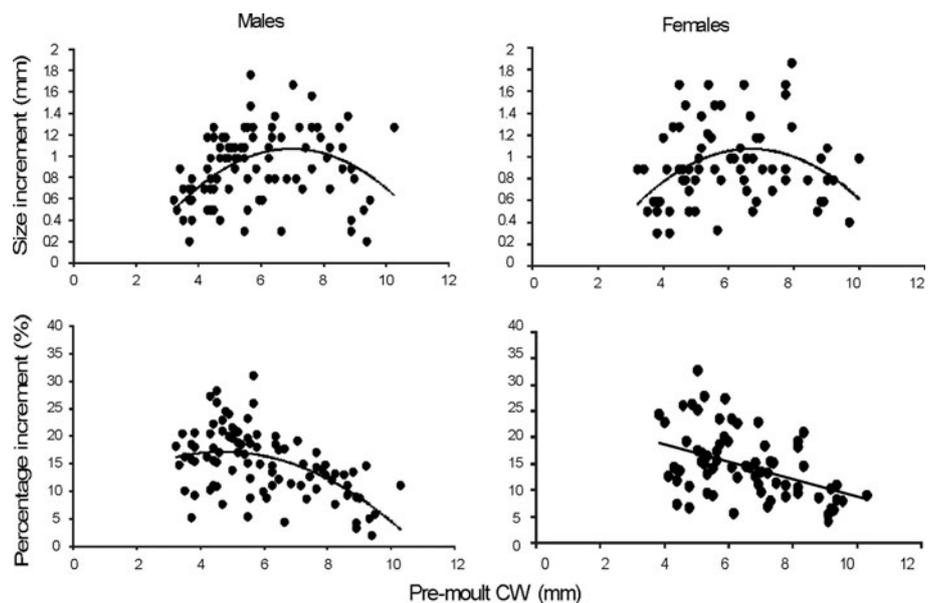
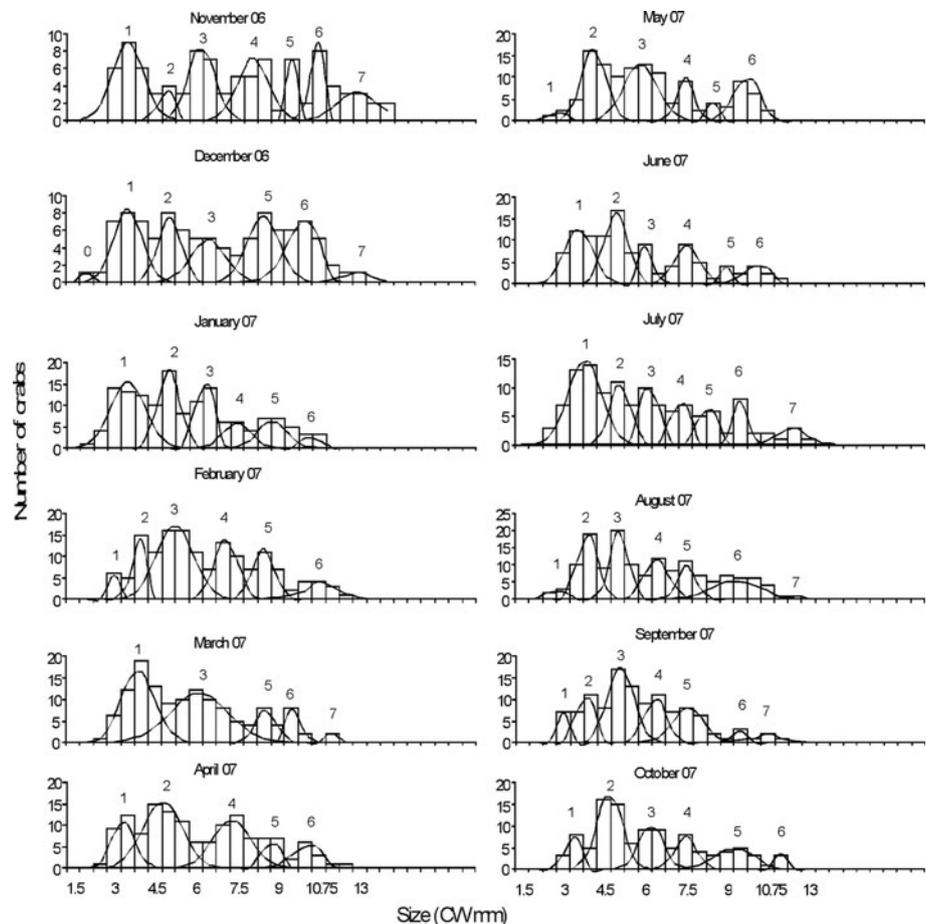


Table 2 Growth of *H. planatus* expressed as functions of absolute increment and per cent increment on crab size, which are plotted in Fig. 3

Sex	Method	Equation of regression	<i>n</i>	<i>r</i> ²	<i>F</i>	<i>P</i>
Female	Size increment	SI = -0.04 pre-moult CW ² + 0.57 pre-moult CW - 0.82	73	0.14	10.01	0.0023
	Per cent increment	PI = -1.84 pre-moult CW + 27.32	73	0.21	18.4	0.0001
Male	Size increment	SI = -0.04 pre-moult CW ² + 0.57 pre-moult CW - 0.93	100	0.21	16.76	0.0001
	Percent increment	PI = -0.45 pre-moult CW ² + 4.25 pre-moult CW + 7.14	100	0.28	7.77	0.0064

n sample size, *r*² coefficient of determination, *F* statistic, *P* associated probability

Fig. 4 Monthly size frequency distributions of male *H. planatus*. Modal groups fitted by least squares method (see Table 3, method described by Bas et al. 2005) and adapted from MIX procedure by Macdonald and Pitcher (1979)

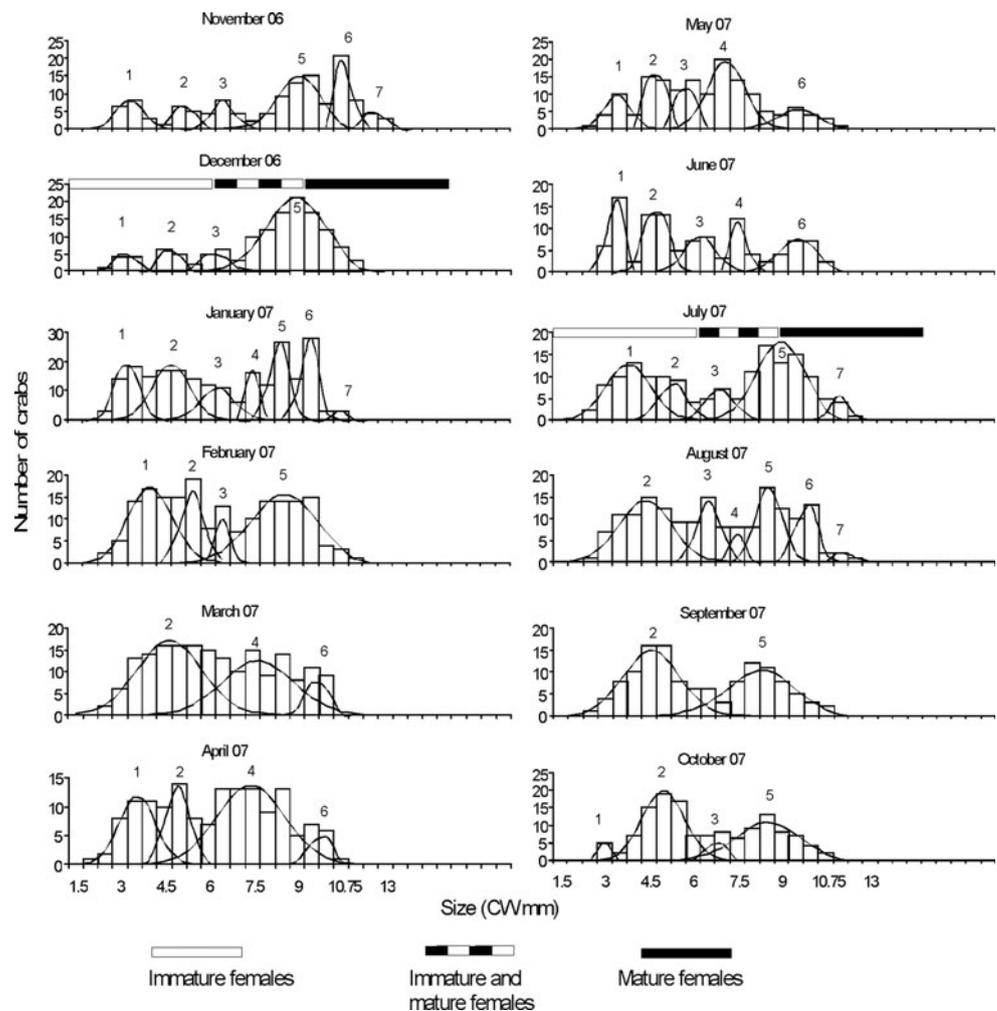


found in the field (Table 3), probably corresponding to the stage Crab II. Crab I obtained from larval experiments is 1.1 mm CW (Diez et al. 2012), and considering the size increment reported here (Table 2), the assigning of the modal group 0 to the stage Crab II is reasonable. The modal group 1 for both males and females occurred in high proportions in two different periods: summer (January–March) (max: 0.37 and 0.33 for males and females, respectively) and early winter (June–July) (max: 0.36 and 0.29 for males and females, respectively) (Tables 3, 4). In some months (e.g. November, April, July), the modal group 1 showed values of standard deviation higher in females than males (Tables 3, 4). This pattern is consistent

with the moult increment observed in the laboratory, in which the size increment of crabs showed a higher variability in female than in males in the range size of 2.5–6.99 mm CW (Fig. 3).

Modal groups including male and female crabs of the range size 2.5–6.99 (modal groups 2–3–4) were present during most of the study period. In females, the modal group 5, which includes the size at maturity 9.6 mm CW, occurred in November–February and July, the time of the year when the terminal pubertal moult takes place (Fig. 5). The modal group 7, corresponding to sizes >10 mm CW (Table 4), presented the greatest temporal discontinuity, probably because few females reached these sizes and

Fig. 5 Monthly size frequency distributions of female *H. planatus*. Modal groups fitted by least squares method (see Table 3, method described by Bas et al. 2005) and adapted from MIX procedure by Macdonald and Pitcher (1979). White and black bars indicate the size ranges of immature and mature females, respectively, placed in months when the pubertal terminal moult occurs



therefore had low abundances at the population and were only detectable only in some months like November, January, July and August (Fig. 5).

In males, at least six modal groups were observed throughout the year (Fig. 4). The modal groups (3–4) corresponding to intermediate mean sizes showed the highest values of standard deviation (max: 1.04; Table 3). This pattern also coincides with the variability observed in the moult increment of males (Fig. 3). The modal group 7 corresponding to higher mean sizes was always present in low proportions (max: 0.11) and only in a few months (e.g. November–December 2006 and July–September 2007) (Fig. 4).

Discussion

Results of this study provide first information on the growth of *H. planatus* in Southern South America. Specifically, we studied moult frequency in the field, moult

increment in the laboratory and analysed the size frequency distributions of crabs from an intertidal zone of the Beagle Channel. Studies on growth of hymenosomatid crabs are very limited (e.g. Richer de Forges 1977; Gao et al. 1994), and the present article is the first one on Hymenosomatidae that links laboratory and field growth data. In a previous study, Richer de Forges (1977) shows the growth of *H. planatus* with animals kept in the laboratory. Our results demonstrate that this species has a variable growth pattern in both sexes which could be explained by the presence of both immature and mature individuals, in a same range size.

The Beagle Channel population of *H. planatus* exhibits different moult temporal patterns according to size. Small crabs moult during early spring and late summer, which coincides with the period observed in the Kerguelen Islands population (Richer de Forges 1977). In the Beagle Channel, a typical sub-Antarctic environment, these periods are characterized by the beginning of an increase in sea surface temperature and primary productivity in early

Table 3 Modal groups of size frequency distributions of males *H. planatus* fitted by least squares through the procedure described by Bas et al. (2005)

Mes	0	1	2	3	4	5	6	7	χ^2	<i>P</i>
Nov-06		3.50 ± 0.55 0.26	4.81 ± 0.17 0.06	6.19 ± 0.48 0.21	8.08 ± 0.54 0.20	9.51 ± 0.03 0.01	10.50 ± 0.30 0.13	12.80 ± 0.98 0.11	7.27	0.99
Dec-06	1.86 ± 0.12 0.01	3.52 ± 0.52 0.22	5.06 ± 0.40 0.15	6.48 ± 0.62 0.15		8.48 ± 0.58 0.22	10.00 ± 0.65 0.23	12.86 ± 0.73 0.03	3.18	0.99
Jan-07		3.50 ± 0.62 0.33	5.00 ± 0.40 0.25	6.31 ± 0.30 0.18	7.50 ± 0.50 0.10	8.80 ± 0.50 0.11	10.30 ± 0.30 0.04		5.95	0.99
Feb-07		3.01 ± 0.01 0.00	3.86 ± 0.20 0.12	5.24 ± 0.65 0.38	7.10 ± 0.42 0.20	8.49 ± 0.38 0.15	10.80 ± 0.90 0.08		5.37	0.99
Mar-07		3.90 ± 0.60 0.37		6.13 ± 1.04 0.44		8.59 ± 0.35 0.10	9.64 ± 0.20 0.07	11.43 ± 0.04 0.01	0.47	1.00
Apr-07		3.35 ± 0.40 0.16	4.80 ± 0.70 0.39		7.33 ± 0.69 0.28	8.78 ± 0.22 0.07	10.15 ± 0.60 0.11		3.12	0.99
May-07		2.78 ± 0.17 0.03	4.13 ± 0.42 0.29	5.85 ± 0.60 0.32	7.50 ± 0.30 0.12	8.50 ± 0.00 0.00	9.80 ± 0.50 0.20		5.23	0.99
June-07		3.57 ± 0.50 0.29	4.95 ± 0.42 0.32	6.16 ± 0.17 0.10	7.55 ± 0.44 0.18	9.03 ± 0.04 0.01	10.19 ± 0.50 0.10		3.93	0.99
July-07		3.81 ± 0.60 0.36	5.11 ± 0.37 0.16	6.20 ± 0.30 0.14	7.30 ± 0.28 0.10	8.30 ± 0.33 0.09	9.52 ± 0.27 0.08	12.10 ± 0.80 0.06	6.22	0.99
Aug-07		2.77 ± 0.25 0.03	3.91 ± 0.35 0.23	5.08 ± 0.33 0.22	6.45 ± 0.42 0.17	7.57 ± 0.30 0.10	9.40 ± 0.89 0.16	11.90 ± 0.14 0.09	4.69	0.99
Sept-07		2.96 ± 0.18 0.05	3.81 ± 0.28 0.16	5.11 ± 0.47 0.36	6.38 ± 0.37 0.17	7.59 ± 0.55 0.19	9.36 ± 0.19 0.03	10.60 ± 0.75 0.04	8.46×10^{-12}	1
Oct-07		3.31 ± 0.19 0.11	4.72 ± 0.45 0.38	6.25 ± 0.42 0.20	7.51 ± 0.36 0.13	9.30 ± 0.73 0.17	11.39 ± 0.13 0.02		0.16	1

Size (in mm CW) ± standard deviation and proportions of modal groups are shown. Critical value $\chi^2 = 27.58$, χ^2 statistic, *P* associated probability of goodness of fit

Table 4 Modal groups of size frequency distributions of females *H. planatus* fitted by least squares through the procedure described by Bas et al. (2005)

Mes	1	2	3	4	5	6	7	χ^2	<i>P</i>
Nov-06	3.37 ± 0.44 0.14	5.19 ± 0.32 0.08	6.52 ± 0.35 0.11		9.12 ± 0.70 0.40	10.99 ± 0.33 0.21	12.50 ± 0.41 0.05	1.92	0.99
Dec-06	3.18 ± 0.30 0.07	4.73 ± 0.20 0.08	6.20 ± 0.40 0.08		9.00 ± 1.00 0.77			5.70	0.99
Jan-07	3.25 ± 0.37 0.17	4.74 ± 0.60 0.25	6.32 ± 0.54 0.13	7.58 ± 0.16 0.07	8.42 ± 0.31 0.19	9.42 ± 0.27 0.18	10.61 ± 0.07 0.02	2.46	0.99
Feb-07	4.05 ± 0.72 0.33	5.47 ± 0.38 0.16	6.58 ± 0.21 0.06		8.59 ± 1.10 0.45			3.99	0.99
Mar-07		4.70 ± 1.10 0.50		7.70 ± 1.20 0.40		9.70 ± 0.35 0.08		5.56	0.98
Apr-07	3.60 ± 0.62 0.24	4.97 ± 0.40 0.18		7.46 ± 1.15 0.52		9.85 ± 0.39 0.06		5.64	0.99
May-07	3.46 ± 0.43 0.14	4.74 ± 0.24 0.19	5.75 ± 0.24 0.14	7.15 ± 0.62 0.40		9.61 ± 0.70 0.13		5.71	0.99
June-07	3.34 ± 0.21 0.21	4.76 ± 0.37 0.26	6.27 ± 0.50 0.19	7.64 ± 0.22 0.14		9.61 ± 0.64 0.21		0.46	0.99
July-07	3.83 ± 0.74 0.29	5.34 ± 0.45 0.12	6.91 ± 0.46 0.10		9.00 ± 0.80 0.45		11.50 ± 0.44 0.05	4.56	0.99
Aug-07		4.40 ± 0.87 0.36	6.55 ± 0.39 0.16	7.47 ± 0.22 0.04	8.57 ± 0.45 0.23	9.90 ± 0.40 0.15	11.85 ± 0.17 0.06	4.85	0.99
Sept-07		4.60 ± 0.93 0.55			8.32 ± 1.12 0.45			3.95	0.99
Oct-07	3.00 ± 0.04 0.01	5.01 ± 0.69 0.51	6.76 ± 0.17 0.07		8.57 ± 1.03 0.41			1.16	0.99

Critical value $\chi^2 = 27.58$. Size (in mm CW) ± standard deviation and proportions of modal groups are shown. χ^2 statistic, *P* associated probability of goodness of fit

spring, reaching the maximum temperature in summer (Almandoz et al. 2011). Although in crustacean decapods endogenous factors impinge on frequency of moulting, environmental variables could affect the moult cycle (see Chang 1995 for a review). The seasonal pattern of moulting observed in small sizes of *H. planatus* has also been found in other cold water species, even in other decapods of the Beagle Channel (e.g. *Paralomis granulosa*, large juvenile and adult *Lithodes santolla*) (Lovrich and Vinuesa 1995; Lovrich et al. 2002).

During the studied period, all mature females were in intermoult stage, which indicates the absence of ecdysis once maturity is reached. Namely, the pubertal moult is a terminal moult. By contrast, morphometrically mature, large males of *H. planatus* show evidence of moulting after the size of morphometric maturity (ca. 9 mm CW, Diez and Lovrich 2010), particularly during summer months (February–March). In addition to the morphometric change at the pubertal moult, where chela shows a first allometric positive change, some males exhibit a second morphometric change in their chela, being significantly longer and wider at 10.6 mm CW (Diez and Lovrich 2010). This pattern suggests that males continue moulting, likely corresponding to modal groups 6 and 7 (Fig. 4), after the first morphometric change. However, from our variable data, it was difficult to determine the number of moults between these two morphometric changes. The terminal moult in males, if present, could occur at the moult stage corresponding to this second allometric change of the chela. By judging the size and abundance of these males in the population (10.1–13.6 mm CW, 6.2 % of male population; Diez and Lovrich 2010), it is probable that not all males pass through this moulting event. Furthermore, it is likely that the lifetime after the male terminal moult may be relatively brief and crabs die shortly afterwards.

In the Beagle Channel, the per cent size increment per moult of *H. planatus* was variable in small crabs and showed a tendency to decrease in larger sizes. This pattern is also observed in other crustacean decapods, both in species with indeterminate growth (e.g. *Munida gregaria*, *L. santolla*, *Neohelice granulata*, *Ucides cordatus*) (Vinuesa et al. 1990; Tapella 2002; Luppi et al. 2004; Mokhtari et al. 2008) as well as in species with determinate growth (e.g. *Maja squinado*) (Sampedro et al. 2003). Growth requires energetic resources before and after ecdysis, in order to moult and to develop gametes in reproductive organs, being antagonistic processes for a fixed energy budget (Hartnoll 1985).

In *H. planatus* females, this opposed relationship begins before reaching the maturity size. This involves a change in energy allocation: part of the energy assigned to growth during the immature phase is diverted to reproduction, with the consequent marked decrease in the per cent size

increment per moult. In fact, *H. planatus* shows one of the highest reproductive output among Brachyura species (ca. 20 % of the body weight per egg batch; Hines 1982; Diez and Lovrich 2010) only exceeded by parasitic pinnotherids species (Hines 1992). Like other hymenosomatids (McLay and Van den Brink 2009), *H. planatus* females can only lay eggs after the pubertal moult, when the abdomen acquires the shape to accommodate the egg mass (Vinuesa and Ferrari 2008). Hence, its high reproductive output can be related with the presence of a terminal pubertal moult. We hypothesize that the terminal pubertal moult is an advantageous feature that allows females to maximize their investment in reproduction after their terminal moult. Having all the energy devoted to reproduction is particularly important in the sub-Antarctic environment that enables *H. planatus* to produce two egg batches per year, which, in turn, allow us to further postulate that determinate growth is an advantageous feature in case of invasion to the Antarctica (Diez and Lovrich 2010).

By contrast, *H. planatus* males attain the gonadal maturity at 3.6 mm CW (Diez and Lovrich 2010), and the process of sexual maturity competes with growth (Hartnoll 1985), as follows. This size at gonadal maturity corresponds to young animals: the smallest male with spermatozoa at deferens ducts is 2.2 mm CW, likely attributable to stages Crab II or Crab III. This is a size relatively small compared to female gonadal maturity or pubertal/terminal moult attained in the range of 7.0–9.6 mm CW (Diez and Lovrich 2010).

The analysis of the modal groups from size frequency distributions of the Beagle Channel population is novel for *H. planatus*. We preferred to use the term “modal groups” instead of instars or cohorts, because of the great variability of moulting increment. However, the first two smaller modal groups likely correspond to juvenile instars, because crabs of the same instar further larger could belong to different modal groups, as aforementioned. We recognize the limitation of our analysis since both applied methods (Bhattacharya’s and MIX) have subjective decisions on, for example, the number of modal groups. A formal and more objective modal analysis of the size structure of the *H. planatus* population (e.g. Smith and Jamieson 1989; Lovrich and Vinuesa 1995; Lovrich et al. 1995; Smith and Botsford 1998; Lovrich et al. 2002) was hampered by different factors. First, the high variability of size increment at moulting combined with the quadratic function that relates the moult increment with the crab size (Fig. 3) makes individuals that belong to a modal group could remain in this same modal group while others crabs could move to the next modal group, even after two moult periods. Alternatively at moulting, small crabs could “skip” a modal group and go fell into the next one. Second, modal groups were present at all samplings, without the

possibility of identifying an instar that could have matched with a modal group, with the exception of the very small sizes. Third, the blurring modes, particularly in females, as a result of the accumulation of adult, terminally moulted individuals >7 mm CW from different size classes. Although modes remained in the same size range during all the studied period (Figs. 4, 5) suggesting that modes are instars, averages of modal groups (Tables 3, 4) contradict this perception, since for two contiguous modal groups, average sizes can be similar. Hence, the analysis of the modal displacements of any cohorts through the study period is complex and can be speculative, even though modal groups can be traced in the population.

Nevertheless, based on the high proportions of modal groups corresponding to small sizes, it is possible to confirm two recruitment periods or juvenile migrations from settlement places (Diez et al. 2011): summer (January–March) and early winter (June–July). Both periods coincide with the two spawning per year of this species (Diez and Lovrich 2010) and with the two larval cohorts found in the meroplankton assemblage of the Beagle Channel (Lovrich 1999). The existence of these two juvenile cohorts in two different periods, the high variability recorded in the moult increment in the laboratory (Fig. 3) and the presence of a terminal moult suggest that the modal groups could be composed by crabs of different ages and moult stages.

The presence of a terminal moult divides Hymenosomatidae into two groups of species: one maintains the ecdysis after the pubertal moult as *H. orbiculare* females and *Elamenopsis lineata* (Lucas 1980). Another fraction is composed of several species of *Halicarcinus* spp. and *Amarinus* spp. which have a pubertal terminal moult (Richer de Forges 1977; Lucas 1980; Vinuesa and Ferrari 2008). This pattern of development has been recorded for some families of decapods. For example, within the Majoidea group, the pubertal and terminal moults are one and the same moult (Hartnoll 2001). *H. planatus* arrives at the pubertal moult with ripe ovaries (Diez and Lovrich 2010), and although its mating system is still unknown, we suggest that this species probably has a mating strategy similar to the “Majoid” group established by McLay and López Greco (2011). Nevertheless, the presence of a terminal moult in males of certain majoid crabs has been largely controversial (Conan and Comeau 1986; Dawe et al. 1991) and was corroborated recently (Fonseca et al. 2008).

The terminal pubertal moult of *H. planatus* females could occur in two different periods: December and July (Diez and Lovrich 2010). The modal groups that contain the size corresponding to maturity (i.e. modal group 5, Fig. 5) presented the highest proportions in December and July. In this context, in which females vary in the number of moults to attain sexual maturity, it is complex to estimate the age of maturity, by calculating the time elapsed

since the arrival to intertidal zone (~3.6 mm CW; Diez et al. 2011) to the maturity size (ca. 9 mm AC; Diez and Lovrich 2010). However, according to the variability in size increment (Table 1; Fig. 3) and an intermoult period of ca. 90 days (estimated from individuals that moulted twice in captivity, (Diez 2011)), females could take 5–9 moult instars (ca. 15–27 months) to attain the size at maturity. Females *H. planatus* of the Kerguelen Islands population take 27 months to reach the size at maturity of 14.1 mm CW, probably at crab instar 12 (Richer de Forges 1977). These differences in size at maturity between both populations could be related to differences in the temperature regimes between the Beagle Channel and Kerguelen Islands. Temperature may affect the growth pattern (Hartnoll 2001) altering the number and sizes of moults that precede the terminal moult as it occurs in, for example, *Chionoecetes opilio* (Burmeister and Sainte-Marie 2010).

Within Hymenosomatidae, the terminal moult may have evolved as part of a strategy of small size and a high reproductive rate (McLay and Van den Brink 2009). This is an important trait in the life history of the sub-Antarctic population of *H. planatus*. The cessation of growth allows allocating most resources to reproduction, favouring the reproductive success in a highly seasonal environment with constrained availability of energetic resources, such as the sub-Antarctic one.

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