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To cite this article: Martín Varisco, Julia Colombo, Tomás Isola & Julio Vinuesa (2016): Growth and maturity of the spider crab *Halicarcinus planatus* (Brachyura: Hymenosomatidae) females in the southwestern Atlantic Ocean. Can these parameters be influenced by the population sex ratio?, *Marine Biology Research*, DOI: [10.1080/17451000.2016.1183792](https://doi.org/10.1080/17451000.2016.1183792)

To link to this article: <http://dx.doi.org/10.1080/17451000.2016.1183792>



Published online: 28 Jun 2016.



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ORIGINAL ARTICLE

Growth and maturity of the spider crab *Halicarcinus planatus* (Brachyura: Hymenosomatidae) females in the southwestern Atlantic Ocean. Can these parameters be influenced by the population sex ratio?

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ABSTRACT

The *Halicarcinus planatus* populations of the southwestern Atlantic Ocean show a highly variable sex ratio and a large size overlapping between females in the last immature instar (ADO) and mature (MAT) females. We hypothesized that these facts are related and that female impregnation has a central role in this relation. Non-impregnated ADO females delay maturity and would continue to grow, leading to size overlapping. This scenario is most probable in populations with a scarcity of males and could affect the growth, maturity and population structure. The sex ratio and female size distribution of several populations of the southwestern Atlantic Ocean were analysed. Growth and maturity were studied in two populations with different sex ratios (Camarones, a population with males, and Rada Tilly, a population where no males were found). Size overlapping was not related to the population sex ratio. Size overlapping was due to a variable moult increment and, to a lesser extent, to delayed maturity. Females mated before terminal moult in both populations. However, in Camarones, physiological maturity was not related to impregnation, while in Rada Tilly, vitellogenic oocytes were observed only in impregnated females. Also, differences in the number of spermatophores in female spermathecae were related to the sex ratio. Our results showed that the morphological maturity pattern of females was not influenced by the population sex ratio. However, physiological maturity was related to female impregnation and sex ratio. Also, the variation in the number of spermatophores suggests differences in the mating system related to the sex ratio.

ARTICLE HISTORY

Received 15 October 2015
Accepted 20 April 2016

RESPONSIBLE EDITOR

Ingo Wehrtmann

KEYWORDS

Delayed maturity; female impregnation; sex ratio; terminal moult

Introduction

The spider crab *Halicarcinus planatus* (Fabricius, 1775) is a small brachyuran crab of the family Hymenosomatidae. Its geographic distribution is closely associated with the Antarctic Circumpolar Current: from Bahía de Taltal (35°S) to Cape Horn in Chile, and along the Tierra del Fuego and Patagonian coasts to 38°S in Argentina (Boschi et al. 1992). It is also found around the Malvinas (Falkland) Islands (Atlantic Ocean), Prince Edward, Crozet and Kerguelen Islands (Indian Ocean), and Macquarie, Campbell and Auckland islands, up to the Cook Strait (Pacific Ocean) (Melrose 1975). On the Patagonian coast, *H. planatus* is common on rocky shores, lower intertidal and sublittoral bottoms, and occurs down to a depth of about 10–15 m (Vinuesa 2005). Crabs are more abundant in sheltered areas and can also be found on exposed coasts but in places protected from the onslaught of

the waves and where water is retained. The *H. planatus* populations of the southwestern Atlantic Ocean exhibit a high variation in sex ratio. In some populations (e.g., Puerto Deseado: López Gappa et al. 1982; Vinuesa & Ferrari 2008a, 2008b; Ferrari et al. 2010; or Rada Tilly: Vinuesa et al. 2011), males are very scarce, whereas in other populations (e.g., Bahía Brown: Diez & Lovrich 2013; or Camarones: Julio Vinuesa 2007, personal communication) males are abundant. The causes of these variations are unknown. However, an early male dispersal to subtidal cryptic microhabitats has been proposed to explain the deviation in sex ratio (Vinuesa et al. 2011; Diez & Lovrich 2013).

The growth pattern among hymenosomatids is variable: some species as *Hymenosoma orbiculare* Desmarest, 1823 and *Elamenopsis lineata* A. Milne-Edwards, 1873 have indeterminate growth (Broekhuysen 1955; Lucas 1980), whereas other species, including *H. planatus*, show determinate growth (Lucas &

Hodgkin 1970; Richer de Forges 1977; Lucas 1980; Vinuesa & Ferrari 2008a; McLay & Van den Brink 2009; Diez & Lovrich 2013). Different traits related to the growth of *H. planatus* have been studied in the Kerguelen Islands (Richer de Forges 1977), Puerto Deseado (Vinuesa & Ferrari 2008a), Comodoro Rivadavia (Vinuesa et al. 2011) and the Beagle Channel (Diez & Lovrich 2013). Different stages in females according to the abdomen morphology have been identified (Vinuesa & Ferrari 2008a): immature (IMM), adolescent (ADO), which refers to the last instar before terminal moult, and mature (MAT). A common feature in *Halicarcinus* spp. populations is the significant size overlapping between ADO and MAT females (Vinuesa & Ferrari 2008a; Vinuesa et al. 2011). According to McLay & Van den Brink (2009), size overlapping in *H. cookii* Filhol, 1885 females is related to variable moult increments in immature crabs and precocious maturity in the female fraction. Vinuesa & Ferrari (2008b) suggested that size overlapping could be related to the fact that if ADO females are not impregnated, they moult into a new ADO stage without allometric changes between the carapace and the abdomen.

Size and age at maturity play a main role in the life cycle of species because selection pressures change drastically (Stearns 1992). Sexual maturity in decapods has been traditionally analysed from three points of view: (a) morphometric maturity (which refers to changes in the relative growth of secondary sexual characteristics), (b) physiological maturity (which refers to the presence of mature gonads) and (c) functional maturity (which refers to the capacity to mate) (Somerton 1980; Paul 1992; Corgos & Freire 2006). The sequence in which these events occur is variable in different life histories. In some hymenosomatid species such as *Amarinus lacustris* (Chilton, 1882), *A. paralacustris* (Lucas, 1970) and *H. cookii*, females may mate in a morphologically immature stage (Lucas 1980; McLay & Van den Brink 2009). Also, in *H. planatus* from Ría Deseado (Santa Cruz), all females mate and develop their gonads at the ADO stage (Vinuesa & Ferrari 2008a, 2008b).

Time of maturity is an allocation decision that results from the balance between costs and benefits of starting reproduction investment at this age (Stearns 1992; Ramirez Llodra 2002). This decision is affected by several environmental variables, energy support and population context. Mating occurs before terminal (pubertal) moult in *H. planatus* females, and based on the fact that a lower probability of mating is expected in populations with a low number of males, we considered that the sex ratio of *H. planatus* populations

affects the growth pattern of females, time of maturity and female size distribution of the population. The following hypotheses were tested: (1) in populations with few males, size overlapping between ADO and MAT females is larger than in populations with abundant males; (2) size overlapping is due to a delayed pubertal moult in the absence of impregnation; and (3) impregnation is necessary for females to reach physiological and gonadal maturity in populations with few and abundant males. Here, we analysed the relation between sex ratio and size overlapping between ADO and MAT females in several *H. planatus* populations of the southwestern Atlantic Ocean. Growth was studied in two populations with different sex ratios (Camarones and Rada Tilly) to determine whether size overlapping could result either from a maturity delay in the absence of impregnation or from a variable moult increment. We also studied the relation between physiological maturity and impregnation in both populations.

Materials and methods

Study area

Samplings were conducted along the coasts of Patagonia and Tierra del Fuego, between 42° and 54°S. The sampling areas comprised two biogeographic provinces: the Magellanic and the Argentine. The coastal water is a mixture of subantarctic water from the Cape Horn Current and low-salinity water from the Magellan plume. The latter, formed by the discharge from the Strait of Magellan, extends along the inner shelf of southern Patagonia (Palma et al. 2008). North of San Jorge Gulf, the area is more influenced by warm temperate waters of the Brazil current. Along the coast of Patagonia, the average tidal amplitude ranges between 6.14 m (Puerto Lobos, Chubut) and 8.67 m (Río Gallegos, Santa Cruz). The tidal amplitude in Tierra del Fuego is lower due to conflicting influences of tidal waves from the Pacific and Atlantic Oceans. In Atlantic waters, rocky shores are mainly formed by consolidated limestone. Basaltic rocky shores can also be found in some areas as Camarones or Bustamante Bay (Chubut).

Sampling

In the austral summer of 2010, crabs were collected on rocky shores of several locations of the southwestern Atlantic Ocean: Puerto Lobos (41°59'S, 65°04'W), Nuevo Gulf (42°48'S, 64°53'W), Camarones (44°50'S, 65°43'W), Bustamante Bay (45°08'S, 66°32'W), Rada

Tilly (45°56'S, 67°33'W), Puerto Deseado (47°45'S, 65°55'W), Desvelos Bay (48°06'S, 65°54'W), San Julián (49°15'S, 67°40'W), Strait of Magellan (52°23'S, 69°28'W), San Pablo Cape (54°17'S, 66°41'W) and Ushuaia (54°48'S, 68°18'W). In Brown Bay (54°51'S, 67°30'W) samplings were carried out in December 2014 (Figure 1). Crabs were collected manually in intertidal environments and by scuba diving in subtidal environments. Crabs were initially stored in sealed bags and subsequently fixed in 4% formalin. These samples were used to determine population sex ratio and size overlapping.

To analyse growth and maturity, females of *Halicarcinus planatus* were collected in the intertidal zone of Camarones and Rada Tilly. Samplings for these experiments were carried out in autumn (April and May) of 2013, 2014 and 2015, because this time has higher moult activity and is close to the beginning of the reproductive period (Vinuesa & Ferrari 2008a; Vinuesa et al. 2011).

Laboratory procedures

Sex ratio and size distribution

In the field samples of the southwestern Atlantic Ocean populations, the sex ratio (expressed as males/males + females) and the operational sex ratio (OSR) were

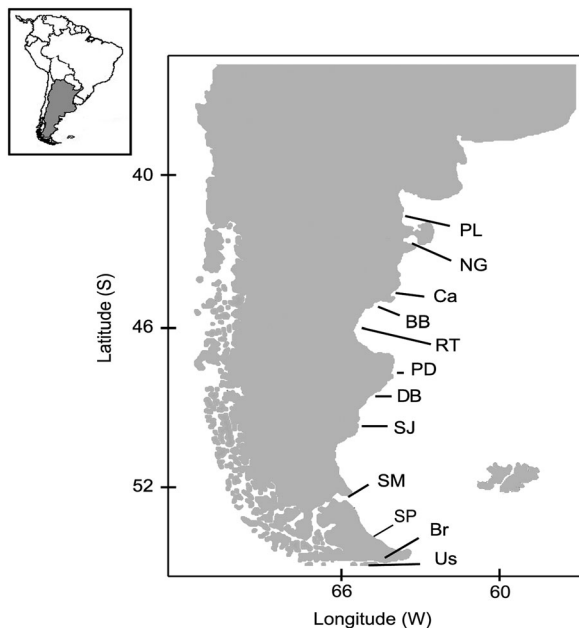


Figure 1. Sampling sites in the southwestern Atlantic Ocean. PL, Puerto Lobos; NG, Nuevo Gulf; Ca, Camarones; BB, Bustamante Bay; RT, Rada Tilly; PD, Puerto Deseado; DB, Desvelos Bay; SJ, San Julián; SM, Strait of Magellan; SP, San Pablo Cape; Br, Brown Bay; Us, Ushuaia.

recorded. The OSR was calculated including only ADO and MAT females. Carapace width (CW) and abdomen width (AW) were measured using a digital caliper (± 0.01 mm) following the criteria of Richer de Forges (1977). According to abdomen morphology, females were classified as IMM, ADO or MAT. The overlapping index was calculated as $OI\% = (CW_{\max\text{ADO}} - CW_{\min\text{MAT}} / CW_{\max\text{MAT}} - CW_{\min\text{ADO}}) \times 100$. This index differs from that used by McLay & Van den Brink (2009) because the morphology of the last juvenile instar of *Halicarcinus planatus* (ADO) is known. The presence and number of spermatophores in ADO females were also recorded by dissection of the spermathecae. Spearman correlation ($H_0: \rho = 0$) was used to test the relation between sex ratio and overlapping index of populations. The correlation was considered significant if $P < 0.05$.

Growth pattern and morphological maturity

Crabs were placed in individual plastic mesh cages in aquaria. Food (*Exosphaeroma* sp. isopods and commercial fish food) was supplied three times a week, and seawater was changed once a week. Premoult ($CW_{(\text{pre})}$) and postmoult ($CW_{(\text{post})}$) sizes were measured. Moult increment was calculated as $MI = CW_{(\text{post})} - CW_{(\text{pre})}$ and relative increment was calculated as $RI = (CW_{(\text{post})} - CW_{(\text{pre})}) / CW_{(\text{pre})}$. The presence of spermatophores was recorded by visual examination of the spermathecae.

A regression was made between $CW_{(\text{pre})}$ and growth indicators ($CW_{(\text{post})}$, MI and RI). Analysis of covariance (ANCOVA) was used to determine whether MI differs between ADO-ADO moult and ADO-MAT moult. The homogeneity of slopes was previously tested. Comparison was considered significant when $P < 0.05$. An independence test was used to evaluate the relation between impregnation and morphological maturity.

Physiological maturity and impregnation

CW and AW were measured in autumn samples from Camarones and Rada Tilly. Females were classified according to the criteria mentioned above. ADO females were dissected and their gonads were removed. Oocytes were classified as previtellogenic and vitellogenic according to Vinuesa & Ferrari (2008b). The presence of vitellogenic oocytes was considered as an indicator of physiological maturity. The diameter of 30 oocytes was measured to the nearest 0.01 mm using a stereoscopic microscope with an ocular micrometer. The presence and number of spermatophores in ADO females were also recorded.

Results

Sex ratio and size overlapping

The sex ratio was not related to the overlapping index of populations (Spearman $\rho = -0.68$; $P = 0.02$). Moreover, no latitudinal patterns in sex ratio and overlapping size were observed. The sex ratio differed from the expected 0.5 in several populations. In six populations, no males were found. Females of *Halicarcinus planatus* reached morphological maturity in a wide CW range in all localities analysed. Size overlapping between immature and mature females was recorded in eight of 11 populations studied (Figure 2). In Puerto Lobos and Nuevo Gulf, the number of ADO females was scarce (five and one, respectively), while no ADO females were found in Brown Bay. In all populations, MAT females were impregnated. In samples without males, females showed only one

spermatophore in their spermathecae, while in populations where males were present the number of spermatophores ranged between 1 and 4 (Table I).

Growth and morphological maturity

The CW of cultured crabs ranged from 5.03 to 11.9 mm and 6.25 to 11.07 for Rada Tilly ($N = 123$) and Camarones ($N = 43$), respectively. In both localities, females showed positive allometric growth ($b > 1$) and MI values were variable. In Camarones, MI was not related to CW_{pre} , while in Rada Tilly MI and CW_{pre} were related. The RI was higher in small crabs and decreased at larger sizes in both localities (Figure 3).

Females of *Halicarcinus planatus* reached morphological maturity in a wide range of sizes in both Camarones (5.96–14.62 mm CW) and Rada Tilly (4.60–12.07 mm). Significant differences were found in MI

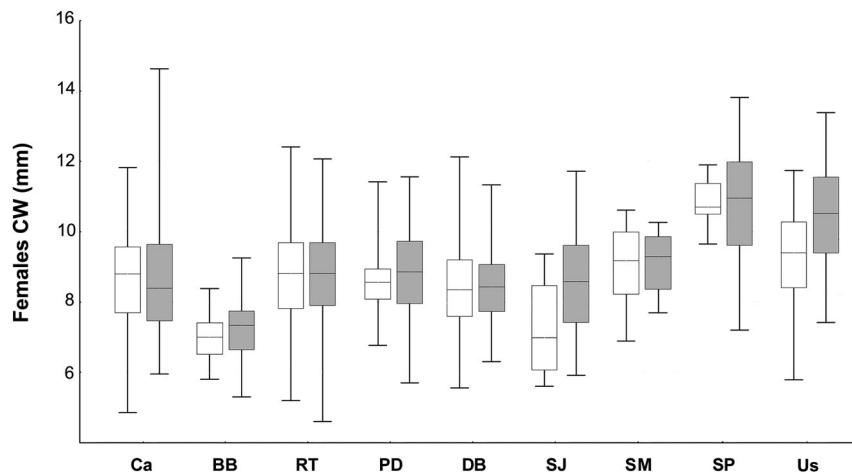


Figure 2. Carapace width of adolescent (white) and mature (grey) females of *Halicarcinus planatus* in several populations of the southwestern Atlantic Ocean. Ca, Camarones; BB, Bustamante Bay; RT, Rada Tilly; PD, Puerto Deseado; DB, Desvelos Bay; SJ, San Julián; SM, Strait of Magellan; SP, San Pablo Cape; Us, Ushuaia. Box plots show the median and inter-quartile range, with whiskers representing the maximum and minimum values.

Table I. Population data of *Halicarcinus planatus* of the southwestern Atlantic Ocean.

Locality	N	SR	P	OSR	♀ CW (mm)	OI (%)	S
Puerto Lobos	247	0.52	0.50	0.46	5.80–14.26	–	1
Nuevo Gulf	48	0.64	0.41	0.56	5.85–12.54	–	1
Camarones	691	0.45	0.49	0.45	5.96–14.62	47.1	1
Bustamante Bay	104	0.02	0.02	0.02	5.31–9.25	52.8	1
Rada Tilly	532	0	<0.01	0	4.60–12.07	99.1	1–3
Puerto Deseado	159	0	<0.01	0	5.51–14.2	89.1	1–4
Desvelos Bay	521	0	<0.01	0	6.31–11.33	56.7	1–3
San Julián	199	0	<0.01	0	5.92–11.71	46.2	1–3
Strait of Magellan	62	0	<0.01	0	7.69–10.26	69.6	1–2
San Pablo Cape	53	0	<0.01	0	7.20–13.82	66.1	1–3
Brown Bay	67	0.34	0.64	0.55	10.87–14.74	–	1
Ushuaia	628	0.01	<0.01	0.01	8.06–13.78	51.2	–

Sex ratio (SR), operational sex ratio (OSR), carapace width (CW) of size at maturity of females, and overlapping index (OI) between adolescent and mature stages, and number of spermatophores (S). The P values indicate the probability of rejecting the null hypothesis of the test of goodness of fit (1:1). Yates' correction was used.

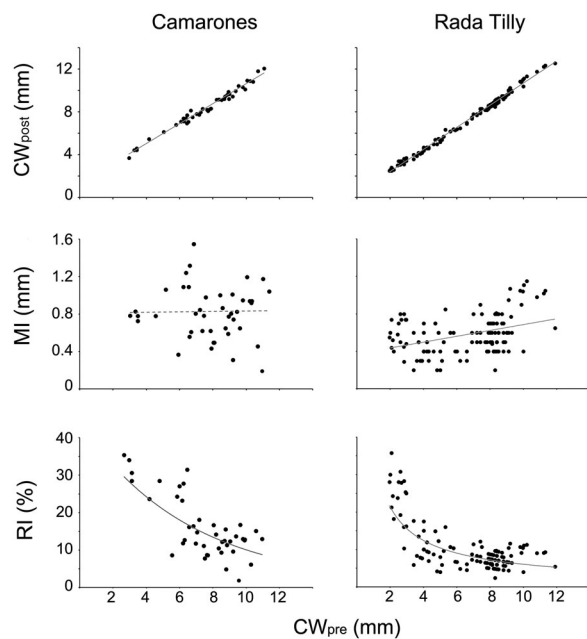


Figure 3. Relation between premoult carapace width of *Halicarcinus planatus* females ($CW_{(pre)}$) and moult indicators: post-moult carapace width ($CW_{(post)}$), moult increment (MI) and relative increment (RI). Continuous and dashed lines represent significant and non-significant regressions, respectively.

values between females that moulted into a mature stage and ADO females that moulted into a new ADO stage in both localities (Figure 4). All females that reached morphological maturity carried spermatophores in their spermathecae. By contrast, females that moulted into a new ADO stage were not impregnated (Table II). MAT females laid eggs 72 h after moulting, while females that moulted into a new ADO stage exhibited no vitellogenic oocytes in their ovaries after moulting.

Field data (2013) showed that the proportion of ADO decreased significantly at the beginning of the reproductive periods (April–May) in both localities. Only 10% of females were ADO before the moulting period at the end of April in Camarones. In Rada Tilly, the proportion of ADO females in the population decreased from 72% in April to 18% in May.

Physiological maturity and impregnation

In both Camarones and Rada Tilly, ovary development began at the ADO stage. In Camarones, mean oocyte size in non-impregnated females was more variable than that in impregnated females. Also, the presence of secondary vitellogenic oocytes was independent of the impregnation of females (χ^2 Yates correction = 0.21, $P = 0.63$). In Rada Tilly, the oocyte size of impregnated females was different from that of non-

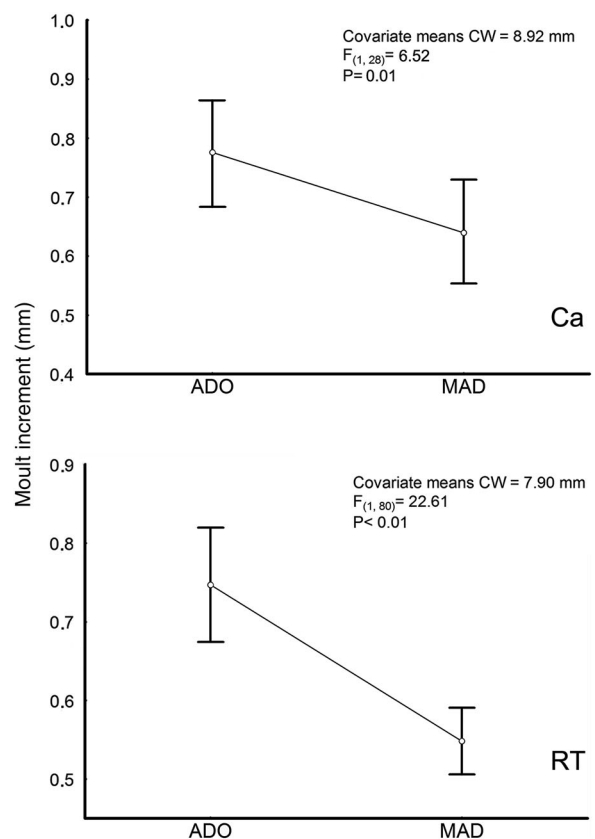


Figure 4. Analysis of covariance between adolescent females (ADO) of *Halicarcinus planatus* that moulted to new ADO stages and ADO that reached morphological maturity (MAT) in Camarones (Ca) and Rada Tilly (RT). Covariate means, F value and probability of rejecting the null hypothesis are indicated for both populations.

impregnated ones (Figure 5). In this population, the presence of secondary vitellogenic oocytes was related to impregnation (χ^2 Yates correction = 5.7, $P = 0.01$).

Discussion

In marine invertebrates, the strategy for resource allocation to growth and reproduction is one of the main aspects of life history. Time at first maturity plays a pivotal role in this strategy and could be influenced by several environmental factors and by the population

Table II. Moulting of *Halicarcinus planatus* females from Rada Tilly and Camarones.

	ADO – ADO		ADO – MAT		No moult		P
	lm	non-lm	lm	non-lm	lm	non-lm	
Rada Tilly	–	14	5	–	3	6	<0.01
Camarones	–	8	20	–	–	2	<0.01

ADO, adolescents; MAT, mature; lm, impregnated females; non-lm, non-impregnated females. The P values indicate the probability of rejecting the null hypothesis of independence of kind of moult (ADO-ADO or ADO-MAT) and impregnation (Fisher exact test).

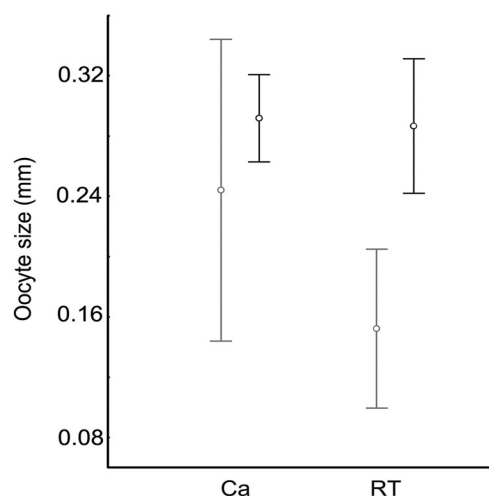


Figure 5. Oocyte size in non-impregnated (grey) and impregnated females (black) of *Halicarcinus planatus* in Camarones (Ca) and Rada Tilly (RT) populations. Vertical lines show standard deviations.

context (Ramirez Llodra 2002). In decapod crustaceans, sexual maturity can be analysed from three points of view: physiological, morphometric and functional maturity. Traditionally, it has been considered that crabs reach morphological maturity before functional maturity. However, some hymenosomatid species, including *Halicarcinus planatus*, mate before morphological maturity (Richer de Forges 1977; Lucas 1980; Vinuesa & Ferrari 2008a, 2008b; McLay & Van den Brink 2009). Females of *H. planatus* develop their gonads and then moult into a morphologically mature stage, and finally lay their eggs. This pattern in the maturity sequence was not influenced by the population sex ratio.

Maturity is an allocation decision that results from the balance between costs and benefits of starting investing in reproduction at this age (Stearns 1992; Ramirez Llodra 2002) and stopping growth in the case of hymenosomatids. Non-impregnated ADO females delay their maturity and moult into a large-size ADO stage (Vinuesa & Ferrari 2008b). McLay & Van den Brink (2009) showed that *H. cookii* females have two strategies, precocious moults and delayed moults, and suggested that these two ways are possible because the net reproductive rate is similar for both strategies. The cost of delaying maturity may be offset by higher fertility in future clutches (Vinuesa & Ferrari 2008a; McLay & Van den Brink 2009; Ferrari et al. 2010). In our study, delayed maturity was recorded in several populations of the southwestern Atlantic Ocean and this strategy was not related to the sex ratio of populations. Regardless of the sex ratio of the population, a low number of females

showed this strategy. A decrease in ADO female abundance was observed in Camarones at the beginning of the reproductive season. In Rada Tilly, where larger proportions of ADO females can be expected due to the scarcity of males, large proportions of ADO females were impregnated and moulted at MAT stages. Similarly, 90% of the ADO females of Puerto Deseado were found to be impregnated before the beginning of the breeding season (Vinuesa & Ferrari 2008a), and in Comodoro Rivadavia most ADO females moulted at MAT stages (Vinuesa et al. 2011). Despite the scarcity of males in these populations, this does not seem to be a limitation for female impregnation.

Delaying the terminal moult could contribute to explaining size overlapping between ADO and MAT stages. However, our results suggest that a variable moult increment is the main factor to explain size overlapping. In *H. cookii*, McLay & Van den Brink (2009) found that size overlapping results from variable moult increments. These authors suggested that the large size range over which *H. cookii* reaches maturity could be related to the timing of the terminal moult. Females that moult in winter have lower moult increments than females that moult in summer. We found no evidence of seasonal effects on moult increments. Variable moult increments were observed in autumn moults and a synchronism in ADO moults has been previously reported (Vinuesa et al. 2011). Moreover, in accordance with the moult increments recorded in immature females of Camarones and ADO size distributions, ADO females could moult three times into new ADO stages in order to explain the maximum size recorded. Also, differences in growth and age at maturity of cohorts can contribute to explaining size overlapping and the decrease in proportion of ADO. Two spawning periods have been recorded in Puerto Deseado (Vinuesa & Ferrari 2008b) and Brown Bay (Diez & Lovrich 2009), and a wide temporal presence of larvae of *H. planatus* in San Jorge Gulf has been reported previously (Vinuesa et al. 2011). Consequently, there are differences in age (and size) in the same annual class. For smaller females, it could be more efficient to mature at a smaller size than to wait until the next season to mature.

In Camarones and Rada Tilly, gonadal development took place entirely during the ADO stage. The short time between terminal moult and egg extrusion provides additional support for this observation. Also, this fact has previously been observed in *H. planatus* populations of Puerto Deseado (Vinuesa & Ferrari 2008a, 2008b) and Brown Bay (Diez & Lovrich 2011), and recorded in other hymenosomatid species (Lucas 1980; McLay & Van den Brink 2009). However, the

relationship between physiological maturity and impregnation showed differences between Camarones and Rada Tilly populations, which could be attributed to differences in sex ratio. In Camarones the development of ovaries was not related to impregnation, while in Rada Tilly, as in Puerto Deseado (Vinuesa & Ferrari 2008a, 2008b), where males are scarce, the development of ovaries is related to impregnation. The role of impregnation in the maturity of ovaries and its implications in the mating system are not clear yet in all sampled populations. We hypothesized that the presence of males could contribute to gonadal development, although we cannot provide data to support this hypothesis.

The populations of *H. planatus* in the southwestern Atlantic Ocean showed a variable sex ratio. Males were very scarce in several populations (Table III). The causes of this deviation are still unknown. Vinuesa et al. (2011) suggested that mature males have cryptic habits in subtidal environments, which makes them difficult to find. According to Diez & Lovrich (2011), the presence of *Macrocystis pyrifera* (Linnaeus) C. Agardh forests in subtidal environments can explain the absence of males in intertidal environments, because males prefer the complex habitat provided by holdfasts. However, males of *H. planatus* have been recorded in intertidal areas with subtidal kelp forests (e.g. Camarones), but not on holdfasts of *M. pyrifera* in other localities, such as Rada Tilly, Puerto Deseado or San Julián (López Gappa et al. 1982; Vinuesa & Ferrari 2008a; Vinuesa et al. 2011).

Brown et al. (1995) proposed that species decrease their performance toward their distribution range limits. Testing this hypothesis, Rivadeneira et al.

(2010) found that in five species of porcellanid crabs of the Chilean coast, the female proportion was maximized at the centre of its range, while at both edges of the distribution the populations tended to be dominated by males. We can also hypothesize that the scarcity of males is a trait of mid-distribution populations and that male abundance is observed in marginal areas of the *H. planatus* distribution range, as in Brown Bay (Beagle Channel), Malvinas (Falkland) Islands and north of Camarones. However, samples taken nearly 50 km west of Brown Bay, in Ensenada Bay ($N=790$), showed only two males during two years of samplings (Lucrecia Ferrari 1981, personal communication). Thus, the mechanism proposed to explain porcellanid sex ratios can hardly be responsible for the strong deviations of *H. planatus*, even in nearby areas. Further studies should be conducted to elucidate this behaviour of the species. Regardless of the causes of sex ratio variations, these differences had no effect on the growth pattern and size overlapping between ADO and MAT females. However, our results show that this has some implications for the reproductive strategy of *H. planatus*. The variation in the number of spermatophores suggests differences in the mating system between populations with abundant males and those with few males. In our study, populations with abundant males carried up to four spermatophores in the spermatheca. Therefore, there would be some sperm competition in the fertilization process, as mentioned for *H. cookii* (Van den Brink & McLay 2009). Moreover, differences in the physiological maturity strategy between the Camarones and Rada Tilly populations could be related to the sex ratio of these populations.

Table III. Summary of sex ratio in different populations of *Halicarcinus planatus* of the southwestern Atlantic Ocean.

Localities	Habitat sampling	Sex ratio	References
Puerto Lobos	Intertidal rocky shores, long-line mussel cultures	0.52	Present study
Nuevo Gulf	Intertidal rocky shores	0.64	Present study
Camarones	Intertidal rocky shores	0.45	Present study
Bustamante Bay	Intertidal rocky shores and <i>Gracilaria gracilis</i> beds	0.02	Present study
Rada Tilly	Intertidal and subtidal rocky shores, long-line mussel cultures, <i>M. pyrifera</i> holdfast and subtidal artificial collectors	0.04/0	Vinuesa et al. (2011) and present study
Puerto Deseado	Intertidal and subtidal rocky shores and <i>M. pyrifera</i> holdfasts	0 (all)	López Gappa et al. (1982), Vinuesa & Ferrari (2008a, 2008b), and present study
Desvelos Bay	Intertidal and subtidal rocky shores and <i>M. pyrifera</i> holdfast	0	Present study
San Julián	Intertidal and subtidal rocky shores, mussel culture boxes and <i>M. pyrifera</i> holdfasts	0	Present study
Rio Gallegos	Rio Gallegos estuary	0	Torres & Vargas (2007)
Strait of Magellan	Intertidal and subtidal rocky shores and <i>M. pyrifera</i> holdfasts	0	Present study
San Pablo Cape	Intertidal rocky shores	0	Present study
Brown Bay	Intertidal rocky shores	0.5/0.4	Diez & Lovrich (2011) and present study
Ushuaia	Intertidal and subtidal rocky shores	0	Present study

Acknowledgements

We thank Gustavo Lovrich for allowing us to check samples from kelp holdfasts of the Beagle Channel during 1999–2001 and Lucrecia Ferrari for her unpublished data on the Beagle Channel and Malvinas (Falkland) Islands. We also thank the editor and anonymous reviewers for their careful reading of our manuscript and their constructive comments and suggestions.

Funding information

This work was supported by the Universidad Nacional de la Patagonia San Juan Bosco.

Disclosure statement

No potential conflict of interest was reported by the authors.

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