

UNIVERSIDADE FEDERAL DO RIO GRANDE DO SUL
INSTITUTO DE BIOCÊNCIAS
DEPARTAMENTO DE ZOOLOGIA
LABORATÓRIO DE CARCINOLOGIA

Trabalho de Conclusão de Curso:

**Fecundity and egg volume of the shore crab *Pachygrapsus transversus*
(Gibbes, 1850) (Decapoda: Grapsidae) in Rio Grande do Sul**

Raquel Peñas Torramilans

Orientadora: Profa. Dra. Mariana Terossi Rodrigues Mariano

PORTO ALEGRE - RS

2019

**Fecundity and egg volume of the shore crab *Pachygrapsus transversus*
(Gibbes, 1850) (Decapoda: Grapsidae) in Rio Grande do Sul**

Raquel Peñas Torramilans

Trabalho de Conclusão de Curso, apresentado à
Comissão de Graduação do Curso de Ciências
Biológicas da Universidade Federal de Rio Grande
do Sul, como parte dos requisitos para a obtenção
do grau de Bacharelado em Ciências Biológicas

Aprovado em 3 de julho de 2019

BANCA EXAMINADORA

Ms. Pedro Augusto da Silva Peres

Dra. Kelly Martinez Gomes

Dra. Mariana Terossi Rodrigues Mariano

*Esas olas verdes, mansas, esas espumas blanquecinas
donde se mece nuestra pupila, van como rozando nuestra
alma, desgastando nuestra personalidad, hasta hacerla puramente
contemplativa, hasta identificarla con la Naturaleza.*

Pio Baroja

ACKNOWLEDGMENT

I want to thank you:

to Professora Mariana Terossi, for the guidance, initiative and confidence she has put in me since the first day that I started this work and my adventure in Brazil.

to all my family, especially father, mother and brothers to be present from the distance and let me follow all the opportunities that are given to me.

to the Laboratorio de Carcinologia, first, to all those who participated in the field trips: Mariana Terossi, Mariana Marques, Karmine, Ana, Amanda, Fernanda, and second, those that caused that there was always coffee: Augusto, Felipe, Emily, Diego, Paula, Victoria, Camila... in general, for everything they have taught me directly or indirectly.

to the Universidade Federal de Rio Grande do Sul and the Universidad de Alicante to create the agreement that has made me able to do this work many kilometers from my house, and that has helped me to grow both academically and personally.

to friends, those who I met in Brazil and those who are at home, specifically to Alberto and Raquel, to help me trust myself and support me day by day.

to finish... to Raúl, for the calls 11,011 km distance, that they encouraged me, on the one hand, to continue loving him, and on the other to continue wanting to work with the marine sciences.

ABSTRACT

Pachygrapsus transversus is an abundant crab in the intertidal ecosystems in tropical and subtropical coast of Atlantic and Pacific Ocean. In tropical regions has a continuous breeding. This study aims to investigate the fecundity and egg volume of *P. transversus* in a subtropical region (Torres, Rio Grande do Sul, Brazil) in two seasons. Ovigerous females were sampled in summer and autumn 2019 at Praia Prainha sited in Rio Grande do Sul. In the laboratory they were identified, measured in relation to carapace width, and the eggs were classified according to their development stages, counted and measured. The main results were: fecundity was correlated positively with the size of the female ($\rho=0.5898$, p-value < 0.05); females produced eggs in both seasons presenting the highest fecundities in summer; the egg volume was higher in autumn (p-value < 0.05) and was larger than those found in lower latitudes; the egg volume increased during its development and it was not detected egg loss. Thus, as expected, the reproduction of *P. transversus* presented seasonal and latitudinal differences, these differences are attributed to the environmental conditions. Moreover, some females were carrying larvae in the abdomen providing additional parental care to the brood. Apparently, this is the first case reported in *Pachygrapsus*. It is important to continue researching on reproductive aspects of *P. transversus* in all seasons in the south of Brazil, since it has not been studied yet.

Key words: Atlantic Ocean, Brazil, reproduction, latitude, seasonality

RESUMO

Pachygrapsus transversus é um caranguejo abundante nos sistemas intertidais na costa tropical do Atlântico. Nas regiões tropicais apresenta reprodução contínua ao longo do ano. O objetivo deste estudo foi investigar a fecundidade e o volume de ovos de *P. transversus* na região subtropical (Torres, Rio Grande do Sul, Brazil) em duas estações do ano. Fêmeas ovígeras foram amostradas no verão e outono de 2019 na Praia Prainha em Torres. No laboratório elas foram identificadas, medidas quanto a largura da carapaça, e os ovos foram divididos em estágios de desenvolvimento, contados e medidos. Os principais resultados foram: a fecundidade foi positivamente correlacionada com o tamanho da fêmea ($\rho=0.5898$, $p\text{-value} < 0.05$); fêmeas produziram ovos nas duas estações, sendo os maiores valores encontrados no verão; o volume dos ovos foi maior no outono ($p\text{-value} < 0.05$) e foram maiores que aqueles encontrados em latitudes menores; durante o desenvolvimento, o volume dos ovos aumentou e não foi detectada perda de ovos. Assim, como esperado, a reprodução de *P. transversus* apresentou diferenças sazonais e latitudinais, estas diferenças são atribuídas a condições ambientais. Além disso, algumas fêmeas estavam carregando larvas no abdômen provendo um cuidado parental adicional para a prole. Aparentemente, este é o primeiro caso reportado para *Pachygrapsus*. É importante continuar pesquisando os aspectos reprodutivos do *P. transversus* em todas as estações do sul do Brasil, uma vez que ainda não foi estudado.

Palavras-chave: Oceano Atlântico, Brasil, reprodução, latitude, sazonalidade

SUMMARY

INTRODUCTION	7
<i>Pachygrapsus transversus</i>	7
Reproduction	8
METHODS AND MATERIALS	11
Study area	11
Sampling and laboratory analysis	11
Data analysis	13
RESULTS	15
Ovigerous females	15
Fecundity and egg volume	16
Parental care	19
Egg loss and increased egg volume	19
DISCUSSION	22
Ovigerous females	22
Fecundity and egg volume	22
Parental care	23
Variations with latitude	24
Egg loss and increased egg volume	24
CONCLUSIONS	26
BIBLIOGRAPHY	27

Fecundity and egg volume of the shore crab *Pachygrapsus transversus* (Gibbes, 1850) (Decapoda: Grapsidae) in Rio Grande do Sul

INTRODUCTION

Pachygrapsus transversus

The infraorder Brachyura, known as one of the most diversified aquatic invertebrate taxa, contains all true crabs and is composed of over 7250 species in 104 families (DAVIE et al., 2015; MA et al., 2019). Grapsidae, commonly known as shore crabs, is one of these families and it has 8 genera with 40 species (NG et al., 2008; IP et al., 2015). One of these genera is *Pachygrapsus* Randall, 1840, with 14 species distributed worldwide (POUPIN et al., 2005).

The brachyuran crab analyzed in this study was *Pachygrapsus transversus* (Gibbes, 1950), this species occurs over a wide geographic range: western Atlantic from USA (North Carolina) to Uruguay (Montevideo) including some islands from Caribbean Sea and Bermuda, eastern Atlantic from South Portugal to Namibia including Canary Islands, Madeira and Cape Verde Islands, Mediterranean Sea, and Denmark (Copenhagen, introduced) (RATHBUN, 1918; CHRISTIANSEN, 1969; MANNING & HOLTHUIS, 1981; WILLIAMS, 1984; MELO, 1996; SCHUBART et al., 2005).

Pachygrapsus transversus is an abundant species in the intertidal zone in tropical and subtropical regions of the Brazilian coast (FLORES & NEGREIROS-FRANSOZO, 1999). This species occurs on rocky surface, climbing over them just above or below the water surface feeding or hide in crevices (HARTNOLL, 1965; FLORES & NEGREIROS-FRANSOZO, 1999). It can also be found in association to biogenic substrata, specifically sand reefs built by the sabellariid polychaeta *Phragmatopoma caudata* Krøyer in Mörch, 1863 and mussel beds formed by *Mytilaster solisianus* (d'Orbigny, 1842) (FLORES & NEGREIROS-FRANSOZO, 1999; BOSA & MASUNARI, 2002). These substrata may provide shelter and food resources for the associated fauna (HECK & HAMBROOK, 1991, THIEL & ULLRICH, 2002). Those reefs may hold very dense aggregations of young grapsids (SPIVAK et al., 1994) where they

find shelter in empty polychaeta tubes or other small refuges originated from the hydrodynamism (FLORES & NEGREIROS-FRANSOZO, 1999).

Pachygrapsus transversus is not only one of the most abundant grapsids on the Brazilian coastline but is also considered a key species in intertidal ecosystems. This is an omnivorous species, feeding on both animal and algae (OGAWA, 1977), and it may impact the structure of rocky shore assemblages (CHRISTOFOLETTI et al., 2010). Similarly, it participates in other food and energy chains both marine and terrestrial as it can be consumed by other species like fish, birds, racoons (ABELE et al., 1986) or frogs (SAZIMA, 1971).

Reproduction

After fertilization, brachyuran species carry the eggs attached to pleopods forming a mass of eggs (COBO & OKAMARI, 2008; TEIXEIRA et al., 2017). They protect the eggs long enough during their development, investing large amounts of energy in brood care so that the egg contains all the required nutrients (WEAR 1974; FERNÁNDEZ et al., 2000).

Studies related to the fecundity of organisms provide us with a great deal of information on animal populations in order to better understand their reproductive strategies and how the population evolves (GARCIA-MONTES et al., 1987). In some decapods, fecundity is measured by the number of eggs produced and is directly related to the size of the animal (HINES 1982; COREY & REID, 1991; MANTELATTO & FRANSOZO, 1997). Egg production and egg development is limited, in part, by climatic conditions, especially in species inhabiting more extreme environments (COBO & OKAMARI, 2008).

The number of eggs is also influenced by factors such as the stage of development of the embryo (GARDNER, 1997; TUCK et al., 2000). In most Pleocyemata, the size of the eggs increases as the egg develops, occupying all available space (WEAR, 1970; WEAR 1974; JONES & SIMONS, 1983; LARDIES & CASTILLA, 2001) consequently, the number of eggs decreases throughout the incubation (OTTO et al., 1989; PÉREZ, 1990; REID & COREY, 1991; NORMAN & JONES, 1993; LUPPI et al., 1998; COMEAU et al., 1999). Moreover, the largest and therefore most nutrient-rich eggs will be found at higher latitudes (CLARKE, 1979; LARDIES & WEHRTHMANN, 2001; TEROSSI et al., 2010). This trend that relates the size of eggs with the latitudes is known as Thorson's rule (MILEYKOVSKY, 1971) and it is

considered as an adaptation to protect the eggs to the low temperatures during the incubation period.

Knowing the reproduction patterns of the inhabitants of rocky coasts is fundamental to better understand when they reproduce, fecundity, larval dynamics, movements of zoeas and recruitment of megalopes and juvenile crabs in the system. Two breeding patterns are known in Brachyura (WENNER et al., 1974; SASTRY, 1983), the first, continuous, when they can produce eggs throughout the year. This would be the case for tropical crustaceans, as the temperature of the water is quite constant. The second, seasonally, only they produce eggs in a few months indicated, when the environment is favorable for the larvae to survive. This would be the case in temperate regions, as an adaptation of species to environmental conditions and the seasonal temperature variation. Therefore, reproduction usually will be continuous at lower latitudes, and, as latitude increases, the reproductive period will be restricted to times when water temperature is higher (WENNER et al., 1974; SASTRY, 1983).

In the case of *P. transversus*, in temperate regions it has been seen to have seasonal reproduction, it reproduces in some months of the year, for example, in the eastern Mediterranean Sea, from May to September (ARAB et al., 2015), *Pachygrapsus marmoratus* have also seasonal reproduction with higher proportions in summer in the southern Black Sea, Turkey (AYDIN et al., 2014). On the other hand, in southeastern Brazil (Ubatuba, SP), ovigerous females of *P. transversus* are found throughout the year, with more egg production in the summer (December to February) (FLORES & NEGREIROS-FRANSOZO, 1998, 1999).

The studies of *Pachygrapsus transversus* egg production in Brazil are in Ceará (OGAWA & ROCHA, 1976), Pernambuco (CÂMARA DE ARAÚJO et al., 2016), Rio de Janeiro (CAMPOS & OSHIRO, 2001) and São Paulo (FLORES & NEGREIROS-FRANSOZO, 1997). In other countries, there are studies in Panama (ABELE et al., 1986), eastern Mediterranean (ARAB et al., 2015) and Jamaica (HARTNOLL, 1965). Although it has a wide distribution, and being one of the most important grapsids in the rocky coast because of its great abundance and interaction in the trophic network, still

The aim of this study is to know more about the egg production of *Pachygrapsus transversus* in Torres, state of Rio Grande do Sul, Brazil, this is the southernmost study area analyzed so far. The specific objectives are:

- 1) Analyze if there is a seasonal difference in the fecundity of *P. transversus* comparing between two seasons (summer and autumn);
- 2) Compare the egg number and size among the stages of development;
- 3) Compare the fecundity and egg size with other studies done in other latitudes with the same species.

METHODS AND MATERIALS

Study area

The study was conducted in Praia Prainha sited in Torres, state of Rio Grande do Sul, Brazil (29°20'40.1"S 49°43'36.1"W) (**Figure 1**). Ovigerous females of the genus *Pachygrapsus* were collected during the low tide in the intertidal zone in summer (February) and autumn (May) 2019. The water temperature was measured with a thermometer at time of collection being 24°C in summer and 22°C in autumn.

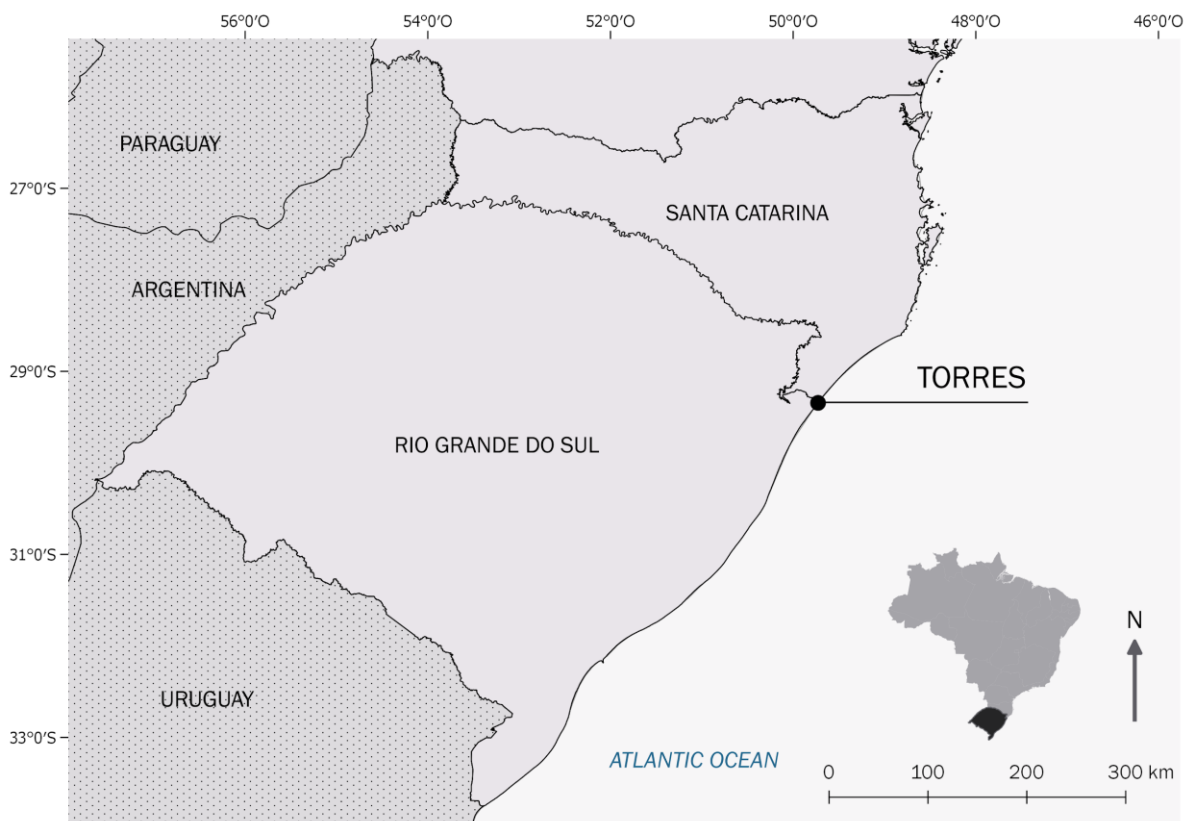


Figure 1 - Localization of the study area in Torres, Rio Grande do Sul.

Sampling and laboratory analysis

The crabs were obtained mostly in *Phragmatopoma* reefs in the rocks using a knife to break small parts of the reef, followed by visual inspection for crabs inhabiting small crevices. The initial purpose was sampled approximately 60 ovigerous females in each season. After collected, the crabs were put in little individual bags to transport to laboratory, where they were frozen.

The specimens were identified according POUPIN et al. (2005) and the carapace width (CW) was measured with a digital caliper rule to the nearest 0.01 mm (**Figure 2**).

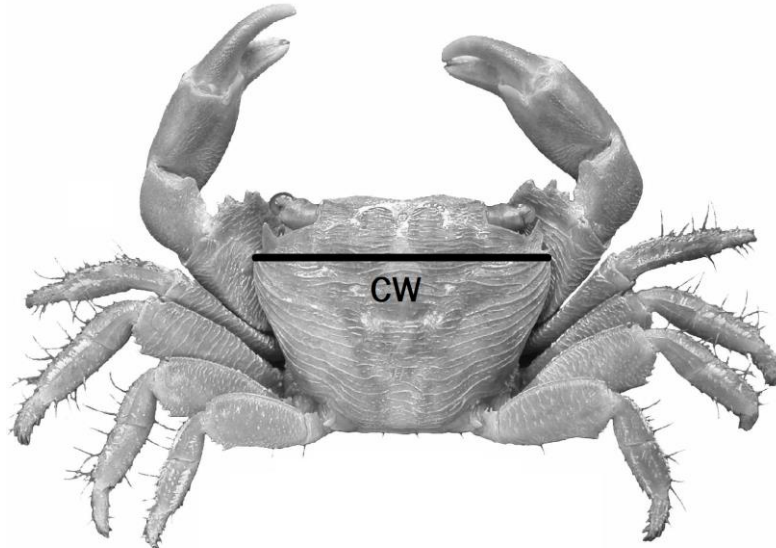


Figure 2 – *Pachygrapsus transversus*. Representation of the carapace width (22.5 mm - CW). (Modified from POUPIN et al. 2005).

The egg batch was carefully extracted from the pleopods and put it in a quadruplicate petri dish to count all the eggs with a manual counter under stereomicroscope. The development of the eggs was subdivided into three different stages according to WEHRTMANN (1990) (**Figure 3**): I. uniform yolk; II. eye pigment barely visible; III. eyes clearly visible, abdomen free. Some females were found with larvae attached to the pleopods (**Figure 3**). To analyze the fecundity, only eggs in the first stage of development were considered (HARTNOLL, 2006).

Of a total of 15 eggs randomly chosen from each female were measured the maximum and the minimum axis with a *camera lucida* in order to calculate the total volume using the formula for oblate spheroid according to TURNER & LAWRENCE (1979):

$$v = \pi \times (a_1)^2 \times (a_2) / 6$$

Where v= volume (mm³), a₁ = maximum axis, a₂ = minimum axis.

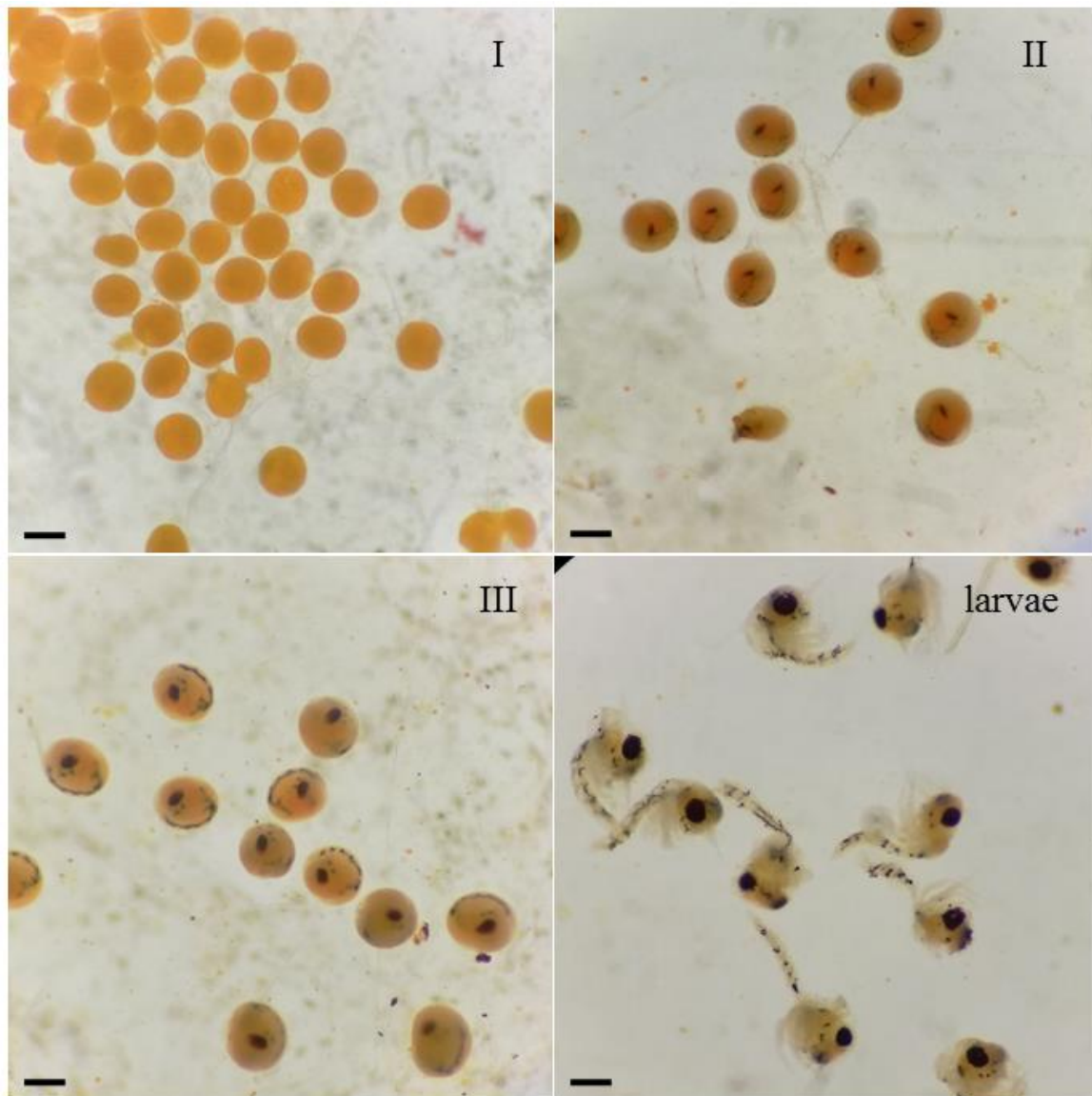


Figure 3 - Eggs in stages I, II and III, and larvae, collected in Torres, RS. Scale = 0.25 mm

Data analysis

To test the normality of the data (female size, egg number and egg volume) it was done Kolmogorov Smirnov-test for both samples using $\alpha=0.05$.

The CW between seasons were compared with a Kruskal-Wallis test. In order to better represent the results, it was done a boxplot.

The relationship between female size and fecundity and between the female size and egg volume was tested using correlation tests.

It was done a one-way ANCOVA to test the differences of the number of eggs in each stage of the egg between the two studied seasons (summer and autumn 2019) using as a covariable the CW and $\alpha=0.01$. To see the differences between the egg volume between the two studied months in each stage it was done a Kruskal-Wallis test ($\alpha=0.05$). To represent the results, two linear regressions were done to see the relation between the number of eggs and the CW of the females, and to see the relation between the size of the egg and the CW of the female.

With the aim to see if there was egg loss various one-way ANCOVA were done to test the differences between all the stages of the egg development in the two studied seasons (summer and autumn 2019), using CW as a covariable and $\alpha=0.01$. For the increasing egg volume, Kruskal-Wallis test were done ($\alpha=0.05$). The representation used in this case were bargraphs.

For every ANCOVA it was tested the homogeneity of variances with a Bartlett test. The data didn't follow the homoscedasticity, even with transformation, consequently, to do the tests it was used $\alpha=0.01$. Also, it was tested the homogeneity of regressions to see the differences between the slopes.

Test and representations were done with VassarStats, the statistical program R (version 3.3.3) and Microsoft® Office Excel.

RESULTS

Ovigerous females

A total of 113 ovigerous females were sampled, 64 in summer and 49 in autumn. Both samples follow a normal distribution (February: $D=0.087896$, $p\text{-value}=0.673$, May: $D=0.12413$, $p\text{-value}=0.4371$). There were no differences in the CW sizes between the studied seasons ($H=6.3482$, $p\text{-value}=0.1175$) (**Table 1**, **Figure 4**). In summer, females were found distributed among all size classes, being the most abundant class, with 13 females, between 9.20 and 10.59 mm, while in autumn, the sizes were concentrated on a smaller range, being the most abundant, with 15 females, between 10.60 and 11.99 mm (**Figure 5**). The biggest female was found in summer, reaching almost 17 mm.

Table 1 - Carapace width (CW - mm) of the ovigerous females reported in summer and autumn 2019 (mean \pm standard deviation, minimum value-maximum value)

SEASON	n	CW (mm)
summer	64	10.89 ± 2.66 6.42 to 16.88
autumn	49	12.23 ± 1.55 9.09 to 15.33

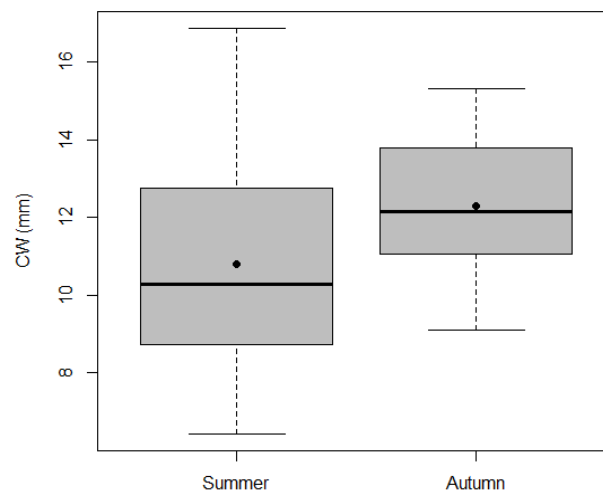


Figure 4 - Comparison of the size of the carapace width (CW - mm) between summer and autumn 2019. The black point represents the mean, and the black line the median of the population.

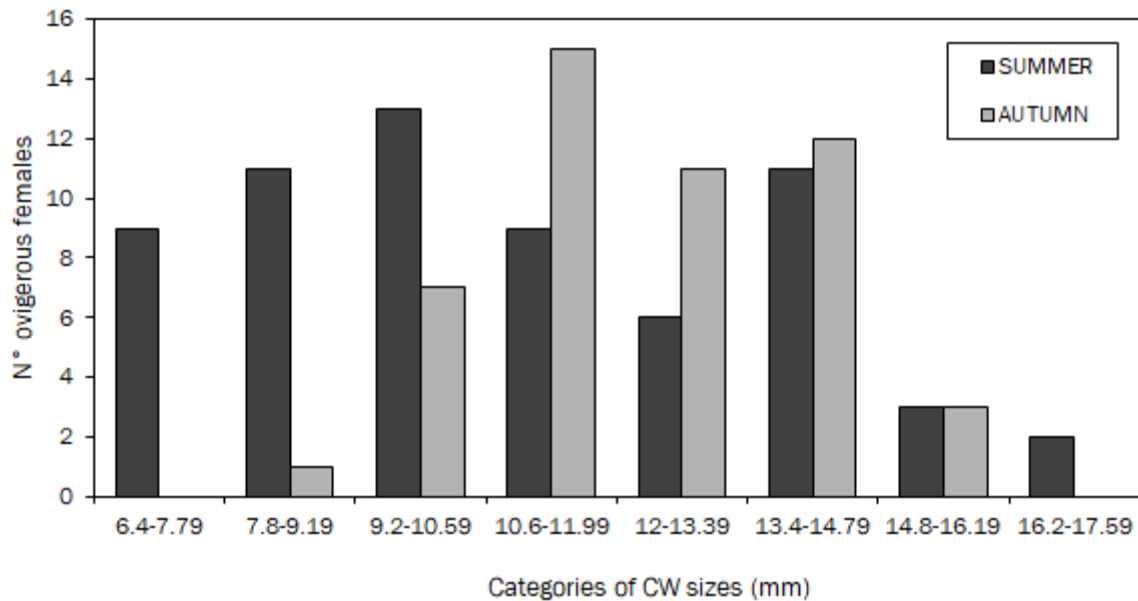


Figure 5 - Number of ovigerous females separated into categories of different sizes of the carapace width (CW - mm) collected in summer and autumn 2019.

Fecundity and egg volume

The data, both in number of eggs and volume of eggs, follow a normal distribution in the two months studied (**Table 2**).

Fecundity, the number of eggs in stage I, was significantly correlated with the size of the female with a 58.98% ($t=5.2163$, $p\text{-value}=3.357E-06$, $\rho=0.5898$).

Fecundity ranged from 828 to 10487 in summer, while in autumn it ranged from 693 to 3006 (**Table 3**). Comparing the two regression lines (**Table 4**, **Figure 6A**), they have significantly different slopes ($F=6.87$, $p\text{-value}=0.0116$), probably influenced by the difference of size females between the months, then with the influence of the covariable, as the regressions are not homogeny and it cannot be possible detect in which season the egg production is higher. Even that graphically, there is a tendency with fecundity being higher in summer than in autumn.

The volume of the eggs wasn't related significantly with the size of the ovigerous females ($t=0.45401$, $p\text{-value}=0.6543$).

In the case of the volume of eggs of the first stage, varied from 0.0069 to 0.011 mm³ in summer while in autumn was from 0.0073 to 0.0144 mm³ (**Table 3**). The volume of eggs found in autumn is significantly higher than in summer (H=25.392, P-value=5E-07) (**Table 4, Figure 6B**).

Table 2 - Results of the Kolmogorov Smirnov-test to test the normality of the data (bold: significant; *partially significant)

		n° eggs	Egg volume
stage I	summer	D = 0.20104 P-value = 0.167	D = 0.10178 P-value = 0.8951
	autumn	D = 0.11542 P-value = 0.9065	D = 0.098862 P-value = 0.9731
stage II	summer	D = 0.15107 P-value = 0.9095	D = 0.16111 P-value = 0.8664
	autumn	D = 0.38314 P-value = 0.3569	D = 0.3202 P-value = 0.5842
stage III	summer	D = 0.34895 P-value = 0.04995*	D = 0.10888 P-value = 0.9899
	autumn	D = 0.1683 P-value = 0.6609	D = 0.13986 P-value = 0.8492

Table 3 - Number and volume of the eggs of the ovigerous females reported in summer and autumn 2019 (mean \pm standard deviation, minimum value-maximum value).

		summer		autumn		
	n	n° eggs	Egg volume (mm ³)	n	n° eggs	Egg volume (mm ³)
stage I	29	2952 \pm 2335 828 - 10487	0.0089 \pm 0.0009 0.0069 - 0.0110	24	1722 \pm 671 693-3006	0.0112 \pm 0.0018 0.0073 - 0.0144
stage II	12	2003 \pm 1214 246 - 4645	0.0105 \pm 0.0019 0.0119 - 0.0153	5	1395 \pm 597 1033 - 2452	0.0130 \pm 0.0011 0.0119 - 0.0148
stage III	14	1416 \pm 1367 512 - 5932	0.0114 \pm 0.0022 0.008 - 0.0159	17	1317 \pm 752 527 - 3601	0.0154 \pm 0.0024 0.0125 - 0.0219

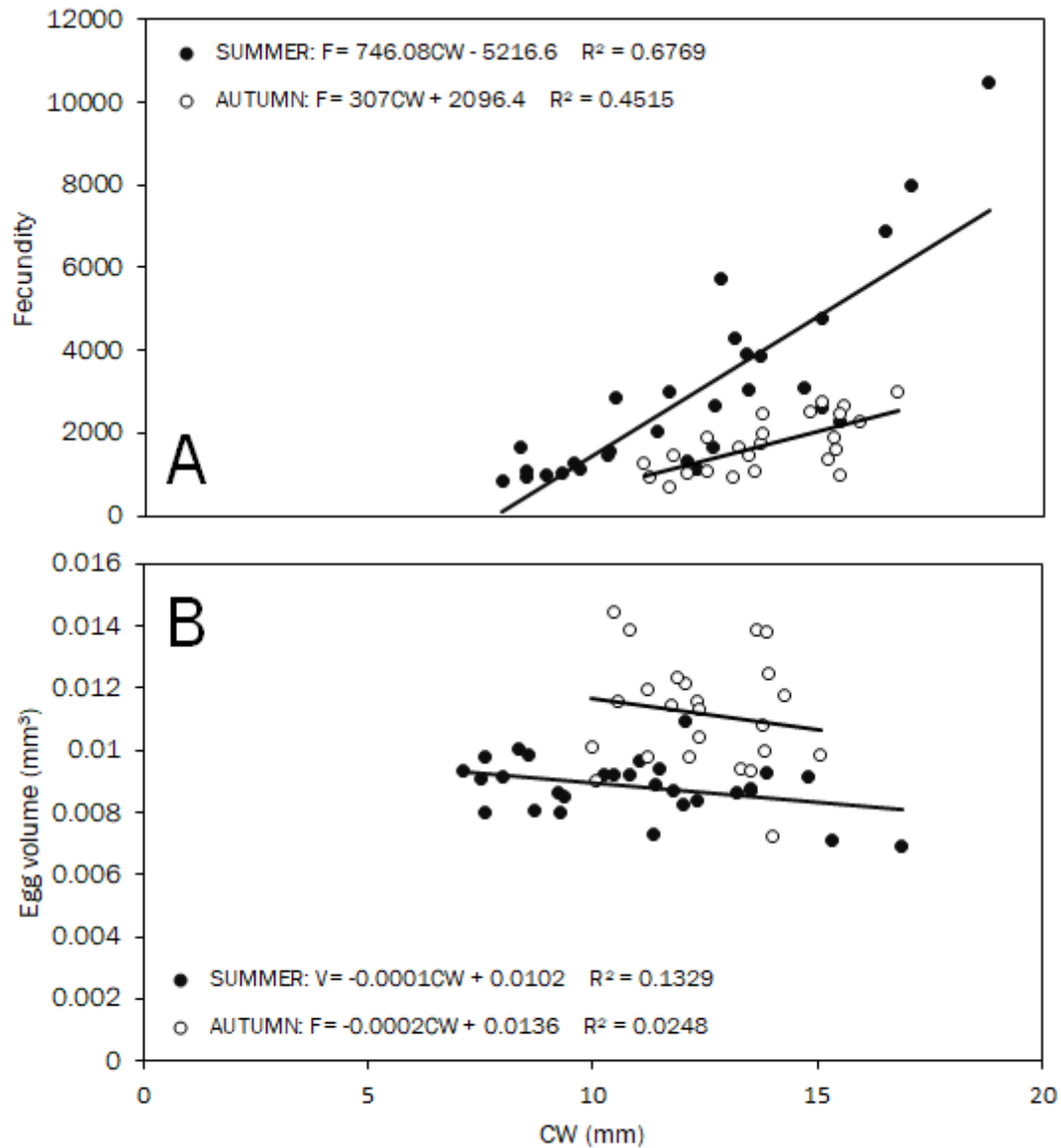


Figure 6 - Lineal regression between (A) fecundity (number of eggs in stage I) and (B) egg volume (mm^3) in stage I with the carapace width (CW - mm) in both studied seasons (summer and autumn 2019).

Table 4 - Results of the tests done comparing the number of eggs (ANCOVA) and the egg volume (Kruskal-Wallis) in each stage of the egg between the two studied seasons (summer and autumn 2019, bold = significant, *partially significant, ($\alpha=0.01$ for ANCOVA, $\alpha=0.05$ for Kruskal-Wallis).

		stage I	stage II	stage III
n° eggs	Homogeneity of regressions	F = 6.87 P-value = 0.0116*	F = 0.08 P-value = 0.7852	F = 14.74 P-value = 0.0007
	ANCOVA	F = 45.33 P-value = 2E-08	F = 2.74 P-value = 0.1203	F = 38.44 P-value = 1E-06
egg volume	Kruskal-Wallis	H=25.392 P-value= 5E-07	H=6.4 P-value=0.1141	H=15.756 P-value= 7E-05

Parental care

A curiosity not previously reported in *Pachygrapsus*, were the cases of extended parental care found in twelve crabs (10.6%), nine individuals in summer and three in autumn. At the time of counting the eggs of the females, it was seen that in the abdomen they possessed the first larvae (**Figure 3**), these females were excluded of the egg development analysis.

Egg loss and increased egg volume

Both in summer and autumn there is a visual loss of eggs between the stages comparing the medias (**Figure 7**). The total egg loss from the first stage until the last one was of 52% in summer and 23.5% in autumn (**Table 5**). Statistically, there wasn't significant egg loss between any stages even though we see the percentage of loss is quite high.

In the case of volumes, the size of the egg increases as it develops. In summer, this difference in volume is significant in the change from stage I to III, the volume increases by 28.7%, being significantly higher in III ($H=12.062$, $p\text{-value}=5E-04$). For autumn, the volume increased by 37.5%, there are significant differences between all stages, in general, from stage I to III ($H=23.198$, $p\text{-value}=1E-06$) (**Table 6, Figure 8**).

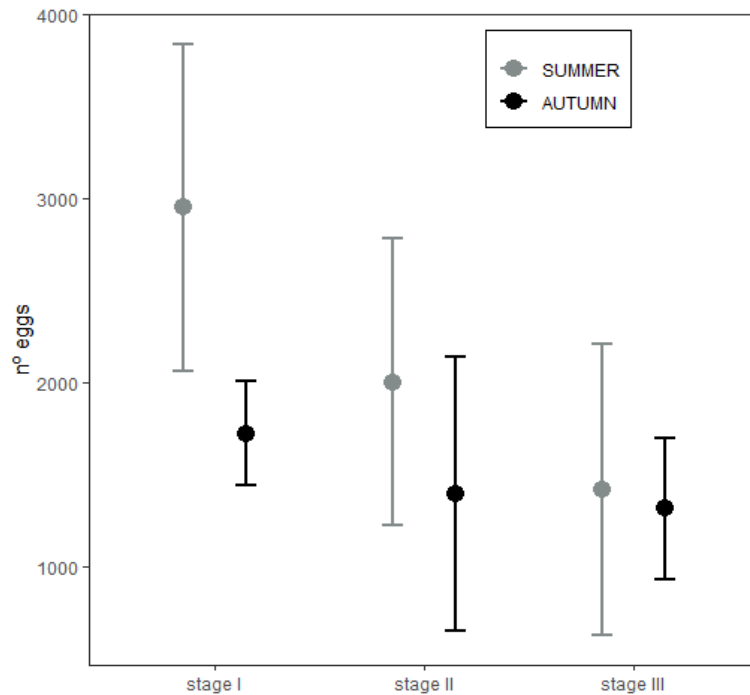


Figure 7 - Representation of the differences of the egg number among stages in the studied months.

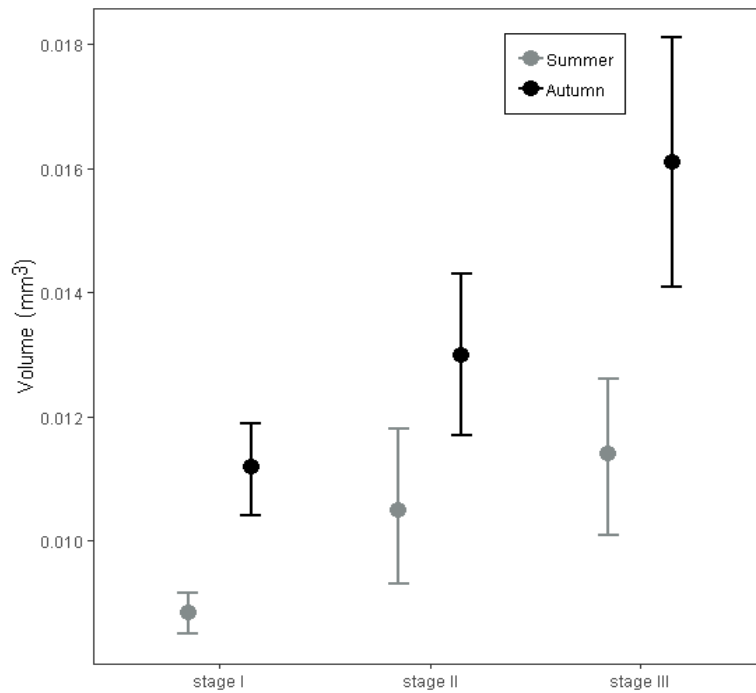


Figure 8 - Representation of the differences of the egg volume among stages in the studied seasons.

Table 5 - Results of the test ANCOVA and percentage of the egg loss between phases and comparing in the two studied seasons (summer and autumn), bold=significant, *partially significant ($\alpha=0.01$).

		I-II	II-III	I-III
SUMMER	%	32.2	29.3	52.0
	Homogeneity of regressions	F = 10.60 P-value = 0.0024	F = 6.68 P-value = 0.0165*	F = 0.58 P-value = 0.4505
	ANCOVA	F = 10.99 P-value = 0.002	F = 1.16 P-value = 0.2925	F = 1.00 P-value = 0.3244
AUTUMN	%	19.0	5.6	23.5
	Homogeneity of regressions	F = 0.67 P-value = 0.4214	F = 0.89 P-value = 0.3578	F = 0.07 P-value = 0.7904
	ANCOVA	F = 2.76 P-value = 0.1084	F = 0.29 P-value = 0.5985	F = 2.39 P-value = 0.1306

Table 6 - Results of the Kruskal-Wallis test and percentage of the increased egg volume between phases and comparing in the two studied seasons (summer and autumn), bold=significant ($\alpha=0.05$).

		I-II	II-III	I-III
SUMMER	%	19.1	6.5	28.7
	Kruskal-Wallis	H=8.0468 p-value= 0.0045587	H=1.3995 p-value=0.2368	H=12.062 p-value= 5E-04
AUTUMN	%	16.3	18.3	37.5
	Kruskal-Wallis	H=5.3346 p-value= 0.02091	H=5.71 p-value= 0.01687	H=23.198 p-value= 1E-06

DISCUSSION

Ovigerous females

It worth to mention that, at the time of collection, it was much easier to find ovigerous females in summer than in autumn, so it was difficult to make the size of the populations equal in both seasons.

The mean of CW agrees with other studies carried out with *P. transversus*, however, the range of sizes in this study is shorter compared to others where specimens of 20 mm have been found in tropical zones and up to 21 mm in temperate zones. This may be related to the trend found in several studies with crustaceans that shows an increase in the size of the individual with latitude (ATKINSON & SIBLY, 1997; ROY & MARTIEN, 2001; MEIRI & DAYAN, 2003, HIROSE et al., 2013). Following this theory, in Torres, RS we would expect to find larger individuals than in studies conducted at lower latitudes, but this evidence is not yet very clear. To better understand these results, it would be good to conduct a study of the population dynamics of *P. transversus* in the Torres area, comparing abundance between males, females, and ovigerous females.

Although ovigerous females were found in both seasons, the number of these females was greater in summer. To better understand the presence of ovigerous females in this region, it would be needed data of the other seasons (winter and spring). It is expected to obtain that *P. transversus* is also a continuous breeding species like in other Brazilian localities since Rio Grande do Sul is a subtropical region. It would also be good to have more studies in temperate zones apart from ARAB et al. (2015) in order to allow more comparisons.

Fecundity and egg volume

The egg production in Brachyura is proportional to the size of the individual, this trend has been observed in several studies with *P. transversus*, for example in Ubatuba, São Paulo (FLORES & NEGREIRO-FRANSOZO, 1997) and in Lebanon, eastern Mediterranean (ARAB et al., 2015). And, also in other species of the genus *Pachygrapsus*, such as *P. marmoratus* in Turkey, Black Sea (AYDIN et al., 2014) and in Lebanon, eastern Mediterranean (ARAB et al., 2015). In this case, this trend is corroborated, in both seasons fecundity increases with the size of the female.

As mentioned above, studies of *P. transversus* fecundity in tropical regions showed that it has a continuous reproduction pattern, with the warmer months being the most productive. These results have not been observed in this study. Although the number of eggs produced in summer is higher than in autumn, there are no significant differences statistically, but maybe because the number of females is not equal in each season. Also, the range of fecundity in summer is wider than in autumn so the standard deviation really affects to the results. These fecundity values differ from all other studies with *P. transversus* except with the work carried out in Rio de Janeiro (CAMPOS & OSHIRO, 2001).

Egg size can be related with temperature, ovigerous females will produce bigger eggs if the temperature is low as an adaptation to the environmental conditions (LARDIES & WEHRTMANN, 2001). In this study, the temperature in autumn was lower than in summer, that is a possible hypothesis for the differences found with the volume. Here, we have punctual data of the temperature from the time of collection, but we believed that the difference between two seasons be higher than two degrees, mainly because it is a subtropical zone.

The volume data reported in this work is difficult to compare with the other studies is that most authors measure the size of the egg by its diameter, they do not contemplate that the egg is not totally spherical, so we do not know if the size they use is the maximum or minimum axis of the egg. In the females of this study, the maximum axis was 0.28 ± 0.0031 mm, ranging from 0.200 to 0.400 mm, greater than those at lower latitudes.

Parental care

About the females found with larva, all the studies carried out with *P. transversus* and its larvae are because they took the females alive and moved them to the laboratory, where they kept them alive until the larval release. A possible explanation for why those females were carrying the larva would be that the females would be waiting for the right moment to let go the larvae. The hatching of larvae in marine invertebrates is related to different environmental periods for example: light and dark and high and low tide (MORGAN, 1995; FAN et al., 2017). For *P. transversus*, the trends found are that specimens released larvae at high tide and during day and night (MORGAN & CHRISTY, 1994; FLORES et al., 2007; BUENO & FLORES, 2010). These last authors also talk about a possible difference in releasing larvae for females

exposed to the waves. At time, we unknown other studies with marine brachyuran species that reported this kind of parental care.

This is possible the first study that found those results in *Pachygrapsus*, on the other hand, it is been reported in other marine and freshwater decapods (DIESEL, 1989; DIESEL & SCHUH, 1993; BOLAÑOS et al., 2004; THIEL, 2003).

Variations with latitude

There is a relationship between egg size and latitude; the females studied have larger eggs than those reported at lower latitudes. This trend had already been found previously in other crustaceans (CLARKE, 1979; LARDIES & WEHRTMANN, 2001; TEROSSI et al., 2010). In Rio Grande do Sul, with subtropical climate, females produce larger eggs than in other regions from Brazil (Pernambuco, Rio de Janeiro and São Paulo), Jamaica and Panama, and therefore, they will produce fewer eggs. Fecundity is lower and eggs are larger than those reported in other studies.

Egg loss and increased egg volume

Even though egg loss it's been reported in Brachyura during the development (FIGUEIREDO et al., 2008; TORRES et al., 2009), it's not the case in this study as comparisons between stages were not significant.

On the other hand, in both seasons the volume of eggs increases significantly as they develop. This change has also been seen in many crustaceans, to cite some, for example: *Nauticaris magellanica* (WEHRTMANN & KATTNER, 1998), *Necora puber* (VALDES et al., 1991) and in *Armases cinereum* (FIGUEIREDO et al., 2008). This increase in volume is related to water consumption. The gain of water during development causes the egg to increase its internal osmotic pressure, which favours hatching. The increase in water also causes the weight of the larvae to decrease, so that when it hatches, it will have a better buoyancy that allows it to swim to the surface and quickly adjust its body temperature (VALDES et al., 1991).

Table 7. Data from *Pachygrapsus transversus* of CW (carapace width), fecundity, egg size or volume obtained from literature.

Localities	CW (mm)	Fecundity	Diameter/Volume	Reference
Tyre, Lebanon 33°16' N, 35°11'E	9.0 to 21.1 14.4 ± 2.5	2860 to 19,967 11,146 ± 5053	0.023 to 0.038 mm 27.5 ± 3.08 mm	ARAB et al., 2015
Jamaica 18°06' N, 77°20'W	-	-	0.25 mm	HARTNOLL, 1965
Fort Amador, Panamá 8°54' N, 79°31' W	9.4 to 13.8	≥15000	0.20 to 0.22 mm	ABELE et al., 1986
Fortaleza, Ceará Brasil 3°43'S, 38°30'W	6 to 15.4 10.06	9222	-	OGAWA, 1976
Recife, Pernambuco Brasil 8°07' S, 34°53' W	2.96 to 18.10 8.53 ± 3.30	350 to 14700 3818 ± 3349	-	CÂMARA DE ARAÚJO et al., 2016
Mangaratiba, Rio de Janeiro Brasil 22°57' S, 44°01' W	8.5 to 20.0	540 to 5273 1770	0.20 to 0.38 mm 0.28 mm.	CAMPOS & OSHIRO, 2001
Ubatuba, São Paulo Brasil 23°25' S, 45°04' W	6 to 13.6	3520 ± 2614	-	FLORES & NEGREIROS- FRANZOZO 1997
Cananéia, São Paulo Brasil 25°01'S, 47°55'W	-	-	0.14 ± 0.012 mm	TISEO et al., 2014
Torres, Rio Grande do Sul Brasil 29°20'S 49°43'W	6.42 to 16.88 11.47 ± 2.34	693 to 10487 2395 ± 1876	0.20 to 0.40 mm 0.28±0.0031 mm 0.0069 to 0.0144 mm ³ 0.0990±0.0018 mm ³	Present study

CONCLUSIONS

- 1) Ovigerous females found in summer had a wide range of sizes compared with autumn.
- 2) Ovigerous females in Rio Grande do Sul were found in both seasons, being more abundant in summer than in autumn.
- 3) Fecundity is related positively to the size of the females.
- 4) Females in summer produced more eggs than in autumn, but not statistically.
- 5) There are differences in the egg volume between summer and autumn.
- 6) In Rio Grande do Sul females produce larger eggs than those in lower latitudes.
- 7) It was found parental care in some females.
- 8) It was not reported egg loss in the studied females.
- 9) The egg volume increases as it develops.

It is important to continue researching the biology and ecology of the species that inhabit intertidal systems since they are very vulnerable to changes produced by human impact. It would be interesting to be able to compare more aspects of the reproduction of *Pachygrapsus transversus* in all the seasons in the southern region of Brazil since it has not been studied yet. It would also be important to observe what effects climate change may have on intertidal communities.

BIBLIOGRAPHY

ABELE, L. G., CAMPANELLA, P. J., SALMON, M. Natural history and social organization of the semiterrestrial grapsid crab *Pachygrapsus transversus* (Gibbes). **Journal of Experimental Marine Biology and Ecology**, vol. 104, no 1-3, p.153-170, 1986.

ARAB, A.; KAZANJIAN, G.; BARICHE, M. Biological traits suggest a niche overlap between two grapsid crabs sharing the rocky intertidal of the eastern Mediterranean. **Journal of the Marine Biological Association of the United Kingdom**, vol. 95, no 8, p. 1685-1692, 2015.

ATKINSON, D; SIBLY, R. M. Why are organisms usually bigger in colder environments? Making sense of a life history puzzle. **Trends in ecology & evolution**, vol. 12, no 6, p. 235-239, 1997.

AYDIN, M; KARADURMUŞ, U; TUNCA, E. Biological characteristics of *Pachygrapsus marmoratus* in the southern Black Sea (Turkey). **Journal of the Marine Biological Association of the United Kingdom**, vol. 94, no 7, p. 1441-1449, 2014.

BOLAÑOS, J.; CUESTA, J.; HERNÁNDEZ, G.; HERNÁNDEZ, J.; FELDER, D. L. Abbreviated larval development of *Tunicotheres moseri* (Rathbun, 1918) (Decapoda, Pinnotheridae), a rare case of parental care in brachyuran crabs. **Scientia Marina**, vol. 68, no 3, p. 373-384, 2004.

BUENO, M.; FLORES, A. A. V. Tidal-amplitude rhythms of larval release: variable departure from presumed optimal timing among populations of the mottled shore crab. **Journal of the Marine Biological Association of the United Kingdom**, vol. 90, no 5, p. 859-865, 2010.

CAMPOS, D. A.; OSHIRO, L. M. Y. Biologia reprodutiva do caranguejo *Pachygrapsus transversus* (Gibbes, 1850) (Crustacea, Decapoda, Grapsidae) da Praia de Ibicuí-RJ. **X Jornada Científica da UFRRJ, Trabalhos Completos**, vol. 11, no 2, p. 209-212, 2001.

CÂMARA DE ARAÚJO, M. S. L.; AZEVEDO, D. S.; SILVA, J. V. C. L.; PEREIRA, C. L. F.; CASTIGLIONI, D. S.. Population biology of two sympatric crabs: *Pachygrapsus transversus* (Gibbes, 1850) (Brachyura, Grapsidae) and *Eriphia gonagra* (Fabricius, 1781) (Brachyura, Eriphidae) in reefs of Boa Viagem beach, Recife, Brazil. **Pan-American Journal of Aquatic Sciences**, vol. 11, no 3, p. 197-210, 2016.

CHRISTIANSEN, M. E. Marine Invertebrates of Scandinavia N°2. **Crustacea Decapoda Brachyura**. vol. 143, Universitetsforlaget, 1969

CHRISTOFOLETTI, R. A.; MURAKAMI, V. A.; OLIVEIRA, D. N.; BARRETO, R. E.; FLORES, A. A. Foraging by the omnivorous crab *Pachygrapsus transversus* affects the structure of assemblages on sub-tropical rocky shores. **Marine Ecology Progress Series**, v. 420, p. 125-134, 2010.

CLARKE, A. On living in cold water: K-strategies in Antarctic benthos. **Marine Biology**, vol. 55, no 2, p. 111-119, 1979.

COBO, V. J.; OKAMORI, C. M. Fecundity of the spider crab *Mithraculus forceps* (Decapoda, Mithracidae) from the northeastern coast of the state of São Paulo, Brazil. **Iheringia. Série Zoologia**, vol. 98, n. 1, p. 84-87, 2008.

COMEAU, M.; STARR, M.; CONAN, G. Y.; ROBICHAUD, G.; THERRIault, J. C. Fecundity and duration of egg incubation for multiparous female snow crabs (*Chionoecetes opilio*) in the fjord of Bonne Bay, Newfoundland. **Canadian Journal of Fisheries and Aquatic Sciences**, vol. 56, no 6, p. 1088-1095, 1999.

COREY, S.; REID, D. M. Comparative fecundity of decapod crustaceans: I. The fecundity of thirty-three species of nine families of caridean shrimp. **Crustaceana**, vol.1, p. 270-294, 1991.

DAVIE, P. J.; GUINOT, D.; NG, P. K. Systematics and classification of brachyura. **Treatise on zoology-anatomy, taxonomy, biology. The crustacea**, vol. 9 part C-II, Brill, p. 1049-1130, 2015.

DIESEL, R. Parental care in an unusual environment: *Metopaulias depressus* (Decapoda: Grapsidae), a crab that lives in epiphytic bromeliads. **Animal Behaviour**, vol. 38, no 4, p. 561-575, 1989.

DIESEL, R.; SCHUH, M. Maternal care in the bromeliad crab *Metopaulias depressus* (Decapoda): maintaining oxygen, pH and calcium levels optimal for the larvae. **Behavioral Ecology and Sociobiology**, vol. 32, no 1, p. 11-15, 1993.

FAN, T. Y.; HSIEH, Y. C.; LIN, K. H.; KUO, F. W.; SOONG, K.; MCRAE, C. J.; EDMUNDS, P. J.; FANG, L. S. Plasticity in lunar timing of larval release of two brooding pocilloporid corals in an internal tide-induced upwelling reef. **Marine Ecology Progress Series**, vol. 569, p. 117-127, 2017.

FERNÁNDEZ, M.; BOCK, C.; PÖRTNER, H.-O. The cost of being a caring mother: the ignored factor in the reproduction of marine invertebrates. **Ecology Letters**, vol. 3, no 6, p. 487-494, 2000.

FIGUEIREDO, J.; PENHA-LOPES, G.; ANTO, J.; NARCISO, L.; LIN, J. Fecundity, brood loss and egg development through embryogenesis of *Armases cinereum* (Decapoda: Grapsidae). **Marine Biology**, vol. 154, no 2, p. 287-294, 2008.

FLORES, A. V.; NEGREIROS-FRANSOZO, M. L. The use of linear and volumetric variables in estimating fecundity in the shore crab *Pachygrapsus transversus* (Gibbes, 1859) (Crustacea, Decapoda, Brachyura). **VII COLACMAR, Congreso Latino-Americano Sobre Ciências do Mar**, p. 319-320, 1997.

FLORES, A. A. V.; NEGREIROS-FRANSOZO, M. L. External factors determining seasonal breeding in a subtropical population of the shore crab *Pachygrapsus transversus* (Gibbes, 1850) (Brachyura, Grapsidae). **Invertebrate reproduction & development**, vol. 34, no 2-3, p. 149-155, 1998.

FLORES, A. A. V.; NEGREIROS-FRANSOZO, M. L. On the population biology of the mottled shore crab *Pachygrapsus transversus* (Gibbes, 1850) (Brachyura, Grapsidae) in a subtropical area. **Bulletin of Marine Science**, v. 65, no 1, p. 59-73, 1999.

FLORES, A. A. V.; MAZZUCO, A. C. A.; BUENO, M. A field study to describe diel, tidal and semilunar rhythms of larval release in an assemblage of tropical rocky shore crabs. **Marine biology**, vol. 151, no 5, p. 1989-2002, 2007.

FLORES, A. A. V.; GOMES, C. C.; VILLANO, W. F. Source populations in coastal crabs: parameters affecting egg production. **Aquatic Biology**, vol. 7, no 1-2, p. 31-43, 2009.

GARCÍA-MONTES, J. F.; GRACIA, A; SOTO, L. A. Morphometry, relative growth and fecundity of the gulf crab, *Callinectes similis* Williams, 1966 (Decapoda: Portunidae). **Ciencias Marinas**, vol. 13, no 4, p. 137-161, 1987.

GARDNER, C. Effect of size on reproductive output of giant crabs *Pseudocarcinus gigas* (Lamarck): Oziidae. **Marine and Freshwater Research**, vol. 48, no 7, p. 581-587, 1997.

HARTNOLL, R. G. Notes on the marine grapsid crabs of Jamaica. **Proceedings of the Linnean Society of London**. Oxford University Press, p. 113-147, 1965.

HARTNOLL, R. G. Reproductive investment in Brachyura. **Hydrobiologia**, vol. 557, no 1, p. 31-40, 2006.

HECK, K. L.; HAMBROOK, J. A. Intraspecific interactions and risk of predation for *Dyspanopeus sayi* (Decapoda: Xanthidae) living on polychaete (Filograna implexa, Serpulidae) colonies. **Marine Ecology**, vol. 12, no 3, p. 243-250, 1991.

HINES, A. H. Allometric constraints and variables of reproductive effort in brachyuran crabs. **Marine Biology**, vol. 69, no 3, p. 309-320, 1982.

HIROSE, G. L.; FRANSOZO, V.; TROPEA, C.; LÓPEZ-GRECO, L. S.; NEGREIROS-FRANSOZO, M. L. Comparison of body size, relative growth and size at onset sexual maturity of *Uca uruguayensis* (Crustacea: Decapoda: Ocypodidae) from different latitudes in the south-western Atlantic. **Journal of the Marine Biological Association of the United Kingdom**, vol. 93, no 3, p. 781-788, 2013.

IP, B. H.; SCHUBART, C. D.; TSANG, L. M.; CHU, K. H. Phylogeny of the shore crab family Grapsidae (Decapoda: Brachyura: Thoracotremata) based on a multilocus approach. **Zoological Journal of the Linnean Society**. vol.174, no 2, p. 217-227, 2015.

JONES, M. B.; SIMONS, M. J. Latitudinal variation in reproductive characteristics of a mud crab, *Helice crassa* (Grapsidae). **Bulletin of Marine Science**, vol. 33, no 3, p. 656-670, 1983.

LARDIES, M. A.; WEHRTMANN, I. S. Latitudinal variation in the reproductive biology of *Betaeus truncatus* (Decapoda: Alpheidae) along the Chilean coast. **Ophelia**, vol. 55, no 1, p. 55-67, 2001.

LARDIES, M.; CASTILLA, J. Latitudinal variation in the reproductive biology of the commensal crab *Pinnaxodes chilensis* (Decapoda: Pinnotheridae) along the Chilean coast. **Marine Biology**, vol. 139, no 6, p. 1125-1133, 2001.

LUPPI, T. A.; BAS, C. C.; SPIVAK, E. D.; ANGER, K.. Fecundity of two grapsid crab species in the Laguna Mar Chiquita, Argentina. **Archive of fishery and marine research**, vol. 45, p. 149-166, 1998.

MA, K. Y., QIN, J., LIN, C., CHAN, T., NG, P. K. L., CHU, K. H., TSANG, L. M. Phylogenomic analyses of brachyuran crabs support early divergence of primary freshwater crabs. **Molecular phylogenetics and evolution**. vol. 135, p. 62-66, 2019.

MANNING, R. B.; HOLTHUIS, L. B. West African Brachyuran crabs. **Smithsonian Contributions to**

Zoology, n. 306, p. 1–379, 1981.

MANTELATTO, F. L. M.; FRANSOZO, A. Fecundity of the crab *Callinectes ornatus* Ordway, 1863 (Decapoda, Brachyura, Portunidae) from the Ubatuba region, São Paulo, Brazil. **Crustaceana**, p. 214-226, 1997.

MEIRI, S.; DAYAN, T. On the validity of Bergmann's rule. **Journal of biogeography**, vol. 30, no 3, p. 331-351, 2003.

MELO, G. A. S. **Manual de identificação dos Brachyura (Caranguejos e Siris) do litoral brasileiro**. São Paulo: Plêiade, 1996.

MILEIKOVSKY, S. A. Types of larval development in marine bottom invertebrates, their distribution and ecological significance: a re-evaluation. **Marine Biology**, vol. 10, no 3, p. 193-213, 1971.

MORGAN, S. G. The timing of larval release. **Ecology of marine invertebrate larvae**, p. 157-191, 1995.

MORGAN, S. G.; CHRISTY, J. H. Plasticity, constraint, and optimality in reproductive timing. **Ecology**, vol. 75, no 8, p. 2185-2203, 1994.

NG, P. K., GUINOT, D., DAVIE, P. J. Systema brachyurorum: Part I. an annotated checklist of extant brachyuran crabs of the world. **The Raffles Bulletin of Zoology**, vol. 17, no 1, p. 1-286, 2008.

NORMAN, C. P.; JONES, M. B. Reproductive ecology of the velvet swimming crab, *Necora puber* (Brachyura: Portunidae), at Plymouth. **Journal of the Marine Biological Association of the United Kingdom**, vol. 73, no 2, p. 379-389, 1993.

OGAWA, E. F. Notas bioecológicas sobre *Pachygrapsus transversus* (Gibbes, 1850) no Estado do Ceará (Crustacea: Brachyura). **Arquivos de Ciências do Mar**, vol. 17, no 2, p. 107-113, 1977.

OGAWA, E. F.; ROCHA, C. A. S. Sobre a fecundidade de crustáceos decápodos marinhos do Estado do Ceará, Brasil. **Arquivos de Ciências do Mar**, vol. 16, no 2, p. 101-104, 1976.

OTTO, R. S. Fecundity and other reproductive parameters of female red king crab (*Paralithodes camtschatica*) in Bristol Bay and Norton Sound, Alaska. **Proceedings of the International Symposium on King and Tanner Crabs, Anchorage, Alaska**, p. 65-90, 1989.

PEREZ, O. S. Reproductive biology of the sandy shore crab *Matuta lunaris* (Brachyura: Calappidae). **Marine Ecology Progress Series**, vol. 59, p. 83-89, 1990.

POUPIN, J., DAVIE, P. J., CEXUS, J. C. A revision of the genus *Pachygrapsus* Randall, 1840 (Crustacea: Decapoda: Brachyura, Grapsidae), with special reference to the southwest pacific species. **Zootaxa**. vol. 1015, no 1, p. 1-66, 2005.

RATHBUN, M. J. The grapsid crabs of America. **Bulletin of the United States National Museum**, vol. 97, p. 1-461, 1918.

REID, D. M.; COREY, S. Comparative fecundity of decapod crustaceans, II. The fecundity of fifteen species of anomuran and brachyuran crabs. **Crustaceana**, vol 2, p. 175-189, 1991.

ROY, K; MARTIEN, K. K. Latitudinal distribution of body size in north-eastern Pacific marine bivalves. **Journal of Biogeography**, vol. 28, no 4, p. 485-493, 2001.

SANT'ANNA, B. S.; TAKAHASHI, E. L. H; HATTORI, G. Y. Parental care in the freshwater crab *Sylviocarcinus pictus* (Milne-Edwards, 1853). **Open Journal of Ecology**, vol. 3, no 02, p. 161, 2013.

SASTRY, A. N. Ecological aspects of reproduction. **Environmental adaptations**, vol. 8, p. 170-179, 1983.

SAZIMA, I. The occurrence of marine invertebrates in the stomach contents of the frog *Thoropa miliaris*. **Ciência e Cultura**, vol. 23, no 5, p. 647-648, 1971.

SCHUBART, C. D.; CUESTA, J. A.; FELDER, D. L. 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**, v. 13, n. 2, p. 99-113, 2005.

SPIVAK, E.; ANGER, K.; LUPPI, T.; BASA, C.; ISMAEL, D. Distribution and habitat preferences of two grapsid crab species in mar chiquita lagoon (province of Buenos Aires, Argentina). **Helgoländer Meeresuntersuchungen**, vol. 48, no 1, p. 59, 1994.

TEIXEIRA, G. M.; FRANSOZO, V.; GÓES, J. M.; FERNANDES-GÓES, L. C.; HIROSE, G. L.; ALMEIDA, A. C.; FRANSOZO, A. Reproductive investment and multiple spawning evidence in the redfinger rubble crab *Eriphia gonagra* (Brachyura, Eriphioidea). **Nauplius**, vol. 25, no 2017006, p. 1-9, 2017.

TEROSSO, M; WEHRTMANN, I. S.; MANTELATTO, F. L. Interpopulation comparison of reproduction of the Atlantic shrimp *Hippolyte obliquimanus* (Caridea: Hippolytidae). **Journal of Crustacean Biology**, vol. 30, no 4, p. 571-579, 2010.

THIEL, M; ULLRICH, N. Hard rock versus soft bottom: the fauna associated with intertidal mussel beds on hard bottoms along the coast of Chile, and considerations on the functional role of mussel beds. **Helgoland Marine Research**, vol. 56, no. 1, p. 21, 2002.

THIEL, MARTIN. Extended parental care in crustaceans—an update. **Revista Chilena de Historia Natural**, vol. 76, no. 2, p. 205-218, 2003.

TISEO, G. R.; MANTELATTO, F. L.; ZARA, F. J. Is cleistosperry and coenospermy related to sperm transfer? A comparative study of the male reproductive system of *Pachygrapsus transversus* and *Pachygrapsus gracilis* (Brachyura: Grapsidae). **Journal of Crustacean Biology**, vol. 34, no 6, p. 704-716, 2014.

TORRES, P.; PENHA-LOPES, G.; NARCISO, L.; MACIA, A.; PAULA, J. Fecundity and brood loss in four species of fiddler crabs, genus *Uca* (Brachyura: Ocypodidae), in the mangroves of Inhaca Island, Mozambique. **Journal of the Marine Biological Association of the United Kingdom**, vol. 89, no 2,

p. 371-378, 2009.

TUCK, I. D.; ATKINSON, R. J. A.; CHAPMAN, C. J. Population biology of the Norway lobster, *Nephrops norvegicus* (L.) in the Firth of Clyde, Scotland II: fecundity and size at onset of sexual maturity. **ICES Journal of Marine Science**, vol. 57, no 4, p. 1227-1239, 2000.

TURNER, R. L.; LAWRENCE, J. M. Volume and composition of echinoderm eggs: implications for the use of egg size in life-history models. **Reproductive ecology of marine invertebrates**. no 9, p. 25-40, 1979.

VALDES, L.; ALVAREZ-OSSORIO, M. T.; GONZALEZ-GURRIARÁN, E. Incubation of eggs of *Necora puber* (L., 1767) (Decapoda, Brachyura, Portunidae). Volume and biomass changes in embryonic development. **Crustaceana**, vol. 60, no 2, p. 163-177, 1991.

WEAR, R. G. Life-history studies on New Zealand Brachyura: 4. Zoea larvae hatched from crabs of the family grapsidae. **New Zealand Journal of Marine and Freshwater Research**, vol. 4, no 1, p. 3-35, 1970.

WEAR, R. G. Incubation in British decapod Crustacea, and the effects of temperature on the rate and success of embryonic development. **Journal of the Marine Biological Association of the United Kingdom**, vol. 54, no 3, p. 745-762, 1974.

WEHRTMANN, I. S. Distribution and reproduction of *Ambidexter panamense* and *Palaemonetes schmitti* in Pacific Costa Rica (Crustacea, Decapoda). **Revista de Biología Tropical**, p. 327-329, 1990.

WEHRTMANN, I. S.; KATTNER, G. Changes in volume, biomass, and fatty acids of developing eggs in *Nauticaris magellanica* (Decapoda: Caridea): a latitudinal comparison. **Journal of Crustacean Biology**, vol. 18, no 3, p. 413-422, 1998.

WENNER, A. M.; FUSARO, C.; OATEN, A. Size at onset of sexual maturity and growth rate in crustacean populations. **Canadian journal of zoology**, vol. 52, no 9, p. 1095-1106, 1974.

WILLIAMS, A. B. **Shrimps, lobsters, and crabs of the atlantic coast of the eastern United States, Maine to Florida**, 1984.