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AMANDA PORCIUNCULA HORCH

Biologia populacional e reprodutiva do caranguejo porcelanídeo *Pachycheles laevidactylus* (Decapoda: Porcellanidae) no litoral norte do Rio Grande do Sul

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Biologia populacional e reprodutiva do caranguejo porcelanídeo *Pachycheles laevidactylus* (Decapoda: Porcellanidae) no litoral norte do Rio Grande do Sul

Dissertação apresentada ao Programa de Pós-Graduação em Biologia Animal, Instituto de Biociências da Universidade Federal do Rio Grande do Sul, como requisito parcial à obtenção do título de Mestre em Biologia Animal.

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SUMÁRIO

APRESENTAÇÃO

A dissertação está organizada em Resumo, Abstract e quatro capítulos, a fim de analisar a história de vida da espécie de caranguejo porcelanídeo *Pachycheles laevidactylus* no sul do Brasil.

O capítulo I, “Introdução geral”, aborda uma síntese sobre os conhecimentos acerca da espécie *P. laevidactylus* e aspectos da biologia populacional e reprodutiva de crustáceos decápodos. Os capítulos II e III foram redigidos em formato de artigos que serão submetidos a revistas científicas internacionais. O capítulo II compreende uma análise da estrutura populacional e período reprodutivo de *P. laevidactylus* no Rio Grande do Sul. O capítulo III consiste em uma análise dos aspectos reprodutivos de *P. laevidactylus* em duas localidades no sul do Brasil, comparadas entre si e com outros locais ao longo da distribuição da espécie no Atlântico oeste. O capítulo IV, “Conclusão geral”, aborda as conclusões mais relevantes obtidas nesta dissertação.

Os capítulos I, II e IV estão formatados de acordo com as normas da revista Regional Studies in Marine Science. E o capítulo III está formatado de acordo com as regras da revista Nauplius.

RESUMO

A família Porcellanidae ocorre mundialmente em regiões marinhas tropicais e temperadas, e possui por volta de 30 gêneros e 280 espécies. Sete espécies do gênero *Pachycheles* foram reportadas na costa Brasileira, porém somente duas ocorrem no estado do Rio Grande do Sul, *P. chubutensis* e *P. laevidactylus*. *Pachycheles laevidactylus* pode ser encontrado na zona entremarés sob rochas, em tufos de algas ou em bancos de mexilhões. Também podem viver em simbiose facultativa com espécies de Bryozoa ou bancos de areia formados por poliquetas. Esta espécie ocorre do estado do Maranhão no Brasil até Monte Hermoso na Argentina. O presente estudo teve como objetivo investigar a estrutura populacional e biologia reprodutiva de *P. laevidactylus* em duas localidades no sul do Brasil, Torres e Tramandaí. Espécimes foram obtidos sazonalmente durante um ano entre Novembro de 2018 e Agosto de 2019. Os caranguejos foram coletados em bancos de areia de poliquetas nas formações rochosas de Torres e nos pilares da Plataforma Marítima de Tramandaí. A temperatura da água foi medida após o período de coleta em cada localidade. Os animais foram sexados, contados e medidos. Um total de 1534 indivíduos foram coletados, 943 em Torres e 591 em Tramandaí. Enquanto diferenças de tamanho corporal e tamanho dos quelípodos não foram encontradas entre os sexos, o pleon das fêmeas demonstrou ser mais largo que o dos machos. A razão sexual manteve-se 1:1 em todas as estações, mas diferiu entre classes de tamanho. A reprodução foi contínua e megalopae estavam presentes exclusivamente na primavera. A maturidade sexual morfométrica das fêmeas foi maior (5.39 mm CW) que o tamanho da menor fêmea ovígera coletada (3.35 mm CW), enquanto machos tornaram-se morfometricamente maduros em 5.20 mm CW. Um total de 438 fêmeas ovígeras foram identificadas. Os ovos foram medidos, contados e classificados em três estágios. Fêmeas com ovos no estágio I foram mais frequentes e foi observada uma correlação positiva entre tamanho corporal e fecundidade (estágio I). Diferenças sazonais de tamanho foram observadas nas duas localidades, porém diferenças de fecundidade e volume dos ovos em estágio I foram detectadas somente na primavera em Tramandaí. A perda de ovos entre estágios de desenvolvimento ocorreu exclusivamente em Torres. Um aumento similar no volume dos ovos entre os estágios I e II foi detectado nas duas localidades. As diferenças encontradas entre as localidades foram majoritariamente atribuídas à temperatura e à estrutura dos bancos de areia. Os resultados obtidos foram comparados com os dados disponíveis para outras localidades dentro dos limites de distribuição da espécie.

Palavras-chave: razão sexual, maturidade, fecundidade, volume de ovos, sazonalidade

ABSTRACT

The Porcellanidae family occurs in tropical and temperate marine habitats worldwide, comprising around 30 genera and 280 species. Seven species of *Pachycheles* have been recorded along the Brazilian coast, but only two occur in the Rio Grande do Sul state, *P. chubutensis* and *P. laevidactylus*. *Pachycheles laevidactylus* mainly inhabits the intertidal zone, and can be found under rocks, among seaweed or in mussel beds. They can also live in facultative symbiosis with species of Bryozoa or polychaete sand banks. This species occurs from the state of Maranhão in Brazil to Monte Hermoso in Argentina. The present study aimed at investigating the population structure and reproductive biology of *P. laevidactylus* in two locations in southern Brazil, Torres and Tramandaí. Specimens were obtained seasonally during one year from November 2018 until August 2019. The crabs were collected from polychaete sand banks found on the rock formations in Torres and on the pillars of the Maritime Platform in Tramandaí. Water temperature was measured at each location after the sampling period. Animals were sexed, counted and measured. A total of 1534 individuals were sampled, 943 in Torres and 591 in Tramandaí. While differences in body size or cheliped size between sexes were not found, females tended to have larger pleons than males. Sex ratio was 1:1 in all seasons, but differed between size classes. Reproduction was continuous and megalopae were present exclusively in spring. The morphometric sexual maturity for females (5.39 mm CW) was larger than the size of the smallest ovigerous female collected (3.35 mm CW), while males became morphometrically mature at 5.20 mm CW. A total of 438 ovigerous females were identified. Their eggs were measured, counted and classified into three stages. Females with eggs at stage I were the most frequent and a positive correlation between body size and fecundity (stage I) was observed. Seasonal size differences were observed in both locations, but only spring in Tramandaí showed a difference in fecundity and stage I egg volume. Egg loss between developmental stages was seen exclusively in Torres. A similar increase in egg volume was detected between stages I and II in both locations. The differences found between the locations were mainly attributed to temperature and sand bank structure. The results obtained were compared with the data available for other locations within the species distribution.

Key words: sex ratio, maturity, fecundity, egg volume, seasonality

CAPÍTULO I: Introdução geral

1. Introdução

Pachycheles laevidactylus Ortmann, 1892

Os crustáceos da ordem Decapoda Latreille, 1803 possuem uma grande diversidade de histórias de vida e estratégias reprodutivas (Watling e Thiel, 2015; Vogt, 2016). Desta ordem fazem parte, entre outros, os caranguejos, siris, camarões, lagostas, lagostins, ermitões, aeglas e porcelanídeos; eles podem ser encontrados em ambientes marinhos, dulcícolas e semi-terrestres. A infraordem Anomura Milne Edwards, 1832, apesar de apresentar a maior diversidade morfológica, se diferencia dos demais decápodos devido principalmente a redução do quinto par de pereiópodos, por possuírem o último somito torácico móvel e o exópodo do urópodo inteiro (Veloso, 1999). Dentro desta infraordem encontram-se os ermitões, caranguejos-reais, aeglas e os caranguejos de porcelana (Ahyong et al., 2010).

A família Porcellanidae Haworth, 1825, cujos membros são popularmente conhecidos como caranguejos de porcelana, possui distribuição marinha mundial em águas tropicais, subtropicais e temperadas (Veloso, 1999). Eles podem ser encontrados nas zonas entremarés e sublitorais dos oceanos, em locais úmidos e não diretamente expostos quando descobertos pela maré vazante (Veloso, 1999). Diversas espécies apresentam interações comensais ou simbióticas com outros organismos, podendo estes ser de vida livre, como peixes (Werding et al., 2016), camarões (Jensen, 1986), ermitões (Meireles e Mantelatto, 2008), estrelas-do-mar (Hernandéz et al., 2005) e tartarugas (Baeza et al., 2013) ou sésseis e coloniais, como anêmonas (Baeza e Stotz, 2001), esponjas (Hiller e Werding, 2018), recifes de corais

(Gore, 1982) e anelídeos (Werding e Hiller, 2019). Os porcelanídeos são animais primariamente filtradores, desempenhando um importante papel de recuperação da matéria orgânica nas cadeias tróficas dos ecossistemas aquáticos (Veloso, 1999). Em sua maioria não possuem valor comercial (Veloso, 1999), porém algumas espécies são consideradas ornamentais e utilizadas para fins de aquarismo como *Porcellana sayana* (Leach, 1820) (Baeza et al., 2013).

A família possui 30 gêneros descritos e cerca de 280 espécies (Bezerra et al., 2019), destas são encontradas 20 espécies no Brasil distribuídas em 6 gêneros (Ferreira e Melo, 2016). O gênero *Pachycheles* Stimpson, 1858 possui o segundo maior número de espécies dentro do grupo (Osawa e McLaughlin, 2010), por volta de 47 espécies (WoRMS, 2021), sendo sete espécies presentes na costa brasileira (Ferreira e Melo, 2016). *Pachycheles laevidactylus* Ortmann, 1892 é uma espécie que habita majoritariamente a zona entremarés, podendo ser encontrada sob rochas, em tufos de algas ou em bancos de mexilhões (Veloso, 1999). Também podem estar presentes em simbiose não obrigatória com espécies de Bryozoa Ehrenberg, 1831 e em bancos de areia construídos por espécies de Polychaeta Grube, 1850 do gênero *Phragmatopoma* Mörch, 1863 (Ferreira e Melo, 2016). A espécie é conhecida somente da costa oeste do oceano Atlântico (Harvey e De Santos, 1996), ocorrendo de Maranhão no Brasil até Monte Hermoso na Argentina (Ferreira e Melo, 2016).

Biologia populacional e reprodutiva

Em estudos de histórias de vida dos organismos, a relação entre crescimento do indivíduo e reprodução é bastante discutida, principalmente analisando o *trade-off* de energia entre estes dois eventos (Hartnoll, 1985; Clarke, 1987). O crescimento em crustáceos decápodos ocorre em saltos, devido ao processo de muda (ecdise) do exoesqueleto comum aos artrópodos. A taxa de crescimento nesses animais é determinada pelo aumento do tamanho corporal a cada ecdise e o tempo entre mudas (intermuda), ambos os quais não são constantes ao longo da vida (Hartnoll, 1982). Segundo Hartnoll (1982), durante o crescimento, além de mudanças no tamanho corporal, também podem ocorrer mudanças nas proporções das partes do corpo, esse fenômeno é conhecido como crescimento alométrico, quando diferentes áreas do corpo possuem taxas de crescimento distintas. Modificações nas proporções podem ocorrer de forma gradual ao longo de diversas mudas ou de modo abrupto em uma muda (Hartnoll, 1982). Mudanças particularmente extremas são consideradas metamorfoses, como por exemplo, a transição do último estágio larval (megalopa) para o primeiro estágio juvenil (Hartnoll, 1985).

Outra transição importante ocorre entre o último estágio imaturo e o primeiro estágio morfologicamente maduro, conhecida como a muda da puberdade (Hartnoll, 1985). Nas fêmeas, essa muda é particularmente notável pelas mudanças nas estruturas utilizadas para carregar os ovos, como a proporção da largura do pléon em relação à carapaça em caranguejos. Nos machos, essa muda pode acarretar em mudanças nas estruturas utilizadas para corte ou passagem dos espermatóforos para as fêmeas, como aumento dos quelípodos ou modificações nos pleópodos (Hartnoll, 1985). Este fenômeno já foi identificado em diversos grupos de crustáceos decápodos, como Caridea (Pescinelli et al., 2018), Brachyura (Santos et al., 2018) e Anomura (Chaves et al., 2019; Pinheiro et al, 2017). A muda da puberdade estabelece a maturidade sexual morfológica dos indivíduos, que então passam a ser considerados reprodutivos (Hartnoll, 1985). O número de machos e fêmeas aptos a se reproduzir em uma população é utilizado para calcular a razão sexual populacional, que pode ser 1:1 ou enviesada para um dos sexos (Emlen e Oring, 1977).

O tamanho corporal de fêmeas aptas a se reproduzir geralmente está relacionado ao número de ovos que se desenvolvem na parte externa do abdômen. A fecundidade em crustáceos decápodos é medida considerando o número de ovos no estágio inicial de desenvolvimento produzidos a cada evento reprodutivo (Hines, 1982). O tamanho dos ovos é geralmente inversamente proporcional a fecundidade, gerando um padrão de fêmeas com muitos ovos pequenos ou poucos ovos grandes (Vance, 1973a,b). Este padrão de número e tamanho dos ovos também está relacionado com latitude e profundidade dos ambientes marinhos, ambos os aspectos implicam em mudanças na temperatura da água (Clarke, 1987). A relação entre estes aspectos pode ser observada em espécies diferentes, tanto próximas quanto afastadas filogeneticamente, e em populações da mesma espécie que possuem distribuições ao longo dos gradientes (Laptikhovsky, 2006). Há também uma sobreposição deste fenômeno com a plasticidade fenotípica do tamanho dos ovos, observada quando fêmeas de tamanhos similares em uma mesma população produzem ovos maiores em temperaturas menores e vice-versa (Laptikhovsky, 2006).

Crustáceos anomuros marinhos apresentam desenvolvimento indireto e as fêmeas destes animais liberam suas larvas na coluna d’água após o desenvolvimento embrionário (Harvey et al., 2014). As larvas que sobrevivem a este período planctônico eventualmente assentam e tornam-se parte de populações locais (Hadfield, 1986). Esta entrada de novos indivíduos em uma população é chamada de recrutamento (Caley et al., 1996). Segundo este autor, a maioria das populações de invertebrados marinhos são demograficamente abertas e o recrutamento local não é determinado pela reprodução local devido à dispersão dos indivíduos pelas correntes oceânicas durante as fases larvais. No sentido restrito, entretanto, o recrutamento em populações marinhas abertas pode ser estimado pela adição de indivíduos às populações locais após o período de assentamento do último estágio larval planctônico (Caley et al., 1996). Os membros da família Porcellanidae, de modo geral, possuem um desenvolvimento indireto abreviado, passando por dois estágios na fase zoea até o estágio de megalopa (Vela e González-Gordillo, 2016), quando assentam e tornam-se juvenis (Jensen, 1991). Assim, a entrada de indivíduos em estágio de megalopa e a presença de juvenis nas populações de porcelanídeos podem indicar um período de recrutamento para estas populações (Jensen, 1991).

Ao longo da área de distribuição de *P. laevidactylus* há estudos realizados no extremo sul, em Mar del Plata, Argentina sobre razão sexual (Bremec e Cazzaniga, 1984) e aspectos populacionais e reprodutivos (Camiolo e Luppi, 2016), entretanto estes trabalhos analisaram um período sete e três meses de coletas, respectivamente. No Brasil, dois estudos descrevem aspectos reprodutivos da espécie, um realizado no Ceará (Ogawa e Rocha, 1976) e outro em São Paulo (Pinheiro e Fransozo, 1995). Desta forma, faltam dados sobre a influência da sazonalidade nos aspectos populacionais, sobre como são estas populações no Brasil, e sobre os aspectos reprodutivos na região sul do país. Os dados dos estudos prévios serão utilizados para comparação com os dados obtidos no presente estudo.

2. Objetivos

O objetivo geral da presente dissertação de mestrado é estudar a biologia populacional e reprodutiva da espécie *Pachycheles laevidactylus* em duas localidades do litoral norte do Rio Grande do Sul, Brasil.

Os objetivos específicos são analisar a distribuição dos sexos nas classes de tamanho, a razão sexual, o período reprodutivo, a maturidade sexual, o crescimento relativo e o recrutamento a fim de entender a biologia populacional da espécie. E, para compreender a biologia reprodutiva da espécie, analisar a fecundidade, o volume dos ovos, a perda de ovos e aumento de tamanho dos ovos. Por fim, todos estes dados foram analisados de forma comparativa entre as localidades e com outros trabalhos envolvendo a espécie alvo e outras espécies de Porcellanidae.

As hipóteses iniciais para o capítulo 2 são que em ambas as localidades não há diferença de tamanho entre sexos, a razão sexual é 1:1, reprodução e recrutamento são contínuos e o tamanho em que a fêmeas começam a se reproduzir é influenciado por mudanças de latitude (tamanhos menores em temperaturas quentes, tamanhos maiores em temperaturas frias). Considerando o padrão relacionado à influência da latitude na relação entre fecundidade e volume dos ovos, a hipótese inicial para o capítulo 3 é que *P. laevidactylus* seguirá este padrão intra e interespecificamente. Ou seja, a espécie têm uma fecundidade menor e ovos maiores nos locais estudados em comparação com outras populações e outras espécies do gênero em áreas tropicais, assim como uma fecundidade maior e ovos menores quando comparada com outras populações e espécies encontradas em locais de latitude maior.

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CAPÍTULO II:

Population biology of the porcelain crab *Pachycheles laevidactylus* Ortmann, 1892 (Decapoda, Anomura, Porcellanidae) in southern Brazil

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Population biology of the porcelain crab *Pachycheles laevidactylus* Ortmann, 1892 (Decapoda, Anomura, Porcellanidae) in southern Brazil

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Abstract

The population structure, sex ratio, reproductive period, recruitment, size at sexual maturity and relative growth of the porcelain crab *Pachycheles laevidactylus* was analysed from two locations on northern coast of Rio Grande do Sul state, Brazil. The crabs were collected from polychaete colonies seasonally during one year, sexed, counted and measured. A total of 1534 individuals were sampled, 943 in Torres and 591 in Tramandaí. There was no difference in body size or cheliped size between sexes, while females had larger pleons than males. The sex ratio was 1:1 in both locations throughout the year, but was skewed towards either males or females in two size classes. Reproduction was continuous, with a higher frequency of ovigerous females in the coldest seasons, but recruitment occurred exclusively in spring. The morphological sexual maturity for females (5.39 mm CW) was larger than the size of the smallest ovigerous female collected (3.35 mm CW), while males became morphologically mature at 5.20 mm CW. Overall, the species starts reproducing at smaller sizes at locations closer to the edges of its distribution. Chelipeds grow at slower rates in adult females than in juveniles. Males did not show any change in growth pattern from juveniles to adults, but all slopes were different except for pleon somite length.

Key words: sex ratio, reproductive period, recruitment, maturity, relative growth

1. Introduction

The anomuran family Porcellanidae Haworth, 1825 occurs worldwide in tropical and temperate marine habitats, especially in intertidal and subtidal zones (Osawa and McLaughlin, 2010; Ferreira and Melo, 2016). The family comprises around 30 genera and 280 species described (Bezerra et al., 2019). Most porcelain crab species are free-living and can be found on rocky shores, coral reefs and estuarine areas (Veloso, 1999). Some display symbiotic relationships with other organisms, both free-living such as shrimps, hermit crabs, turtles and fishes (Jensen, 1986; Meireles and Mantelatto, 2008; Baeza et al., 2013; Werding et al., 2016) and sessile such as coral reefs, anemones, sponges and annelids (Gore, 1982; Baeza and Stotz, 2001; Hiller and Werding, 2018; Werding and Hiller, 2019). These crabs are known to consume benthic algae and filter plankton from the water column (Veloso, 1999; Zimba et al., 2016), they also serve as food for local predators (Ogawa and Rocha, 1976). They are considered to have little commercial value, but a few species are used in the aquarium trade, such as *Porcellana sayana* (Leach, 1820) (Baeza et al., 2013).

Twenty species of Porcellanidae are currently known from the Brazilian coast, seven of which belong to *Pachycheles* Stimpson, 1858 (Ferreira and Melo, 2016).

Pachycheles laevidactylus Ortmann, 1892 mainly inhabits the intertidal zone, and can be found under rocks, among seaweed or in mussel beds (Veloso, 1999). They can also live in facultative symbiosis with species of Bryozoa or polychaete sand banks of *Phragmatopoma* Mörch, 1863 (Ferreira and Melo, 2016). This species occurs exclusively in the western Atlantic, from the state of Maranhão in northeast Brazil to Monte Hermoso in Argentina (Ferreira and Melo, 2016). No information on the life history of *P. laevidactylus* is known for the south of Brazil, although it is the most frequent Decapoda species in the *P. caudata* Krøyer in Mörch, 1863 sand banks on the northern coast of Rio Grande do Sul state (Zanini et al., submitted). In Argentina, Bremec and Cazzaniga (1984) analysed the reproductive biology and sex ratio of the species, while Camiolo and Lupi (2016) studied its habitat and population structure, heterochely, relative growth, morphological maturity and fecundity.

Considering that this species is the most frequent decapod in the poliquete sand banks on the northern coast of Rio Grande do Sul and little is known about their ecology on the region, the present study aimed at investigating the population biology of the porcelain crab species *Pachycheles laevidactylus* in southern Brazil. The population structure, sex ratio, reproductive period, recruitment, size at sexual maturity and relative growth of individuals from two locations on the northern coast of Rio Grande do Sul state were analysed seasonally over the course of a year. Our initial hypotheses are that there is no difference in body size between sexes, sex ratio is 1:1, reproduction and recruitment are continuous and the size at which females start reproducing is strongly influenced by latutidinal changes (smaller sizes at warmer temperatures, larger sizes at colder temperatures).

2. Material and methods

2.1 Sample collection

Specimens of *Pachycheles laevidactylus* (Fig. 1A) were obtained from two locations on the northern coast of Rio Grande do Sul state, Brazil, Torres (29°20'20.9"S, 49°43'23.0"W) and Tramandaí (30°00'16.7"S, 50°07'49.2"W) (Fig. 1B), during one year: November 2018 (spring), February (summer), May (autumn) and August 2019 (winter). In Torres, the crabs were collected at low tide from rock formations at the shore (Fig. 1D) by two people for 30 minutes. During that time sand banks formed by the polychaete *P. caudata* were searched for crabs by hand using knives. Considering the lack of natural rock formations in the Tramandaí shoreline, the animals were collected at low tide from the pillars of the Maritime Platform (Fig. 1C, D). Samples of *P. caudata* sand banks were removed from the pillars and brought to the beach, where two people examined them for crabs during 30 minutes. Water temperature was measured at each location after the sampling period with a mercury thermometer.

Immediately after collection, the crabs were transported to the laboratory and frozen. The animals were identified according to Ferreira and Melo (2016), counted and sexed considering pleopod presence, number and location (Ferreira, 2015). Males have only the second pleopod present, which is modified as a gonopod, while females only have the third to fifth pleopods, which are long and setose (Baeza and Asorey, 2012; Ferreira, 2015). The following measurements were obtained from the specimens using a 0.01 mm caliper and a light stereomicroscope: carapace length (CL); carapace width (CW); largest cheliped propodus length (LPL); largest cheliped propodus width (LPW); smallest cheliped propodus length (SPL); smallest cheliped propodus width (SPW); second pleon somite length (PSL) and pleopod length (PL). The only pleopod present in males and the pleopod found on the third pleon somite in females were used for PL, always on the left side. Only measurements of intact structures were considered, measurements of structures with injuries were not performed. Considering the differences between locations and collection methods, some analyses (population structure, sex ratio, reproductive period and recruitment) were performed by location. However, considering that the locations are near each other, some analyses (sexual maturity and relative growth) were done with the entire pool of data.

Specimens were preserved in 70% ethyl alcohol and deposited at the Carcinological Collection of the Zoology Department at Universidade Federal do Rio Grande do Sul (DZ/UFRGS), under the catalogue numbers 6921 to 6928.

2.2 Population structure, sex ratio, reproductive period and recruitment

Population structure was analysed according to the size-frequency distribution of individuals. The size classes were calculated using the formula $k = 1 + \log_2 n$, k being the number of classes and n being the total number of specimens (Sturges, 1926). The dimensions of a size class were obtained by dividing the range of CW measurements by k. The frequency of ovigerous females/total females marked the reproductive period. The recruitment was estimated by the presence of individuals in the megalopa phase. Individuals whose sex could not be determined were considered indeterminate (IN).

Statistical analyses were performed using R version 3.6.0 (R Core Team, 2020) and Microsoft Excel. Kolmogorov-Smirnov test was applied to test data normality. Measurements from males and females were compared through Mann-Whitney test. Chi-square test (χ^2) was used to compare the number of males and females (sex ratio) between seasons, size classes and in total. Size data is presented as median (1st quartile; 3rd quartile) and the significance level used was $\alpha = 0.05$.

2.3 Size at functional and morphological sexual maturity

The functional sexual maturity for females was estimated based on the smallest ovigerous female. To determine the morphological sexual maturity of females and males, the measurements were log transformed and a non-hierarchical ‘k-means clustering’ analysis was performed. This method separates the data into a preselected number of groups in order to maximize the variance between groups and minimize the variance within groups. It was used to separate juveniles and adults within each sex. A discriminant analysis (DA) was applied to refine the classification if needed. An analysis of covariance (ANCOVA) was used to compare the intercepts and slopes between juveniles and adults for each relationship. The results determined whether the two groups (juvenile and adults) were best represented by different linear equations or by the same single equation.

2.4 Relative growth

A regression analysis was performed to evaluate the relative growth considering the function $y = ax^b$, where y = dependent variable (CL, LPL, LPW, SPL, SPW, PSL and PL), x = independent variable (CW), a = intercept and b = slope of the regression (Hartnoll, 1982). The value of the constant b was used to establish the growth pattern for each body part, where $b = 1$ was considered isometric growth, $b > 1$ was positive allometric growth and $b < 1$ was negative allometric growth. The values of the constant b were tested using the Student’s t-test.

3. Results

3.1 Population structure

A total of 1534 individuals were collected during the study period. Of the 943 sampled in Torres, 91 (9.7%) were megalopae, 40 (4.2%) were IN, 400 (42.4%) were males, 144 (15.3%) were non-ovigerous females and 268 (28.4%) were ovigerous females (Fig. 2). The highest number of crabs collected was 351 in summer, while the lowest was 128 in autumn (Fig. 2). In Tramandaí 591 individuals were collected, of which 2 (0.5%) were megalopae, 9 (1.5%) were IN, 278 (47.1%) were males, 83 (14.0%) were non-ovigerous females and 218 (36.9%) were ovigerous females (Fig. 2). Winter was the season when the highest number of animals were collected (257), and the lowest (85) was in spring (Fig. 2). Torres had the megalopa with the smallest CW of all (1.46 mm), while the largest individual was an ovigerous female (15.16 mm) (Table 1). In Tramandaí, the CW of individuals varied between 1.62 mm (megalopa) and 15.00 mm (male) (Table 1).

The data showed a non-normal distribution (Torres: D = 0.92785, $p < 0.0001$; Tramandaí: D = 0.97547, $p < 0.0001$). Size comparisons between males and females yielded similar results in both locations (Fig. 3). In Torres, there was no difference in size between males and total females in the following structures: CW (W = 79776, p = 0.088), CL (W = 84456, p = 0.239), LPL (W = 41532, p = 0.353), LPW (W = 42837, p = 0.468), SPL (W = 43272, p = 0.759) and SPW (W = 43841, p = 0.808). Females had significantly larger PSL than males when comparing total individuals (W = 95008, $p <$ 0.0001) and only adults (W = 37136, $p < 0.0001$), as well as a slightly larger PSL between juveniles (W = 16083, p = 0.034). While in Tramandaí, total females were slightly larger than males (W = 40420, p = 0.025). Total males and females did not display a significant difference in CL (W = 44234, p = 0.202), LPL (W = 27195, p = 0.786), LPW (W = 30510, p = 0.658), SPL (W = 31088, p = 0.881) and SPW (W = 31078, p = 0.949). Females also had a significantly larger PSL than males in total (W

= 52610, $p < 0.0001$) and when comparing only adults (W = 28869, $p < 0.0001$), but not between juveniles (W = 4123.5, $p = 0.672$).

3.2 Sex ratio

In both locations, the total sex ratio did not differ significantly from 1:1 (Torres: $\chi^2 = 0.18$; Tramandaí: $\chi^2 = 1.08$; $p > 0.05$) and there was also no difference between the number of males and females in each season ($p > 0.05$). However, in Torres, the females were found in significantly higher numbers in the seventh size class (9.21–10.64 mm; $\chi^2 = 4.26$, $p < 0.05$) (Fig. 4A) and in Tramandaí, males were more abundant in the fourth size class (4.89–6.32 mm; $\chi^2 = 4.06$, $p < 0.05$) and females were more abundant in the seventh size class (9.21–10.64 mm; $\chi^2 = 4.76$, $p < 0.05$) (Fig. 4A).

3.3 Reproductive period and recruitment

Ovigerous females were found all year round in both locations (Fig. 4B). The lowest frequencies of ovigerous females were in spring (Torres) and summer (Tramandaí). The highest frequencies of ovigerous females were in autumn/winter in both locations. The recruitment period was the same for both locations, with megalopa being found only in spring and IN being found mainly in spring/summer in Torres and exclusively in this period for Tramandaí (Fig. 2). The water temperature varied from 15°C in winter (Torres) to 28°C in summer (Tramandaí) (Fig. 4B).

3.4 Size at functional and morphological sexual maturity

The overall smallest ovigerous female was found in Tramandaí (3.35 mm CW, 3.33 mm CL), and appeared in all size classes after that (Fig. 2), signaling the size at functional maturity for females. In Torres, ovigerous females began to appear in the third class (3.45–4.88 mm) and were the only individuals in the tenth class (13.53–15.00 mm) (Fig. 2).

The size of the smallest adult female found through the k-means clustering analysis was 5.39 mm CW, with all the smaller females considered juveniles (Fig. 5). For males, the smallest adult was considered to be at 5.20 mm CW, with all the smaller males considered juveniles. Most relationships showed a significant difference between juveniles and adults for both males and females (ANCOVA, Table 2). CL x CW in females was the only relationship where the slope was the same between juveniles and adults, while the intercept was different. In males, only PSL x CW was better explained by one single linear equation instead of two (Table 2, Fig. 5).

3.5 Relative growth

In the relative growth analysis, CL showed negative allometric growth in all groups (Table 3, Fig. A1). The characters LPL, LPW, SPL and SPW had different growth between juvenile and adult females. Juvenile females had positive allometry for LPL, LPW and SPW, and isometric growth for SPL, while adults had isometric growth for LPL, LPW and SPW, and negative allometric growth for SPL. Juvenile and adult females had positive allometry for PSL and PL. Males did not present any difference in growth pattern between juveniles and adults and all characters other than CL had positive allometric growth (Table 3, Fig. A1). IN individuals presented positive allometry for LPL, LPW and SPW, and isometric growth for SPL and PSL (Table 3). These individuals did not have pleopods and so the PL growth pattern could not be analysed.

4. Discussion

4.1 Population structure

There are both similarities and differences between the *Pachycheles laevidactylus* populations of Tramandaí and Torres. Notably, females were slightly larger than males in Tramandaí only, whereas no such difference could be detected in Torres nor in a *P. laevidactylus* population in Argentina (Bremec and Cazzaniga, 1984). This indicates a lack of size difference between males and females in this species, regardless of the small difference seen in Tramandaí. A similar situation was seen in the species *Allopetrolisthes spinifrons* (H. Milne Edwards, 1837) and *Porcellana sayana*, both species that also live in gregarious communities and have been found to have little or no size difference between males and females (Baeza and Asorey, 2012; Baeza et al., 2013). However, size differences between males and females have been detected in other porcelain crab species, with males generally attaining larger sizes than females (Ahmed and Mustaquim, 1974; Miranda and Mantelatto, 2009; Baeza and Asorey, 2012), although sometimes females can attain the larger sizes (Ahmed and Mustaquim, 1974).

4.2 Sex ratio

The sex ratio of *P. laevidactylus* was 1:1 overall in both locations and did not fluctuate throughout the year. The same has also been found in several other species of Porcellanidae (Ahmed and Mustaquim, 1974; Bremec and Cazzaniga, 1984; Fransozo and Bertini, 2001; Miranda and Mantelatto, 2009; Baeza and Asorey, 2012; Baeza et al., 2013; Bezerra et al., 2019). However, sex ratio did differ from 1:1 in a few size classes. Females were more abundant in the seventh size class (9.21–10.64 mm) in both locations, while males were more abundant in the fourth size class (4.89–6.32 mm) only in Tramandaí. This skewed sex ratio by size agrees with the slight size difference detected between males and females in Tramandaí, since males were more abundant in a smaller size class and females dominated a larger size class. While females were more abundant in a larger size class in Torres as well, the males were not more frequent at any size over another.

The overall sex ratio of these *P. laevidactylus* populations fits within the theory of natural selection. The theory states that natural selection favours a 1:1 sex ratio, and that if producing male or female progeny is equally expensive then the sex ratio is likely to be 1:1 (Wenner, 1972). However, the skewed sex ratio seen in the different size classes of *P. laevidactylus* does not fit the theory, and might be caused by different mortality rates or differential behaviours between sexes (Wenner, 1972), such as ovigerous females hiding deeper into the sand banks for protection or males being more active as they search for mates. Ahmed and Mustaquim (1974) reported a similar pattern for the four species they analysed, where the overall and seasonal sex ratio was 1:1, but in some size classes it deviated in favour of one of the sexes. The two *Pachycheles* species they analysed also showed a tendency towards larger crabs being mostly female, while the opposite occurred in the two *Petrolisthes* Stimpson, 1858 species (Ahmed and Mustaquim, 1974).

4.3 Reproductive period and recruitment

Ovigerous females were collected across all seasons, indicating a continuous reproductive strategy, but with the highest frequency of ovigerous females in the coldest months (autumn/winter). Boschi (1963) observed that ovigerous females of *P. laevidactylus* (cited as *P. haigae*) could be found all year long in Argentina and Ogawa and Rocha (1976) also collected ovigerous females on the northern coast of Brazil along an entire year, but no other study has since analysed its reproductive period in other locations. Some species of porcelain crabs have shown continuous reproduction, *Pachycheles tomentosus* Henderson, 1893, *Pachycheles natalensis* (Krauss, 1843), *Petrolisthes rufescens* (Heller, 1861) in Pakistan (Ahmed and Mustaquim, 1974), *Petrolisthes armatus* (Gibbes, 1850) in Brazil (Oliveira and Masunari, 1995; Miranda and Mantelatto, 2009; Bezerra et al., 2019) and *Porcellana sayana* in Brazil (Baeza et al., 2013) are some examples of this reproductive strategy. In contrast, other species have more restricted reproductive periods, such as *Pachycheles monilifer* (Dana, 1852) in Brazil (Fransozo and Bertini, 2001), *Petrolisthes boscii* (Audouin, 1826) in Pakistan (Ahmed and Mustaquim, 1974), *Petrolisthes laevigatus* (Guérin, 1835) in Chile (Lardies et al., 2004) and *Petrolisthes japonicus* (De Haan, 1849) in Japan (Hamasaki et al., 2020).

The larval stages of *P. laevidactylus* can last between 25 to 31 days (Boschi et al., 1967), until they become megalopae and settle (Jensen, 1991). Individuals in the megalopa stage were collected exclusively during spring in both locations, which indicates a seasonal recruitment period for this species in the region. Despite being present all year long, ovigerous females had higher frequencies in autumn/winter which might lead to the presence of megalopae and IN in spring/summer. Nevertheless, the complete absence of megalopae in other seasons indicates that factors other than temperature are influencing the recruitment period in these populations. This disjointed reproductive and recruitment period was also registered in two populations of *Petrolisthes armatus* in Brazil (Oliveira and Masunari, 1995; Pinheiro et al., 2017). The authors of those studies also found that *P. armatus* in those locations had continuous reproduction, yet seasonal recruitment. However, for another two populations of the same species both continuous reproduction and continuous recruitment were recorded (Miranda and Mantelatto, 2009; Bezerra et al., 2019). This intraspecific plasticity might be especially clear in species with wide distributions and which can occupy diverse environments within that range. Subsequent studies on other populations of *Pachycheles laevidactylus* including all seasons could provide more data on whether this species also presents this intraspecific plasticity along its distributional range.

In contrast to the restricted presence of megalopae, IN individuals and male and female juveniles were found in both spring and summer in Tramandaí, while in Torres they were collected all year long. The disparity between the number of megalopae collected in Torres (91) and Tramandaí (2), as well as the difference between the presence of megalopae and the presence of IN individuals and juveniles, could perhaps be attributed to bias in the different sampling methods applied to each location or the physical habitat differences (horizontal natural rock formations in Torres vs. vertical human made columns in Tramandaí).

4.4 Size at functional and morphological sexual maturity

The smallest ovigerous female found in the present study (3.35 mm CW, 3.33 mm CL) was larger than the ones found in other studies of *P. laevidactylus* in northeastern Brazil (2.8 mm CL; Ogawa and Rocha, 1976 as *P. haigae*), in Mar del Plata, Argentina (2.26 mm CW; Camiolo and Luppi, 2016) and in Monte Hermoso, Argentina (3.0 mm CW; Bremec and Cazzaniga, 1984 as *P. haigae*), and similar to southeastern Brazil (3.3 mm CL; Pinheiro and Fransozo, 1995 as *P. haigae*). The size of the smallest ovigerous female is often used to signal the onset of functional sexual maturity for females, and is known to vary between species and between populations of the same species (Hines, 1989; Hirose et al., 2013).

Wehrtmann et al. (2012) also reported a difference in size at onset of functional sexual maturity for populations of *Petrolisthes armatus* along its distributional range. The authors observed that females became ovigerous at smaller sizes in Pacific Costa Rica compared to Brazil, and concluded that this shift might be related to environmental factors such as temperature. Similar patterns are known for other decapod species (Hines, 1989; Castilho et al., 2007; Hirose et al., 2013), where breeding starts at smaller sizes in warmer environments than in colder environments, forming a gradient from lower latitudes to higher latitudes (Blackburn et al., 1999; Blackenhorn and Demont, 2004). But a few cases of the opposite occurring are also known (Terossi et al., 2010). This variation might be due to multiple abiotic and biotic factors, such as latitude, temperature, salinity, habitat, food availability, competition and predation risk (Hirose et al., 2013). Here we see a slight increase in the size of the smallest ovigerous female from the tropical zone (northeastern Brazil) towards the temperate zone (present study), but a decrease from the south of Brazil towards Argentina. Argentina is at the edge of the *P. laevidactylus* distribution range, which could influence the size difference observed between south Brazil and Argentina. Studies have shown that environmental conditions might be less optimal at the edges of an organism's distribution when compared to the central areas, possibly resulting in stress related population and reproductive differences (Wehrtmann et al., 2012; Wassick et al., 2017).

It should be noted that only one of the *P. laevidactylus* studies cited above (Ogawa and Rocha, 1976) conducted their sampling during an entire year, with the added caveat that the authors were focused on fecundity rather than population analysis. The other studies all had shorter sampling periods, the longest lasting 7 months (Bremec and Cazzaniga, 1984). These different sampling periods could have influenced the crab sizes found in those populations when compared to the present study, due to the possible influence of biotic and abiotic factors that could change from season to season.

In the present study, the morphological sexual maturity of females did not match the functional sexual maturity (smallest ovigerous female). The smallest morphologically mature female (5.39 mm CW) was about 2 mm larger than the smallest ovigerous female found (3.35 mm CW). A study done with brachyuran crabs showed that gonadal maturity can occur before morphological changes in relative growth, even for characters related to reproduction (López et al., 1997). These authors also found that the size at onset of gonadal maturity coincided with the size of the smallest ovigerous female, but the percentage of ovigerous females only began to be relevant near the morphometric size of maturity. In porcelain crabs, a difference between functional and morphological maturity was found in another population of *P. laevidactylus* in Argentina (Camiolo and Lupi, 2016) and in *Petrolisthes armatus* in Brazil (Pinheiro et al., 2017). Camiolo and Lupi (2016) calculated the morphological maturity for females at around 4.38 mm CW, smaller than the size found for females in the present study. Once again showing that *Pachycheles laevidactylus* does not follow the usual pattern between reproduction and temperature. The morphological sexual maturity for males was slightly smaller than for females, with the smallest adult male having 5.20 mm CW.

4.5 Relative growth

Individuals of indeterminate sex, females and males showed a negative allometry between carapace length and width, a pattern that was also observed in *Petrolisthes armatus* for both sexes in two studies (Miranda and Mantelatto, 2010;

Wassick et al., 2017) but only females in another (Pinheiro et al., 2017). Heterochely was observed in both males and females in the present study, same as reported for *P. laevidactylus* in Argentina (Camiolo and Luppi, 2016) and as is common in porcelain crabs (Pinheiro et al., 2017). In the study, Camiolo and Luppi (2016) found no significant difference in handedness between males and females. As such, we did not analyse handedness in the present study, and instead, only compared chelipeds by size rather than anatomical side.

The length and width of both chelipeds grew slower than the carapace width in adult females as opposed to juvenile females, especially the length of the smallest cheliped. This change in growth pattern is probably related to energy allocation, since as adults the females tend to direct more energy towards reproduction. In males, the length and width of both chelipeds showed positive allometric growth as juveniles and as adults. Nevertheless, the angular and linear coefficients were different between the two demographic categories, indicating that these structures grow at different speeds. This is even more apparent when comparing the width of both the smaller and the largest chelipes. Regardless of the difference in growth pattern, no size difference could be detected when comparing the measures of the largest and the smallest chelipeds between males and females. The population of *P. laevidactylus* analysed in Argentina also showed positive allometry for the length of the larger cheliped, but isometry for both sexes on the length of the smaller cheliped (Camiolo and Lupi, 2016), as opposed to the males and adult females in the present study. Additionally, the larger cheliped of adult males and females of species from the *Petrolisthes* and the *Allopetrolisthes* genera presented positive allometric growth (Miranda and Mantelatto, 2010; Baeza and Asorey, 2012; Pinheiro et al., 2017), in contrast to the females in this study.

Despite males and females displaying the same growth pattern (positive allometry) for the second pleon somite, adult females had a larger second pleon somite than adult males. However, males had the same growth line for both juveniles and adults, while females did not, showing that the pleon of females grows faster than the pleon of males. The females of *P. laevidactylus* analysed in Argentina showed a similar growth pattern for adults (positive allometry) and different for juveniles (isometry), while the males presented isometric growth rates overall (Camiolo and Lupi, 2016). The relationship between pleon size and sex is very well documented in brachyuran crabs (Hartnoll, 1982; Hirose et al., 2013), and females with pleons larger than males have also been found in the porcelain crab *Petrolisthes armatus* (Miranda and Mantelatto, 2010; Pinheiro, et al., 2017; Wassick et al., 2017) and *Pachycheles laevidactylus* (Camiolo and Lupi, 2016). This difference between sexes is probably related to reproduction, as a larger pleon in females could correlate to more space for egg carrying, and consequently a higher number of eggs (Hartnoll, 1982).

Male and female pleopods are morphologically different in porcellanid crabs, and also have different functions. Only one pair of pleopods is present in males (located on the second pleon somite), it is biramous and modified into a gonopod (Ferreira, 2015). In females, there are three pairs of pleopods, located on the third, fourth and fifth somites; and they are used to hold the egg mass during the ovigerous period (Ferreira, 2015). The pleopods of both males and females showed positive allometric growth overall, which differs from what was seen in a porcelain crab from a different genus. *Petrolisthes armatus* displayed a plasticity in pleopod length growth patterns across its distributional range. In Brazil, the pleopod length in males of *P. armatus* had negative allometric growth and in females it had isometric growth (Miranda and Mantelatto, 2010). In two locations in the Atlantic United States of

America, females had positive allometric growth in both while males had negative allometric growth in one and isometric growth in the other (Wassick et al., 2017). Still, males and females alike use their pleopods during reproduction and might benefit from having longer pleopods as adults, facilitating the transfer of sperm from males to females and influencing the amount of eggs females can hold. This might explain why males and females in the present study presented positive growth.

The present study analysed many aspects of *P. laevidactylus* at two locations in a temperate zone in Brazil for the first time, adding to the knowledge of this species. Some of our initial hypotheses were confirmed, such as the lack of difference in body size between sexes, the 1:1 sex ratio and continuous reproduction. However, others were not. The recruitment period was seasonal and latitudinal differences did not seem to be the most relevant factor influencing the size that females start reproducing or their size at morphological maturity. Further studies focused on the population dynamics of *P. laevidactylus* at the northern edge of its distribution could help elucidate how environmental factors other than latitude and temperature affect its biology.

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Table 1. *Pachycheles laevidactylus*. Carapace width (mm) from individuals sampled in two locations in the northern coast of Rio Grande do Sul state, Brazil. ♂: males; ♀: females; 1st q: 1st quartile; 3rd q: 3rd quartile.

Groups	Torres			Tramandaí		
	Min	Max	Median (1st q; 3rd q)	Min	Max	Median (1st q; 3rd q)
Megalopa	1.46	1.68	1.58 (1.56; 1.60)	1.62	1.63	
Indeterminate	1.48	3.65	2.07 (1.81; 2.28)	1.85	4.45	2.57 (2.10;2.89)
♀	1.75	15.16	6.08 (4.02; 8.02)	2.08	14.05	7.52 (4.73; 9.15)
Ovigerous ♀	3.61	15.16	7.16 (5.61; 9.26)	3.35	14.05	8.13 (6.44; 9.65)
♂	1.80	13.30	5.59 (3.84; 7.69)	2.15	15.00	6.48 (4.68; 8.49)

Table 2. *Pachycheles laevidactylus*. Analysis of covariance (ANCOVA) results for each growth relationship between juveniles and adults of females and males in the northern coast of Rio Grande do Sul state, Brazil. CL, carapace length; CW, carapace width; LPL, largest cheliped propodus length; LPW, largest cheliped propodus width; SPL, smallest cheliped propodus length; SPW, smallest cheliped propodus width; PSL, second pleon somite length; PL, pleopod length; J, juveniles; A, adults; Par, parameter; *significant difference at $p < 0.05$.

Relationship	Group	Par. (log)	F	*p*
CL x CW	♀ (J vs. A)	intercept	8.84	0.003*
		slope	2.89	0.089
	♂ (J vs. A)	-	-	-
		slope	27.28	0.000*
LPL x CW	♀ (J vs. A)	-	-	-
		slope	58.73	0.000*
	♂ (J vs. A)	-	-	-
		slope	29.48	0.000*
LPW x CW	♀ (J vs. A)	-	-	-
		slope	122.26	0.000*
	♂ (J vs. A)	-	-	-
		slope	103.17	0.000*
SPL x CW	♀ (J vs. A)	-	-	-
		slope	8.47	0.003*
	♂ (J vs. A)	-	-	-
		slope	9.68	0.001*
SPW x CW	♀ (J vs. A)	-	-	-
		slope	82.10	0.000*
	♂ (J vs. A)	-	-	-
		slope	50.44	0.000*
PSL x CW	♀ (J vs. A)	-	-	-
		slope	5.64	0.017*
	♂ (J vs. A)	intercept	0.45	0.504
		slope	0.02	0.887
PL x CW	♀ (J vs. A)	-	-	-
		slope	86.35	0.000*
	♂ (J vs. A)	-	-	-

slope 142.81 0.000

Table 3. *Pachycheles laevidactylus*. Relative growth for groups (IN: indeterminate sex; ♀J: juvenile female; ♀A: adult female; ♂J: juvenile male; ♂A: adult male) of individuals sampled in the northern coast of Rio Grande do Sul state, Brazil. CL carapace length; CW carapace width; LPL largest cheliped propodus length; LPW largest cheliped propodus width; SPL smallest cheliped propodus length; SPW smallest cheliped propodus width; PSL second pleon somite length; PL pleopod length; *n* number of individuals; *r* correlation coefficient (all correlations were significant, $p < 0.05$); GP growth pattern; + positive allometry; – negative allometry; = isometry.

Relationship	Group	*n*	Power function $y = ax^b$	r^2	$b \neq 1$	GP
CL x CW	IN	47	$CL = 0.11\ CW^{0.92}$	0.93	Yes	-
	♀J	245	$CL = 0.13\ CW^{0.90}$	0.97	Yes	-
	♀A	424	$CL = 0.12\ CW^{0.92}$	0.98	Yes	-
	♂J	252	$CL = 0.10\ CW^{0.93}$	0.98	Yes	-
	♂A	384	$CL = 0.02\ CW^{0.98}$	0.99	Yes	-
LPL x CW	IN	28	$LPL = 0.20\ CW^{1.26}$	0.93	Yes	+
	♀J	190	$LPL = 0.12\ CW^{1.21}$	0.95	Yes	+
	♀A	334	$LPL = 0.24\ CW^{1.00}$	0.90	No	=
	♂J	191	$LPL = 0.22\ CW^{1.30}$	0.95	Yes	+
	♂A	302	$LPL = 0.01\ CW^{1.16}$	0.95	Yes	+
LPW x CW	IN	28	$LPW = 1.14\ CW^{1.56}$	0.94	Yes	+
	♀J	190	$LPW = 0.94\ CW^{1.41}$	0.90	Yes	+
	♀A	336	$LPW = 0.33\ CW^{1.03}$	0.90	No	=
	♂J	192	$LPW = 1.09\ CW^{1.52}$	0.92	Yes	+
	♂A	307	$LPW = 0.54\ CW^{1.18}$	0.94	Yes	+
SPL x CW	IN	27	$SPL = 0.06\ CW^{0.87}$	0.49	No	=
	♀J	189	$SPL = 0.08\ CW^{1.03}$	0.90	No	=
	♀A	336	$SPL = 0.10\ CW^{0.94}$	0.87	Yes	-
	♂J	189	$SPL = 0.26\ CW^{1.17}$	0.94	Yes	+
	♂A	307	$SPL = 0.13\ CW^{1.09}$	0.94	Yes	+
SPW x CW	IN	28	$SPW = 1.12\ CW^{1.33}$	0.79	Yes	+

	♀J	191	$SPW = 1.03\ CW^{1.25}$	0.91	Yes	+
	♀A	336	$SPW = 0.54\ CW^{0.97}$	0.89	No	=
	♂J	190	$SPW = 1.08\ CW^{1.30}$	0.94	Yes	+
	♂A	307	$SPW = 0.79\ CW^{1.12}$	0.95	Yes	+
PSL x CW	IN	47	$PSL = 0.61\ CW^{1.10}$	0.88	No	=
	♀J	243	$PSL = 0.59\ CW^{1.12}$	0.96	Yes	+
	♀A	421	$PSL = 0.61\ CW^{1.16}$	0.96	Yes	+
	♂J	252	$PSL = 0.49\ CW^{1.02}$	0.97	Yes	+
	♂A	383	$PSL = 0.49\ CW^{1.02}$	0.96	Yes	+
PL x CW	♀J	212	$PL = 3.81\ CW^{2.34}$	0.79	Yes	+
	♀A	407	$PL = 2.67\ CW^{1.71}$	0.92	Yes	+
	♂J	249	$PL = 1.94\ CW^{1.54}$	0.80	Yes	+
	♂A	383	$PL = 1.19\ CW^{1.04}$	0.94	Yes	+

Figure Captions

Figure 1. A) *Pachycheles laevidactylus* Ortmann, 1892. B) Location of the two study areas, Tramandaí and Torres, Rio Grande do Sul, Brazil. C) Photo of the Tramandaí Maritime Platform. D) Photo of the Torres rocky shore. E) Photo of a *Phragmatopoma caudata* Krøyer in Mörch, 1863 sand bank in Tramandaí. Photographs by F.B. Ribeiro (A) and M. Terossi (C–E).

Figure 2. *Pachycheles laevidactylus*. Frequency of individuals by size class (CW = carapace width) in total and separated by season in Tramandaí and Torres. n = number of individuals.

Figure 3. *Pachycheles laevidactylus*. Size of body structures (mm) by sex in Tramandaí and Torres, boxplot (median and quartiles, with outliers). CL = carapace length; CW = carapace width; LPL = largest cheliped propodus length; SPL = smallest cheliped propodus length; LPW = largest cheliped propodus width; SPW = smallest cheliped propodus width; PSL = second pleon somite length. Bold and underlined structures are significantly ($p < 0.05$) different between males and females.

Figure 4. *Pachycheles laevidactylus*. A) Percentage of males found in each size class (CW = carapace width) in Tramandaí and Torres, dark circles indicate a significant ($p < 0.05$) difference between the number of males and females. B) Percentage of ovigerous females (based on the total number of females) and water temperature (°C) by season in Tramandaí and Torres.

Figure 5. *Pachycheles laevidactylus*. Dispersion diagrams of juvenile and adult females and males sampled in the northern coast of Rio Grande do Sul state, Brazil. PSL: second pleon somite length, PL: pleopod length, CW: carapace width.

Figure A1. *Pachycheles laevidactylus*. Dispersion diagrams of juvenile and adult females sampled in the northern coast of Rio Grande do Sul state, Brazil. CL: carapace length, CW: carapace width, LPL: largest cheliped propodus length, LPW: largest cheliped propodus width, SPL: smallest cheliped propodus length, SPW: smallest cheliped propodus width.

Figure 1

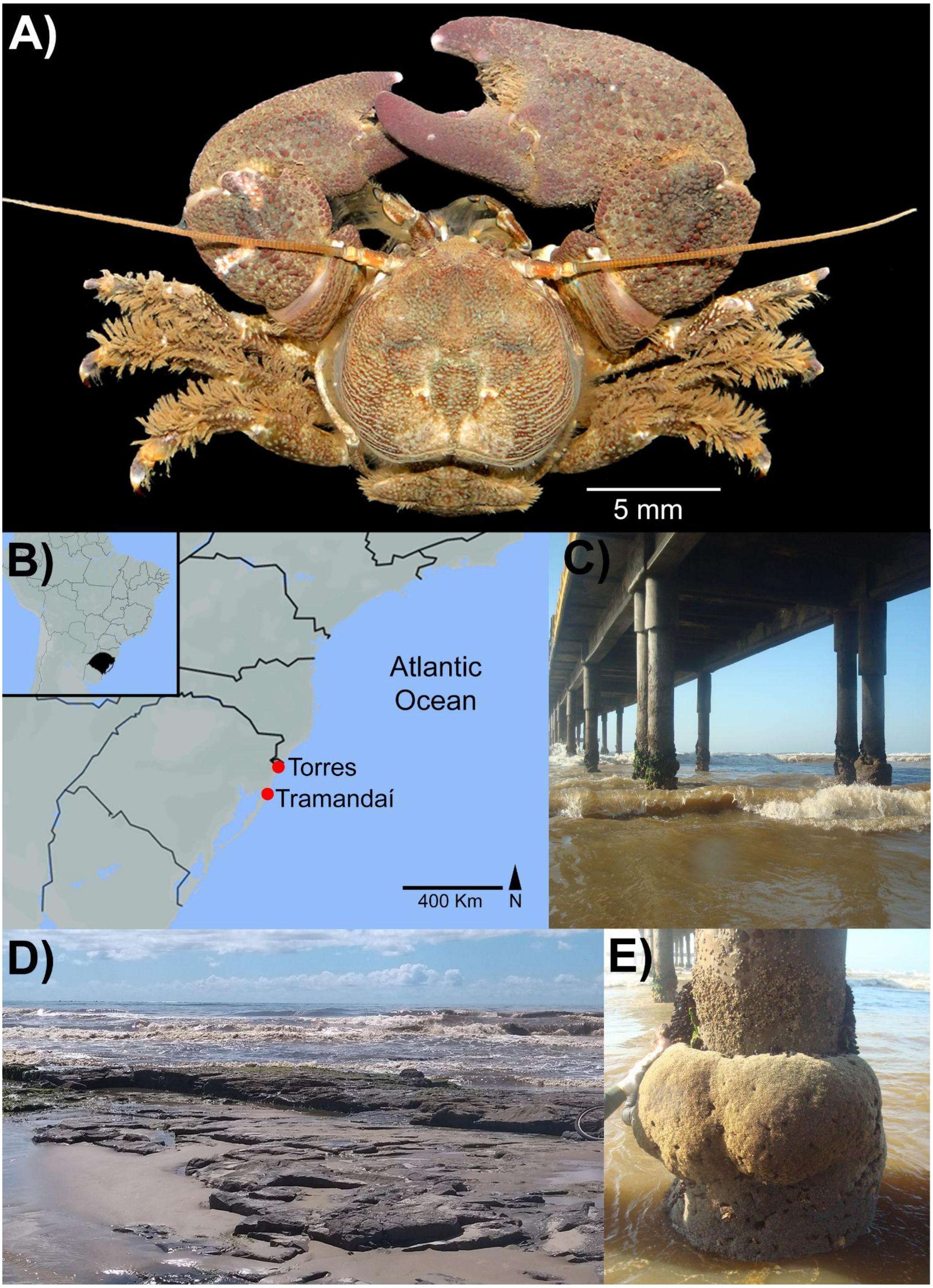


Figure 2

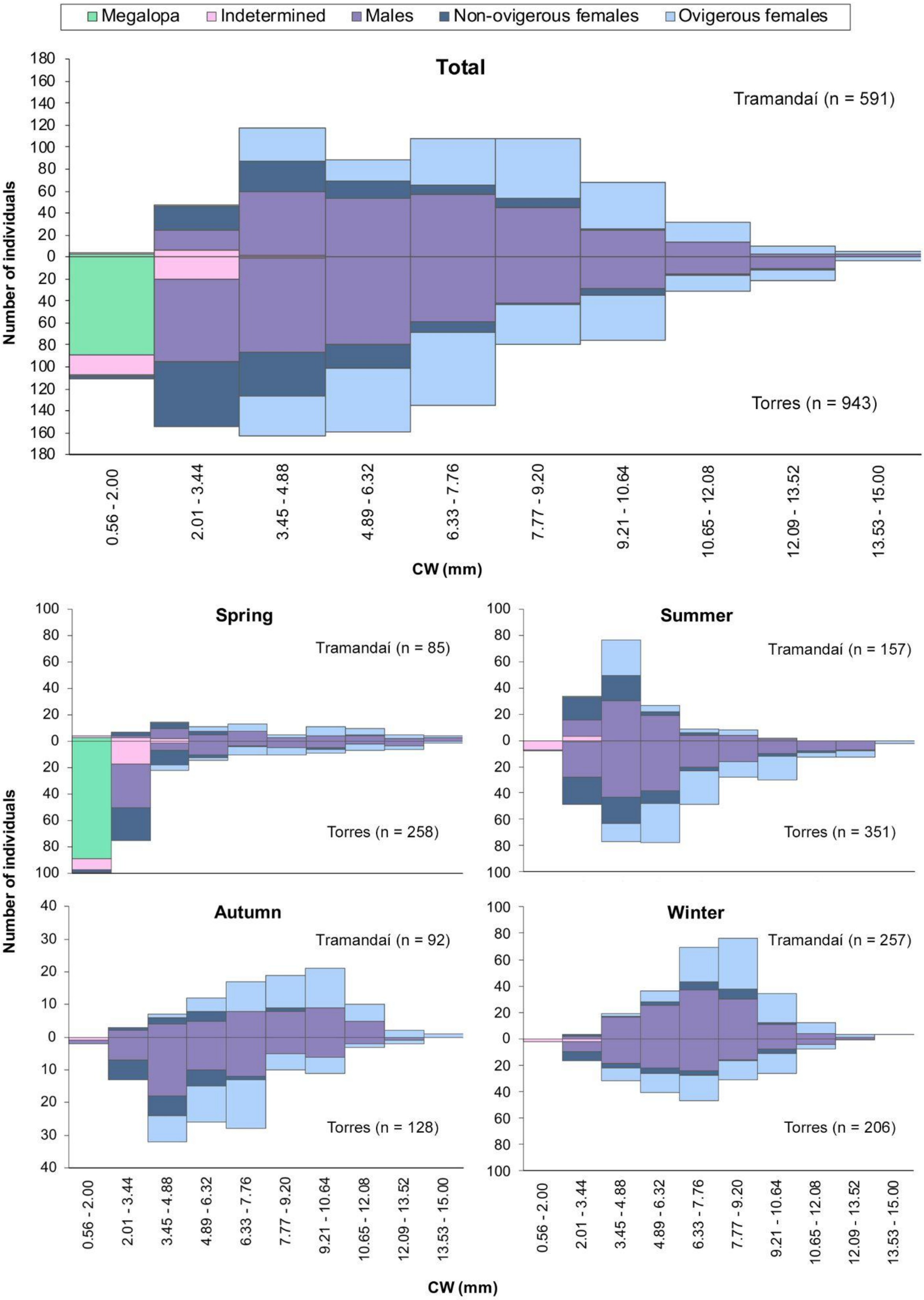
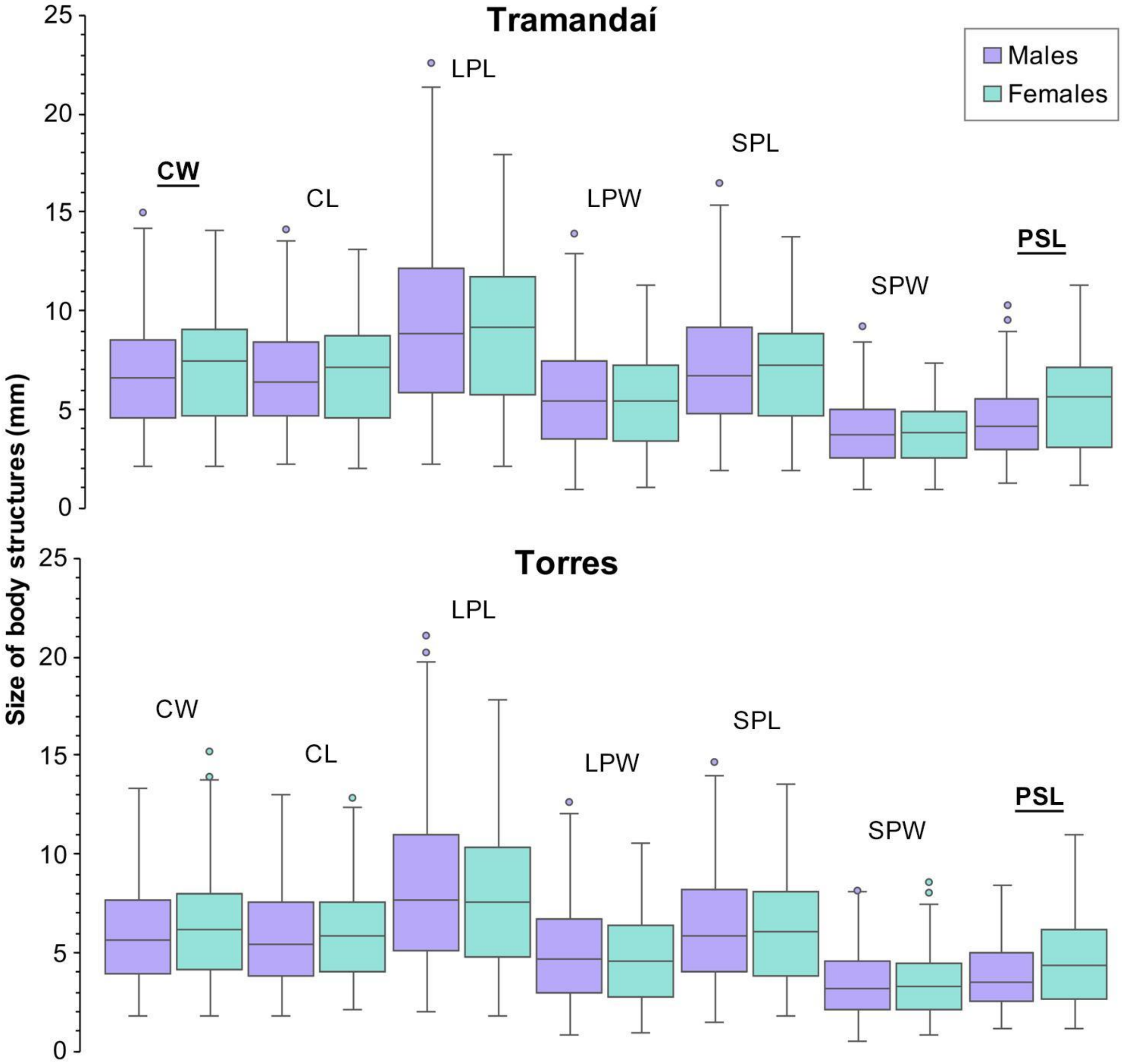

Megalopa
Indetermined
Males
Non-ovigerous females
Ovigerous females
Total
Tramandaí (n = 591)
Torres (n = 943)
Number of individuals
180
160
140
120
100
80
60
40
20
0
20
40
60
80
100
120
140
160
180
0.56 - 2.00
2.01 - 3.44
3.45 - 4.88
4.89 - 6.32
6.33 - 7.76
7.77 - 9.20
9.21 - 10.64
10.65 - 12.08
12.09 - 13.52
13.53 - 15.00
CW (mm)
Spring
Tramandaí (n = 85)
Torres (n = 258)
Summer
Tramandaí (n = 157)
Torres (n = 351)
Autumn
Tramandaí (n = 92)
Torres (n = 128)
Winter
Tramandaí (n = 257)
Torres (n = 206)
100
80
60
40
20
0
40
30
10
CW (mm)

Figure 3



Tramandaí
Males
Females
CW
CL
LPL
LPW
SPL
SPW
PSL
Torres
CW
CL
LPL
LPW
SPL
SPW
PSL
Size of body structures (mm)
25
20
15
10
5
0
25
20
15
10
5
0

Figure 4

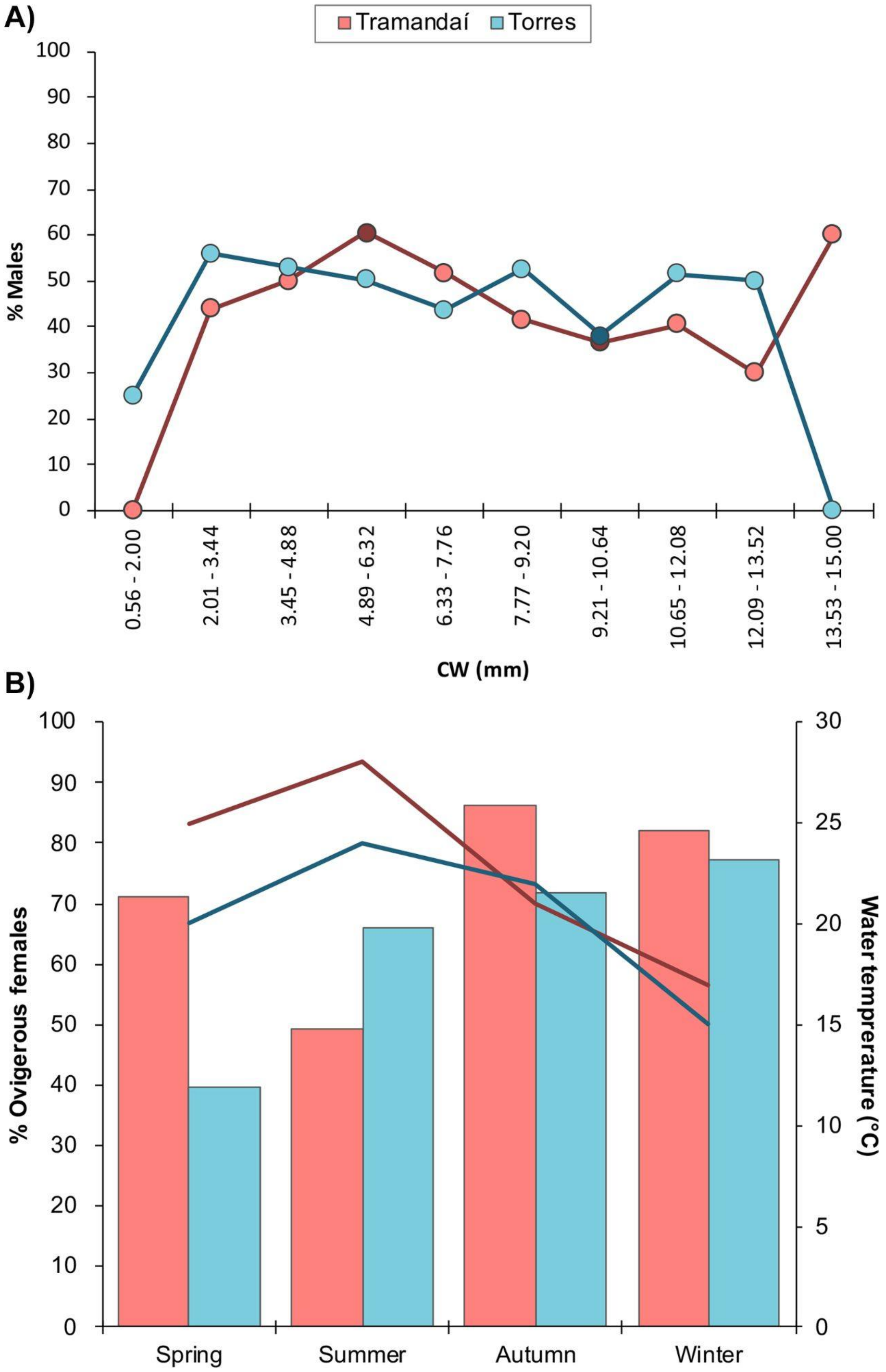
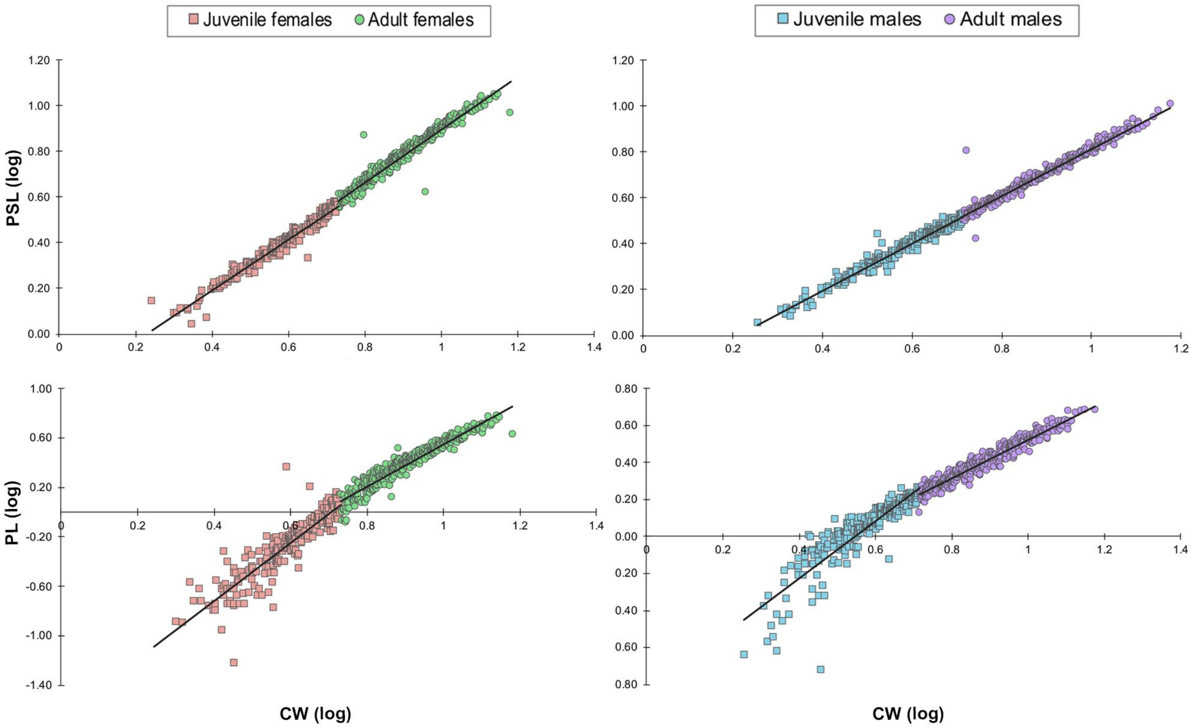
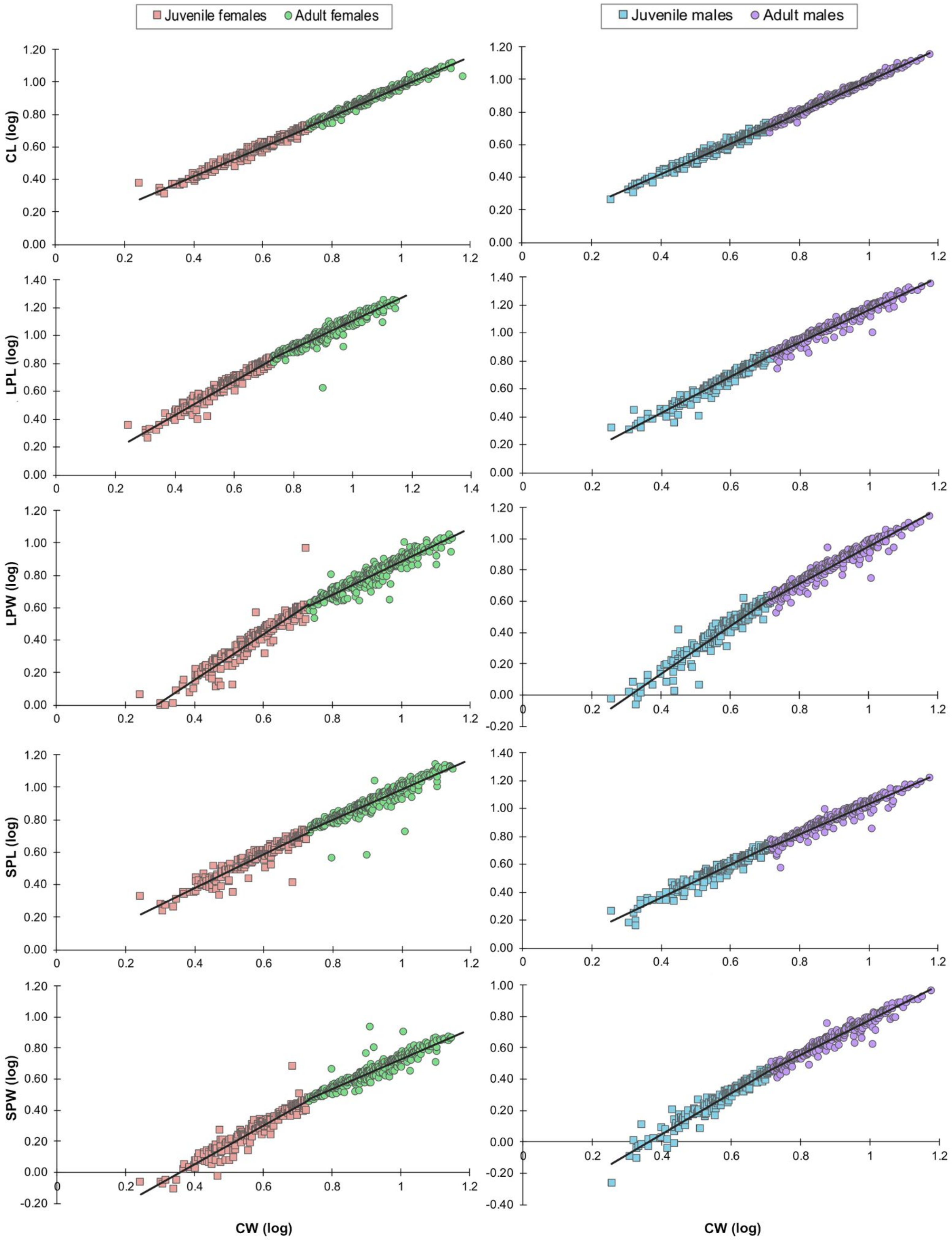

A)
Tramandaí
Torres
% Males
100
90
80
70
60
50
40
30
20
10
0
0.56 - 2.00
2.01 - 3.44
3.45 - 4.88
4.89 - 6.32
6.33 - 7.76
7.77 - 9.20
9.21 - 10.64
10.65 - 12.08
12.09 - 13.52
13.53 - 15.00
CW (mm)
B)
% Ovigerous females
Water temprerature (°C)
100
90
80
70
60
50
40
30
20
10
0
30
25
20
15
10
5
0
Spring
Summer
Autumn
Winter

Figure 5



Juvenile females
Adult females
Juvenile males
Adult males
PSL (log)
PL (log)
CW (log)
CW (log)
1.20
1.00
0.80
0.60
0.40
0.20
0.00
0
0.2
0.4
0.6
0.8
1
1.2
1.4
1.00
0.60
0.20
-0.20
-0.60
-1.00
-1.40
0.80
0.60
0.40
0.20
0.00
0.20
0.40
0.60
0.80

Figure A1


■ Juvenile females ● Adult females
■ Juvenile males ● Adult males
CL (log)
LPL (log)
LPW (log)
SPL (log)
SPW (log)
CW (log)
CW (log)
0
0.2
0.4
0.6
0.8
1
1.2
1.4
-0.40
-0.20
0.00
0.20
0.40
0.60
0.80
1.00
1.20
1.40

CAPÍTULO III:

Reproduction of the porcelain crab *Pachycheles laevidactylus* Ortmann, 1892 (Decapoda, Anomura, Porcellanidae) in southern Brazil: a comparative study in two locations

Será submetido para a revista Nauplius

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Reproduction of the porcelain crab *Pachycheles laevidactylus* Ortmann, 1892 (Decapoda, Anomura, Porcellanidae) in southern Brazil: a comparative study in two locations

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Reproduction of the porcelain crab *Pachycheles laevidactylus* Ortmann, 1892 (Decapoda, Anomura, Porcellanidae) in southern Brazil: a comparative study in two locations

Abstract

The present study analysed the reproductive characteristics of *Pachycheles laevidactylus* in two locations (Tramandaí and Torres) in the south of Brazil. Fecundity, number of eggs and egg volume were analysed during one year and compared between locations and seasons. 438 ovigerous females were collected from sand banks formed by the polychaete *Phragmatopoma caudata* and measured. Eggs were classified into three stages, counted and measured. Water temperature was measured at each location after the sampling period. Females with stage I eggs were more frequent than females with eggs on stages II and III, possibly because it is the longest stage. A positive correlation between female body size and fecundity (stage I) was observed, represented by a power function. Ovigerous females from both locations had a maximum number of eggs higher (around 3000) than previously found for the species in other studies, however, they also reached the largest sizes. Seasonal size differences were observed in both locations, but only spring in Tramandaí showed a difference in fecundity. Conversely, ovigerous females in Torres lost 36,8% of their eggs between stages II and III, while no egg loss was detected in Tramandaí. Stage I egg volume fluctuated between seasons in Tramandaí only, showing a tendency to be smaller in the warmer seasons. A similar increase in egg volume was detected between stages I and II in both locations, 44.4% in Tramandaí and 41.2% in Torres. The differences found between the locations were mainly attributed to temperature and sand bank structure.

Keywords: fecundity, egg volume, egg loss, seasonality

Introduction

Decapod crustaceans are known as a group with highly diverse reproductive patterns (Fernandéz et al., 2020), but two aspects are considered extremely important for all of them, fecundity and egg size. Fecundity is generally defined as the number of fertilized eggs that a female carries in a single brood (Sastry, 1983) and, according to Thorson-Rass' rule, is inversely related to egg size (Laptikhovsky, 2006). Number of eggs and egg size can differ between higher taxa, species and even closely related populations as a response to variations on temperature, food availability, reproductive season and female body size (Laptikhovsky, 2006). As a result, a general pattern related to latitude and depth in marine environments can be seen between number of eggs and egg size (Clarke, 1987). Species living in warmer temperatures tend to have a high number of small eggs, while in cold temperatures eggs tend to be larger but fewer in number (Laptikhovsky, 2006).

Many studies have analysed these reproductive parameters in different crustacean species (Fernandéz et al., 2020), including the widespread porcelain crabs (Pinheiro and Fransozo, 1995; Baeza et al., 2001; Hernáez and Palma, 2003; Hamasaki et al., 2021). Due to their global marine distribution, species of the Porcellanidae Haworth, 1825 family are frequently good models for studies on inter and intraspecific plasticity of fecundity and egg size (Wehrtmann et al., 2012; Wassick et al., 2017; Viña et al., 2018).

Around 280 species have been described for Porcellanidae and classified into 30 different genera (Bezerra et al., 2019). Seven species that belong to the

Pachycheles Stimpson, 1892 genus have been recorded along the coast of Brazil, but only two occur in the state of Rio Grande do Sul, *Pachycheles chubutensis* Boschi, 1963 and *Pachycheles laevidactylus* Ortmann, 1892 (Ferreira and Melo, 2016). The first can generally be found at lower depths, in sandy bottoms or associated with sponges (Veloso, 1999). In contrast, the second lives in algae tufts, mussel beds and under rocks in the intertidal zone (Veloso, 1999). *Pachycheles laevidactylus* is also frequently associated with bryozoans and polychaetes of the *Phragmatopoma* Mörch, 1863 genus. In a survey of crustaceans inhabiting sand reefs of *Phragmatopoma caudata* Krøyer in Mörch, 1863 conducted in the northern coast of Rio Grande do Sul state (Zanini et al., submitted), *P. laevidactylus* was the most frequent decapod found. Furthermore, in a population study conducted in the northern coast of Rio Grande do Sul state, in Torres and Tramandaí, a high percentage of ovigerous females was observed in relation to the total individuals (28% in Torres and 37% Tramandaí) (Horch and Terossi, capítulo II). This species is distributed from Maranhão state in northern Brazil to Monte Hermoso in Argentina (Ferreira and Melo, 2016), and in Brazil, only two studies have been conducted analysing the reproductive biology of this species in the states of Ceará (Ogawa and Rocha, 1976) and São Paulo (Pinheiro and Fransozo, 1995). Camiolo and Luppi (2016) have also recorded the number of eggs of ovigerous females along with information on the population biology of the species in Mar del Plata, Argentina.

Considering that a pattern related to latitude can be seen between fecundity and egg volume (Clarke, 1987) and that these features are fundamental to understand the life-history traits of a species, we tested whether this pattern could be observed intraspecifically and interspecifically in a species of porcelain crab. To accomplish this we analysed the fecundity, number of eggs and egg volume of *P. laevidactylus* during one year in two locations in the south of Brazil (temperate zone). We tested the hypothesis that females have lower fecundity and larger eggs in cold temperatures (temperate areas) when compared to other populations of *P. laevidactylus* in tropical areas, and conversely, higher fecundity and smaller eggs then species found at colder temperatures.

Material and methods

Sample collection

Ovigerous females of *Pachycheles laevidactylus* inhabiting sand banks formed by the polychaete *P. caudata* were obtained from two locations on the northern coast of Rio Grande do Sul state, Brazil, Torres (29°20'20.9"S, 49°43'23.0"W) and Tramandaí (30°00'16.7"S, 50°07'49.2"W). The collections were done once per season during one year: November 2018 (spring), February (summer), May (autumn) and August 2019 (winter). The sampling methods, including a map and photographs, have been described in detail in Horch and Terossi (Capítulo II). All ovigerous females were stored individually to minimize egg loss. Water temperature was measured at each location after the sampling period with a mercury thermometer. They were then transported to the laboratory and frozen. The animals were identified according to Ferreira and Melo (2016) and counted. Carapace width (CW) of all females was measured using a 0.01 mm caliper and a light stereomicroscope.

Specimens were preserved in 70% ethyl alcohol and deposited at the Carcinological Collection of the Zoology Department at Universidade Federal do Rio Grande do Sul (DZ/UFRGS), under the catalogue numbers 6921 to 6928.

Reproductive biology

The size-frequency distribution of ovigerous females followed the population size classes described in Horch and Terossi (Capítulo II). Eggs were carefully removed from the pleon of the females and counted using a manual counter. Embryonic development of the eggs was classified according to Wehrtmann (1990): stage I (eggs without eye pigmentation and with yolk), stage II (eggs with eye pigmentation and yolk) and stage III (fully developed larvae with little or no yolk). To calculate egg volume, the larger (ld) and smaller (sd) diameters were measured of 15 randomly selected eggs from each female and used according to the formula $V = (\pi \times (sd)^2 \times ld)/6$ (Turner and Lawrence, 1979). Measurements were taken using a stereomicroscope equipped with a *camera lucida* to draw the eggs. Only females with eggs at stage I were considered for fecundity analysis, while females with eggs on other stages were used to analyse egg loss and changes in egg volume during embryonic development.

Data analysis

Statistical analyses were performed using Microsoft Excel and R version 3.6.0 (R Core Team, 2020). Kolmogorov-Smirnov and Levene tests were used to analyse data normality and homogeneity. Since data was found to be non-parametric, log transformations were applied before some tests as needed. Regression analysis was performed to compare the number and volume of the eggs in stage I with the CW of each female. Mann-Whitney test was used to compare female CW between locations. Female CW and fecundity were compared between seasons for each location using a Kruskal-Wallis test, followed by a Pairwise Wilcox test when significant. Analysis of covariance (ANCOVA) was applied to compare the number of eggs and egg volume between embryonic stages, and egg volume between seasons, with the CW as covariate. A subsequent Tukey test was performed when significant. The data is presented as median (1st quartile; 3rd quartile) and the significance was considered as $\alpha = 0.05$.

Results

The values of water temperature in Tramandaí were: 25°C (spring), 28°C (summer), 21°C (autumn), 17°C (winter); and in Torres were: 20°C (spring), 24°C (summer), 22°C (autumn), 15°C (winter). A total of 201 ovigerous females were analysed in Tramandaí, of which 12.9% were in spring, 16.9% were in summer, 20.9% were in autumn and 49.3% were in winter. Of the 237 ovigerous females analysed in Torres, 10.1% were in spring, 43.5% were in summer, 17.3% were in autumn and 29.1% were in winter (Fig. 1A). In relation to the egg development stages, in Tramandaí, 70.2% females carried eggs on stage I, 12.9% carried eggs on stage II and 16.9% carried eggs on stage III, and in Torres, 59.5% females carried eggs on stage I, 22.8% carried eggs on stage II and 17.7% carried eggs on stage III (Tab. 1). Except spring in Tramandaí (no females with stage II eggs), all other seasons had females with eggs in the three stages distributed in almost similar proportions (Fig. 1A). Nevertheless, females carrying stage I eggs were more abundant in all seasons in both locations (Fig. 1A).

The size range of the ovigerous females found in Torres was 3.61 mm to 15.16 mm [7.34 (5.91; 9.39) mm], while in Tramandaí the smallest ovigerous female was 3.35 mm and the largest was 14.05 mm [8.13 (6.47; 9.69) mm] (Fig. 1B). Despite the largest ovigerous female being sampled in Torres, a significantly higher number of ovigerous females in the larger size classes were collected in Tramandaí (Mann-Whitney, W = 21446, p = 0.016). Ovigerous females also showed a significant difference in size between seasons in both Torres (Kruskal-Wallis, H = 14.156, p =

0.003) and Tramandaí (Kruskal-Wallis, H = 61.521, $p < 0.0001$) (Fig. 2A). In Torres, the ovigerous females in spring were larger than the ones sampled in all other seasons ($p < 0.005$). However, in Tramandaí, the ovigerous females collected in summer were significantly smaller than the ones present in all other seasons ($p < 0.0001$) (Fig. 2A).

Considering ovigerous females with eggs in the stage I of development (fecundity), the minimum number of eggs found was 1 in both locations, while the maximum number found in Tramandaí was 3000 and in Torres it was 2749 eggs (Tab. 1). In both locations, fecundity showed a significant correlation with female body size ($p < 0.0001$) (Fig. 2B), but no correlation was found between the volume of stage I eggs and body size ($p = 0.24$). When comparing fecundity between locations, ovigerous females in Tramandaí had a significantly higher number of eggs than in Torres (Mann-Whitney, W = 11564, $p = 0.018$; Tab. 1). Fecundity was also different between seasons in Tramandaí (Kruskal-Wallis, H = 44.13, $p < 0.0001$), with the number of eggs in summer being significantly lower than all other seasons ($p < 0.001$) (Fig. 2A). However, fecundity was not significantly different between seasons in Torres (Kruskal-Wallis, H = 5.28, $p = 0.152$) (Fig. 2A). The volume of eggs on stage I was different between seasons in Tramandaí (ANCOVA, F = 14.02, $p < 0.0001$), with the differences between spring–winter ($p < 0.0001$), spring–autumn ($p < 0.001$) and summer–winter ($p = 0.035$) being significant. No difference in the volume of stage I eggs was detected between seasons in Torres (ANCOVA, F = 2.22, $p > 0.09$).

No difference was detected between the number of eggs present at each embryonic stage in Tramandaí (ANCOVA, F = 1.571, $p = 0.21$; Fig. 3A; Tab. 1). However, the number of eggs present at each stage was significantly different in Torres (ANCOVA, F = 7.656, $p < 0.0001$; Fig. 3A; Tab. 1), with the differences between stages I–III ($p < 0.001$) and stages II–III ($p = 0.002$) being significant, but not between stages I–II (*p* = 0.941). Ovigerous females in Torres lost 36,8% of their eggs during embryonic development, the majority of them between stage II and stage III. When comparing egg volume between embryonic stages, the results seen in Torres and Tramandaí were similar. Egg volume was significantly different between embryonic stages in both Torres (ANCOVA, F = 43.405, $p < 0.0001$) and Tramandaí (ANCOVA, F = 27.34, $p < 0.0001$). Stage I was different from stages II and III ($p < 0.0001$), while stages II and III were not significantly different from each other in both Torres ($p = 0.32$) and Tramandaí ($p = 0.92$) (Fig. 3B). The median egg volume in Tramandaí increased 44.4% during development from stage I to stage III, whereas in Torres the egg volume increased 41.2% (Fig. 3B).

Eight females, four from each location, were found carrying larvae (zoea I) on their pleons, sometimes together with eggs in stage III. They were not considered in the analyses.

Discussion

Ovigerous females of *Pachycheles laevidactylus* were found in all seasons. Considering the absolute numbers analysed in this study, the highest number of ovigerous females were in summer in Torres and in winter in Tramandaí. However, a study of the reproductive period (frequency of ovigerous females in relation to total females) in this same region and period reported the highest frequency of ovigerous females in the colder months (autumn-winter) (Horch and Terossi, Capítulo II). In both locations, females with stage I eggs were overall more abundant than females with eggs on stages II and III. The same pattern was seen in two populations of *Petrolisthes armatus* (Gibbes, 1850), where ovigerous females with stage I eggs were also more abundant than stages II and III (Wehrtmann et al., 2012). Probably because what we consider stage I here (egg without eye pigmentation) is longer than the other stages, as also reported for *P. chubutensis* (stages I and II from González-Pisani et al., 2009) and for hermit crabs (stages I to IV from Turra and Leite, 2007).

A positive correlation between female body size and fecundity (number of stage I eggs) was observed in both Tramandaí and Torres, represented by a power function. The same positive correlation with a power function was found in other *P. laevidactylus* populations in São Paulo, Brazil (Pinheiro and Fransozo, 1995) and Mar del Plata, Argentina (Camiolo and Lupi, 2016). Ogawa and Rocha (1976) represented the correlation between fecundity and body size using a linear function in a population in Ceará, Brazil. However, the authors did not specify whether they considered only females with stage I eggs in the analysis, and as such, the results cannot be compared with the present study. A power function has also been a good fit for other species of Porcellanidae, including species in the same genus, such as *Pachycheles monilifer* (Dana, 1852) (Hattori and Pinheiro, 2001; Leone and Mantelatto, 2015) and in other porcelain crabs, such as *Allopetrolisthes angulosus*, *Allopetrolisthes spinifrons, Liopetrolisthes patagonicus, Petrolisthes granulosus* and *Petrolisthes tuberculatus* (Hernáez and Palma, 2003). *Petrolisthes armatus* has shown intraspecific differences in this correlation, with two populations being best represented by a linear function (Wehrtmann et al., 2012) and another with a power function (Pinheiro et al., 2017). A power function indicates that the smaller sized females have a very low number of eggs when compared to the larger females, which in turn have an incrementally higher number of eggs as they grow. Therefore, the relationship between body size and fecundity might be best described by a power function for porcelain crab species, with perhaps a certain level of intraspecific plasticity.

In the present study, the ovigerous females of both locations had a maximum number of eggs higher than any found previously for *P. laevidactylus* in other locations (Tab. 2). The northernmost location analysed for this species is the state of Ceará, Brazil, where the authors found females with the lowest number of eggs (Tab. 2), however, as already mentioned, we cannot affirm that they considered only females with stage I eggs in the analysis. Further south, a maximum of 775 eggs was reported in São Paulo, Brazil. Meanwhile, in Mar del Plata, Argentina, a location almost at the southern edge of the known distribution of *P. laevidactylus*, Camiolo and Lupi (2016) sampled ovigerous females with a number of eggs between 1 and 160. It should be noted that the ovigerous females collected in Tramandaí and Torres reached larger sizes than the ones collected in the studies mentioned above (Tab. 2). Considering the influence of female body size on fecundity, this size difference could perhaps explain the higher number of eggs. As already discussed by Horch and Terossi (Capítulo II), other than Ogawa and Rocha (1976), no other study mentioned above conducted samples during one year, which could influence female body size and consequently fecundity.

The number of eggs found in the present study were also higher than the ones found for other species of the *Pachycheles* genus, as seen in *P. ackleianus* A. Milne-Edwards, 1880, *P. monilifer* (Dana, 1852) and *P. rugimanus* A. Milne-Edwards, 1880 (Tab. 2), as well as a few porcelain crabs of other genera (Reid and Corey, 1991; Wehrtmann et al., 2012, Hamasaki et al., 2021). Even so, ovigerous females of the species *Pachycheles grossimanus* had the largest sizes and highest number of eggs of the genus (Tab. 2). *Polyonyx gibbesi* (Reid and Corey, 1991) and *Allopetrolisthes spinifrons* (Baeza et al., 2001) were observed carrying a higher number of eggs than the ones recorded in the present study as well.

As previously mentioned, female body size directly influences fecundity. This relationship might explain the higher fecundity found in Tramandaí, since a higher number of large ovigerous females were collected in Tramandaí than in Torres. This dissimilarity in female size could be a consequence of the difference between habitats (horizontal natural rock formations in Torres vs. vertical wood columns in Tramandaí), and the different sampling methods employed at each one. Exposure time could also be influencing fecundity, as seen when comparing the fecundity of intertidal and subtidal species of Porcellanidae (Viña et al., 2018), since longer periods of air exposure during low tide could have consequences for daily temperature fluctuations (Stillman and Somero, 2000) and egg oxygenation (Viña et al., 2018). The pillars of the Maritime Platform in Tramandaí might spend less time exposed during low tide than the rock formations in Torres (A. P. Horch, personal observation).

Seasonal differences were observed in both locations. In Tramandaí, ovigerous females were both smaller in size and carried fewer eggs in summer when compared to all other seasons, therefore, the low fecundity was probably influenced by the reduced female size. In Torres, ovigerous females were larger in spring when compared to all other seasons however, no seasonal difference in fecundity was observed. This discrepancy between the two locations might be because the size difference in Torres was not as prominent as the one seen in the summer of Tramandaí. Water temperature might have influenced the difference in both size and fecundity, since summer in Tramandaí was the hottest season of the studied period, 11°C higher than the coldest season (winter) in Tramandaí and 4°C higher than summer in Torres, and studies have shown that high temperatures might be detrimental to porcelain crabs (Stillman and Somero, 2000; Stillman, 2004). A study conducted with *Petrolisthes japonicus* in Japan found a difference in fecundity between the three breeding periods observed for the species, despite its non-continuous reproduction (Hamasaki et al., 2021). Fecundity was also higher in winter than in summer for *Allopetrolisthes spinifrons* in Chile, in a location where the species has continuous reproduction (Baeza et al., 2001).

When comparing the number of eggs present at each stage of embryonic development, ovigerous females showed different patterns in the two locations. No egg loss was detected in Tramandaí, but a significant loss was seen in Torres. This loss occurred between stage II and stage III, therefore females carrying stage III eggs had the lowest numbers of all three stages. None of the previous reproductive studies analysed egg loss in *Pachycheles laevidactylus*, but it is a fairly common occurrence in decapods (Corey and Reid, 1991; Lardies and Wehrtmann, 2001; Terossi et al., 2010), and has been observed in some other porcelain crabs (Reid and Corey, 1991; Lardies and Wehrtmann, 1996; Förster and Baeza, 2001; Wassick et al., 2017; Hamasaki et al., 2021). However, Hernáez and Palma (2003) analysed reproductive parameters of five species of Porcellanidae and did not observe significant egg loss between embryonic stages for any of the species, which corroborated the results found by López et al. (1997) for *Petrolisthes granulosus*. Egg loss was also not detected in a population of *Pachycheles monilifer* in Brazil (Leone and Mantelatto, 2015). When it does occur in porcelain crabs, egg loss is accidental and might be attributed to general movement by the ovigerous females, pleon fanning or active grooming of the egg mass by the 5th pereopod during development (Förster and Baeza, 2001). Contrary to other decapods (Terossi et al., 2010), the results obtained in a study with *Petrolisthes violaceus* show that an increase in egg volume during development does not lead to egg loss due to space constraints (Förster and Baeza, 2001).

The lack of correlation between the volume of stage I eggs and female body size (CW) seen for *P. laevidactylus* has been recorded for other decapod crustaceans as well (Terossi et al., 2010; R. Peñas-Torramilans, A. P. Horch and M. Terossi, unpublished data), including porcelain crabs (Wassick et al., 2017). However, none of the previous studies conducted with *P. laevidactylus* analysed the egg volume in those locations, making it impossible to compare our current results. The volume of stage I eggs stayed constant throughout the year in Torres. In contrast, egg volume was significantly different between seasons in Tramandaí. With the exception of summer and autumn, stage I eggs tended to be smaller in the warmer seasons (spring and summer) when compared to the colder seasons (autumn and winter). Perhaps this variation between locations might also be due to the wider temperature fluctuations recorded in Tramandaí, which had an 11°C (17–28°C) difference between summer and winter compared to the 9°C (15–24°C) recorded in Torres. A similar phenomenon to what was seen in the fecundity comparisons.

A significant increase in egg volume was detected during embryonic development in both locations. This increase occurs between stage I and stage II, with no change seen between stage II and III. Studies have also shown an increase in volume during egg development in *Pachycheles chubutensis* (González-Pisani et al., 2009), *P. monilifer* (in Hattori and Pinheiro, 2001), *Petrolisthes armatus* (in Reid and Corey, 1991; Wehrtmann et al, 2012), *P. granulosus* (in López et al., 1997; Hernáez and Palma, 2003), *P. laevigatus* (in Lardies and Wehrtmann, 1996) and *Liopetrolisthes patagonicus* (in Hernáez and Palma, 2003). This increase in egg size during development is usually attributed to embryo growth (Hernáez and Palma, 2003) and higher water content (Lardies and Wehrtmann, 1996; López et al., 1997), both of which are limited by characteristics of the egg membrane (Lardies and Wehrtmann, 1996).

Interestingly, the change in egg volume between developmental stages was the only similarity between the reproductive aspects of *P. laevidactylus* in Tramandaí and Torres.

Temperature is generally considered as an important factor for reproduction, leading to patterns such as females in lower latitudes having many small eggs and females in higher latitudes having few large eggs (Clarke, 1987; Laptikhovsky, 2006). This pattern does not represent the known fecundity of *Pachycheles laevidactylus* at different locations along its distributional range, since ovigerous females found at low latitudes (Ceará, Brazil; Ogawa and Rocha, 1976) had fewer eggs than females found at higher latitudes (São Paulo, Brazil; Pinheiro and Fransozo, 1995; present study). Likewise, when comparing the fecundity observed in São Paulo (Pinheiro and Fransozo, 1995) with Tramandaí and Torres, females in the present study had a higher number of eggs than in São Paulo. Conversely, the fecundity of the ovigerous females in Argentina (Camiolo and Lupi, 2016) was similar to Ceará (Ogawa and Rocha, 1976), but lower than both São Paulo (Pinheiro and Fransozo, 1995) and the present locations.

Eight ovigerous females were found carrying some larvae, frequently alongside stage III eggs. This could be because at the time of collection these ovigerous females were in the process of releasing their offspring or by the rupture of the membrane of some or all stage III eggs present during the freezing and thawing process. Ovigerous females of *Petrolisthes japonicus* in Japan were also found carrying hatching eggs (Hamasaki et al., 2021), but no possible explanation was provided by the authors.

In conclusion, the differences in fecundity observed between *Pachycheles laevidactylus* populations could not be linked to latitude changes, and the species did not follow the expected pattern. Instead of higher fecundity and smaller eggs in warmer temperatures (lower latitude) and lower fecundity and larger eggs in colder temperatures (higher latitude), *P. laevidactylus* shows lower fecundity at the edges of its distribution and higher fecundity at the present locations. As such, our initial hypothesis was not supported. The correlation between latitude and egg volume could not be tested, since this is the first study to analyse this feature in *P. laevidactylus*. Further reproductive studies with this species should include egg volume analyses and how it relates to latitude and fecundity. Aspects other than water temperature and latitude appear to be influencing the species' reproductive pattern, perhaps food availability, microhabitat differences (which species they live in symbiosis with), ocean currents and human interactions might be responsible for the variation observed. It is important to document species that do not fit within the expected reproductive patterns, so that we can investigate why and widen our understanding of how life-history traits are influenced by the environment.

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Table 1. *Pachycheles laevidactylus*. Number of eggs and volume (mm^3) for each embryonic developmental stage from two locations in the northern coast of Rio Grande do Sul state, Brazil. n: number ovigerous females; Range: minimum–maximum; 1st Q: 1st quartile; 3rd Q: 3rd quartile.

		Number of eggs				Egg volume (mm^3)			
	n	Range	Median	1st Q	3rd Q	Range	Median	1st Q	3rd Q
Tramandaí									
Stage I	141	1–3000	258	59	593	0.04–0.20	0.10	0.07	0.14
Stage II	26	1–2260	434	168	695	0.13–0.20	0.17	0.16	0.18
Stage III	34	2–1256	307	28	488	0.06–0.29	0.18	0.15	0.21
Torres									
Stage I	141	1–2749	133	32	408	0.04–0.19	0.10	0.08	0.13
Stage II	54	2–1516	132	41	315	0.07–0.23	0.15	0.13	0.17
Stage III	42	1–1528	84	15	278	0.07–0.24	0.17	0.14	0.19

Table 2. Ovigerous female size (mm) and number of eggs from species of the *Pachycheles* genus. n: number of ovigerous females; Range: minimum–maximum; SD: standard deviation; na: not available in the literature. * carapace width, other measurements are of carapace length; **median (1st quartile; 3rd quartile); ***the authors considered fecundity as eggs in stage I, others did not mention that.

Species	Location	Sample collection	n	Body size (mm)		Number of eggs		Reference
				Range	Mean ± SD	Range	Mean ± SD	
P. ackleianus A. Milne-Edwards, 1880	Florida, USA	Jan., Jul., Oct.	20	2.8–4.32	3.72	24–143	62.7	Reid and Corey, 1991***
P. grossimanus (Guérin, 1835)	Montemar, Chile	1 year	8	7.5–20.5	na	5968	na	Antazana et al., 1965***
P. laevidactylus Ortmann, 1892	Ceará, Brazil	1 year	111	2.8–9.8	4.3	14–157	34	Ogawa and Rocha, 1976
	São Paulo, Brazil	Jul., Sept., Nov.	157	3.33–9.6	6.38 ± 1.56	2–775	156.1 ± 117.6	Pinheiro and Fransozo, 1995***
	Torres, Brazil	1 year	237	3.61–15.16*	7.34 (5.91; 9.39)**	1–3000	133 (32; 408)**	Present study***
	Tramandaí, Brazil	1 year	201	3.35–14.05*	8.13 (6.47; 9.69)**	1–2749	258 (59; 593)**	Present study***
	Mar del Plata, Argentina	Apr., May, Jun.	na	2.26–na*	na	1–160	na	Camiolo and Lupi, 2016
P. monilifer (Dana, 1852)	Florida, USA	Jun., Jul., Sept.	22	4.16–8.24*	6.01*	8–286	113.32	Reid and Corey, 1991***
	São Paulo, Brazil	Aug. to May	180	3.3–8.8	6.1 ± 1.2	2–511	135 ± 126	Hattori and Pinheiro, 2001***
	São Paulo, Brazil	Summer (once in Spring and Autumn)	48 35	3.31–8.48* 2.62–5.95*	5.4 ± 1.1* 4.7 ± 0.9*	na na	174 ± 228 53.6 ± 52.8	Leone and Mantelatto, 2015***
P. rugimanus A. Milne-Edwards, 1880	Florida, USA	Mar., Jun., Oct.	8	3.2–5.92	4.19	10–235	94.25	Reid and Corey, 1991***

Figure Captions

Figure 1. *Pachycheles laevidactylus*. Ovigerous females carrying eggs in stage I, stage II and stage III sampled in Tramandaí and Torres, Rio Grande do Sul, Brazil distributed by seasons (A) and size classes (B). CW: carapace width.

Figure 2. *Pachycheles laevidactylus*. Size and fecundity (stage I eggs) of ovigerous females sampled in Tramandaí and Torres, Rio Grande do Sul, Brazil. A) Boxplot (median and quartiles, with outliers) by seasons. Four values (outliers) of fecundity higher than 2000 eggs were excluded from the graph, three from Tramandaí (spring: 2444 and 2015; autumn: 3000) and one from Torres (spring: 2749). B) Regressions between carapace width (CW) and fecundity.

Figure 3. *Pachycheles laevidactylus*. Median (1st quartile; 3rd quartile) of the number of eggs (A) and egg volume (B) at each embryonic stage of development (I–III) in Tramandaí and Torres, Rio Grande do Sul, Brazil.

Figure 1

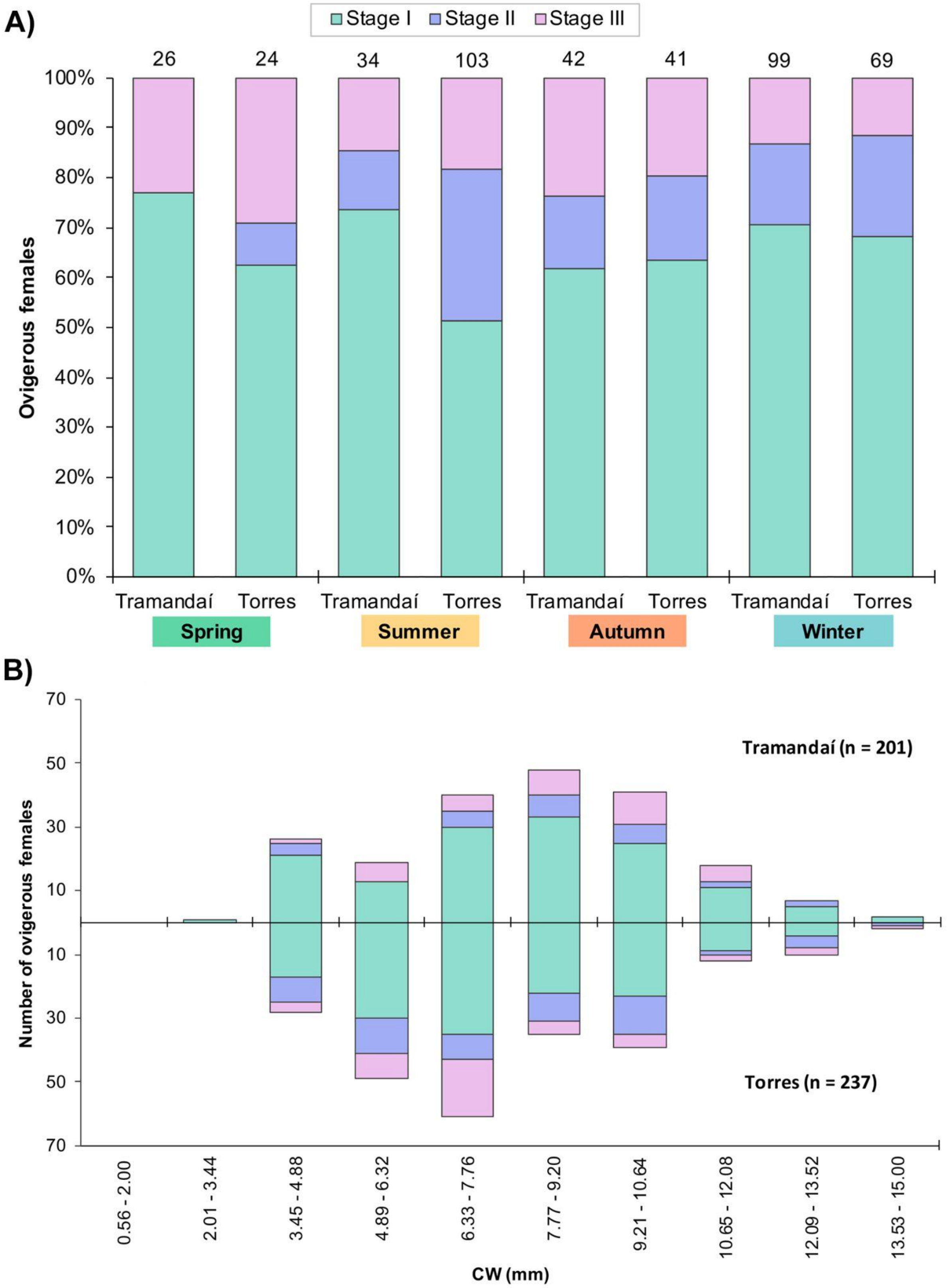

A)
Stage I
Stage II
Stage III
26
24
34
103
42
41
99
69
100%
90%
80%
70%
60%
50%
40%
30%
20%
10%
0%
Ovigerous females
Tramandaí
Torres
Tramandaí
Torres
Tramandaí
Torres
Tramandaí
Torres
Spring
Summer
Autumn
Winter
B)
70
50
30
10
10
30
50
70
Number of ovigerous females
Tramandaí (n = 201)
Torres (n = 237)
0.56 - 2.00
2.01 - 3.44
3.45 - 4.88
4.89 - 6.32
6.33 - 7.76
7.77 - 9.20
9.21 - 10.64
10.65 - 12.08
12.09 - 13.52
13.53 - 15.00
CW (mm)

Figure 2

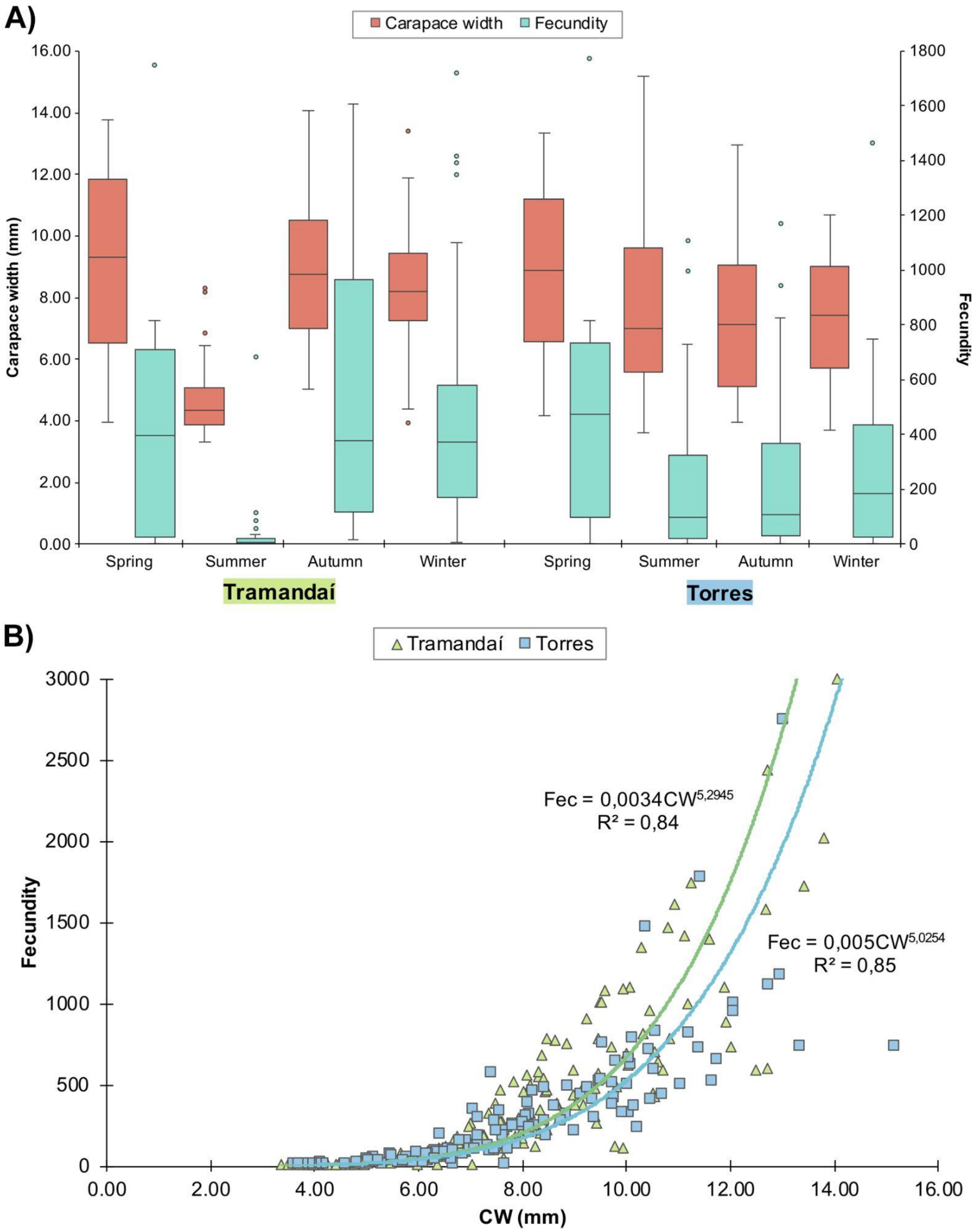
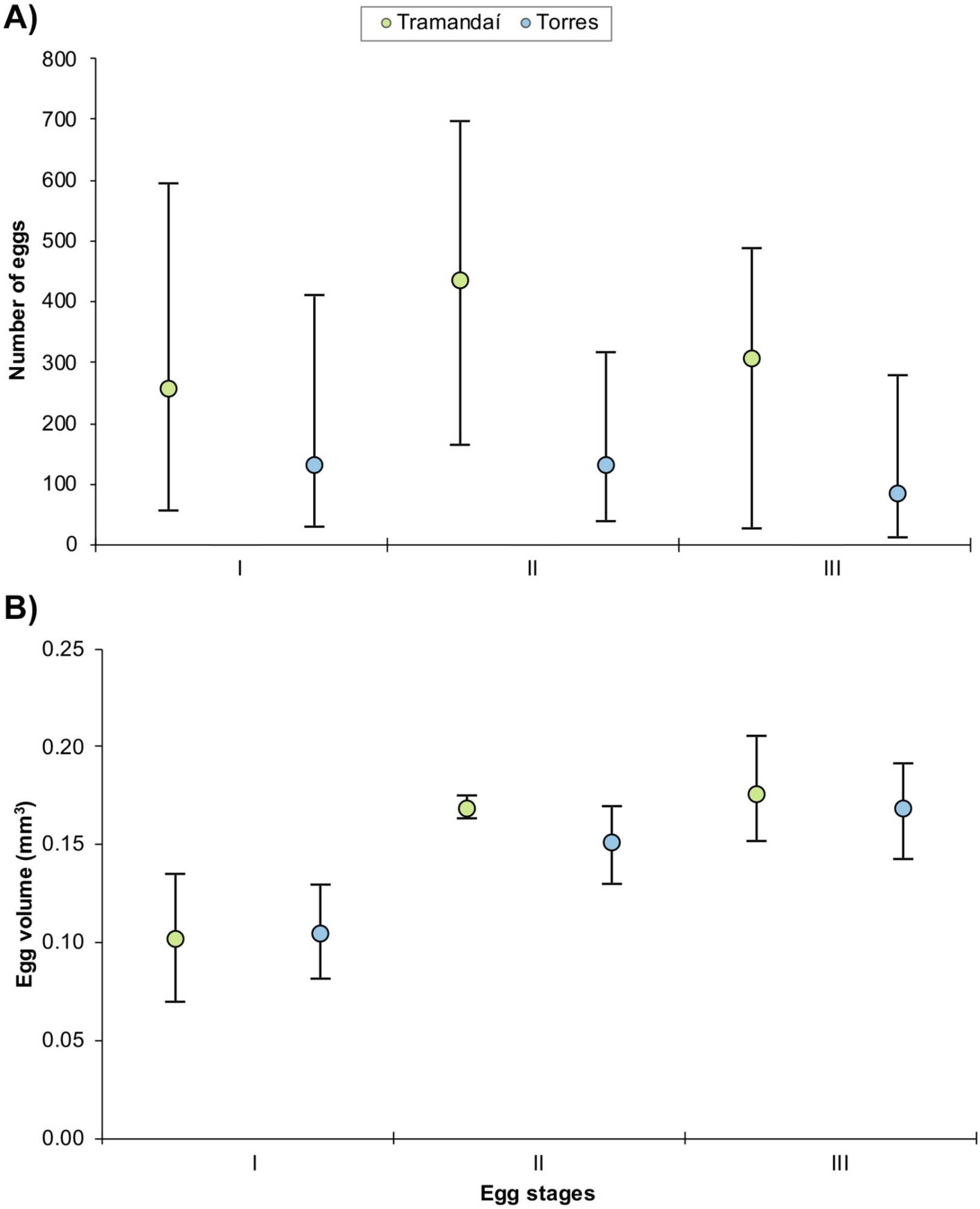

A)
Carapace width
Fecundity
Carapace width (mm)
16.00
14.00
12.00
10.00
8.00
6.00
4.00
2.00
0.00
Fecundity
1800
1600
1400
1200
1000
800
600
400
200
0
Spring
Summer
Autumn
Winter
Spring
Summer
Autumn
Winter
Tramandaí
Torres
B)
Tramandaí
Torres
Fecundity
3000
2500
2000
1500
1000
500
0
0.00
2.00
4.00
6.00
8.00
10.00
12.00
14.00
16.00
CW (mm)
Fec = 0,0034CW^5,2945
R² = 0,84
Fec = 0,005CW^5,0254
R² = 0,85

Figure 3


A)
Tramandaí
Torres
800
700
600
500
400
300
200
100
0
Number of eggs
I
II
III
B)
0.25
0.20
0.15
0.10
0.05
0.00
Egg volume (mm³)
I
II
III
Egg stages

CAPÍTULO IV: Conclusão geral

Estudos populacionais e reprodutivos são essenciais para o conhecimento científico sobre as espécies e para esforços de conservação. O presente trabalho é o primeiro a analisar a história de vida do caranguejo de porcelana *Pachycheles laevidactylus* Ortmann, 1892 na região Sul do Brasil. Também foram realizadas importantes comparações destes aspectos ecológicos da espécie com informações de estudos conduzidos em outros locais ao longo da sua ampla distribuição no Atlântico oeste, apontando diferenças e similaridades.

Pachycheles laevidactylus aparenta não possuir diferença de tamanho corporal entre fêmeas e machos, porém o pleon das fêmeas adultas se mostrou maior que o dos machos adultos. Essa diferença se deve provavelmente a aspectos reprodutivos, pois fêmeas com pleons maiores podem carregar um número maior de ovos. De modo geral, a espécie manteve uma razão sexual 1:1 durante o ano, porém foram encontrados maiores números de fêmeas ou machos em algumas classes de tamanho. *Pachycheles laevidactylus* apresentou reprodução contínua no sul do Brasil, como já havia sido observado em populações no Ceará e Argentina. Apesar disso, pode-se observar uma maior frequência de fêmeas ovígeras durante os meses frios. Megalopas foram coletadas somente na primavera em ambas as localidades, apontando um recrutamento sazonal.

Foi encontrada uma diferença entre o tamanho da menor fêmea ovígera (3.35 mm CW) e o tamanho de maturidade sexual morfológica das fêmeas (5.39 mm CW). Enquanto a maturidade morfológica dos machos foi calculada em 5.20 mm CW. Considerando o tamanho da menor fêmea ovígera encontrada, a começa a se reproduzir em tamanhos menores nas extremidades da sua distribuição (Ceará, Brasil e Mar del Plata, Argentina), enquanto em localidades mais centrais isto ocorre em tamanhos maiores (Rio Grande do Sul e São Paulo, Brasil). A maturidade morfológica das fêmeas também ocorreu em um tamanho maior no Rio Grande do Sul quando comparado com a Argentina. O presente estudo analisou o crescimento relativo de *P. laevidactylus* pela primeira vez no Brasil. Indivíduos de sexo indeterminado, fêmeas e machos apresentaram o mesmo padrão de crescimento para a comprimento da carapaça (alometria negativa). Foi observado que o comprimento e a largura de ambos os quelípodos cresce em um ritmo mais lento quando comparado com a largura da carapaça em fêmeas adultas, do que em fêmeas juvenis. Fêmeas juvenis e adultas apresentaram alometria positiva para o pleon e o primeiro pleópodo. A relação entre o comprimento da carapaça e a largura da carapaça foi a única onde a reta das fêmeas juvenis e das adultas possui a mesma inclinação, mas intercepto diferentes. Machos não apresentaram diferença de alometria entre juvenis e adultos, e todas as estruturas (exceto comprimento da carapaça) apresentaram alometria positiva. Para machos, a relação entre o pleon e a largura da carapaça foi melhor representada por uma única reta, enquanto todas as outras relações foram representadas por retas com inclinações e interceptos diferentes entre juvenis e adultos.

Fêmeas carregando ovos em estágio I foram mais abundantes que fêmeas com ovos em estágio II ou III, possivelmente devido a maior duração deste estágio. Foi encontrada uma correlação positiva entre fecundidade (ovos em estágio I) e tamanho corporal em Torres e Tramandaí, representada por uma função de potência, similar ao encontrado em outras localidades. O tamanho máximo das fêmeas ovígeras coletadas em Torres e Tramandaí foi maior do que em outras localidades, e o mesmo foi observado quanto ao número máximo de ovos contados. Também houve variação de tamanho e número de ovos entre as estações do ano em Tramandaí, apontando uma possível influência da temperatura da água na fecundidade. A diferença ocorreu na primavera, quando foram encontradas fêmeas menores e com um número também menor de ovos. Por outro lado, uma variação no número de ovos entre estações não foi observada em Torres. Considerando o desenvolvimento embrionário, a perda de ovos não foi observada nas fêmeas de Tramandaí, todavia em Torres houve uma diminuição no número de ovos entre os estágios II e III.

Não houve correlação entre o tamanho das fêmeas e o volume dos ovos em estágio I, similar a outros porcelanídeos. O volume dos ovos em estágio I manteve-se constante durante o ano em Torres, porém mudou em Tramandaí. Esta mudança possivelmente ocorreu devido a maior amplitude de temperatura medida em Tramandaí, com uma tendência de os ovos serem menores durante os meses quentes e maiores durante os meses frios. A única similaridade reprodutiva encontrada entres as duas localidades estudadas foi o aumento de volume dos ovos durante o desenvolvimento embrionário. O aumento ocorreu somente entre os estágios I e II.

A temperatura da água é geralmente considerada um fator importante para a reprodução de espécies marinhas, resultando em um padrão observado onde fêmeas em menores latitudes possuem muitos ovos pequenos, e fêmeas em latitudes maiores carregam poucos ovos maiores. A fecundidade de *Pachycheles laevidactylus* não aparenta seguir este padrão, no entanto outros estudos focados em analisar o volume dos ovos são necessários para melhor elucidar a plasticidade reprodutiva observada na espécie ao longo da sua distribuição.