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Individual growth and mortality of *Rhithropanopeus harrisii* (Decapoda: Panopeidae) in the estuarine region of Patos Lagoon, Southern Brazil

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ABSTRACT

The present investigation aimed to estimate the individual growth and mortality of an invasive species found in the estuarine region of Patos Lagoon (Southern Brazil). For 20 months crabs were sampled, and in the laboratory specimens of *Rhithropanopeus harrisii* (Gould, 1841) were measured (carapace width, CW, and weight). Carapace width data was utilized for a modal progression analysis and to estimate the individual growth curve (von Bertalanffy growth model), and a size-converted catch curve. Von Bertalanffy parameters estimated were $CW_\infty = 16.92$ mm and $k = 1.28$ year^{-1}. Maximum longevity was estimated at 3.5 years. Instantaneous total mortality was estimated at 2.17 ± 0.30 year^{-1}. It has been suggested that longevity may be explained by a low predation impact on *R. harrisii*, which, as a consequence, may lead to slow individual growth of this species in the estuarine region of Patos Lagoon.

KEYWORDS

Crab, longevity, modal progression, population ecology, predation

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INTRODUCTION

The introduction of non-native species in the environment is a constant threat for terrestrial and marine biodiversity, and an important issue in environmental global change (Simberloff *et al.*, 2013). Each river basin has a characteristic faunal composition, with its endemic species bound by natural geographic barriers, and anthropogenic changes have led to losses in biodiversity and the increased likelihood of bio-invasions (van der Velde *et al.*, 2002). Crustaceans are understood to be the main group of invasive species on continental and regional scales (Hänflig *et al.*, 2011).

Rhithropanopeus harrisii (Gould, 1841) (Decapoda: Panopeidae) is a native crab from North America (Atlantic Coast), distributed from New Brunswick (Canada), through the north of the Gulf of Mexico (Florida, USA), to Mexico, Panama, and Venezuela (Williams, 1984; Rodriguez and Suarez, 2001; Roche *et al.*, 2009). It is an euryhaline species, in which adults are found in water with salinity from 0.5 to 40 ppt (Boyle *et al.*, 2010). This species is typically cryptic and found under stones and in vegetation, but an association with oyster reefs or debris, muddy and sandy substrates have been also reported (Brockerhoff and McLay, 2011). *Rhithropanopeus harrisii* is noted to outcompete native species (Brockerhoff and McLay, 2011) and to spread white spot baculovirus, with potential impacts on aquaculture and commercial harvests (Hayes and Sliwa, 2003).

The occurrence of *R. harrisii* in the estuarine region of the Patos Lagoon (Southern Brazil) has been reported by D'Incao and Martins (1998), with specimens caught from 1982 to 1985 at several locations in the estuary, *e.g.*, from the breakwater up to 40 km into the estuarine region such as "Praia do Barro Duro" (Pelotas City). It is not understood whether the introduction was facilitated by ballast water (D'Incao and Martins, 1998) or by ship fouling (Tavares, 2011). This estuarine region is located in the Southwestern Atlantic, on the Subtropical Convergence region and the mouth of the estuary is an access point to the Port of Rio Grande, an important port for Mercosul trading (Vasconcelos and Da Silva Piva, 2007). *Rhithropanopeus harrisii* has been established in this estuarine region, and this species has not been reported in any other estuary on the Brazilian coast (Tavares, 2011).

For the estuarine region of the Patos Lagoon, only one study on the biology of *R. harrisii* is published (Rodrigues and D'Incao, 2015). This paper reported biometric relationships and estimates of the abundance of this species but did not report on individual growth or other population parameters. Invasive species are interesting subjects to study basic processes in population biology, as it is important to understand the life history traits that allow a species to be successfully settled in the environment. Moreover, this basic information can feed demographic models that can be applied for the management of populations of these invaders (Sakai *et al.*, 2001).

The individual growth of an organism is described by its increase in size (or weight) with age. Crustaceans have exoskeletons which must be periodically shed for incremental growth, and this process is called ecdysis. As no hard structures which carry age information are kept, typically, the study of age and growth is carried out using size-based methods such as modal progression analysis (Hilborn and Walters, 1992). Individual growth of *R. harrisii* has been studied in laboratory conditions, using crabs caught from a location in Poland (Turoboyski, 1973). It has been determined that eight to nine ecdyses occur before the adult phase is reached and maximum longevity was estimated at five years (Turoboyski, 1973).

The present investigation aims to estimate the growth curve based on the von Bertalanffy growth model and the total mortality of *R. harrisii* based on samples taken in the estuarine region of the Patos Lagoon.

MATERIAL AND METHODS

Sampling

Samples were taken from July/2015 to March/2017 (20 months). Three rectangular samplers (21.1 × 18.1 × 15.6 cm, 6L; Fowler *et al.*, 2013) were placed at Marinheiros Island ("Ilha dos Marinheiros") (32°02'S 52°19'W), at a location called Bandeirinhas, Patos Lagoon, southern Brazil (Fig. 1). Each sampler was filled with empty shells (bivalves and gastropods) to provide hiding places for the animals.

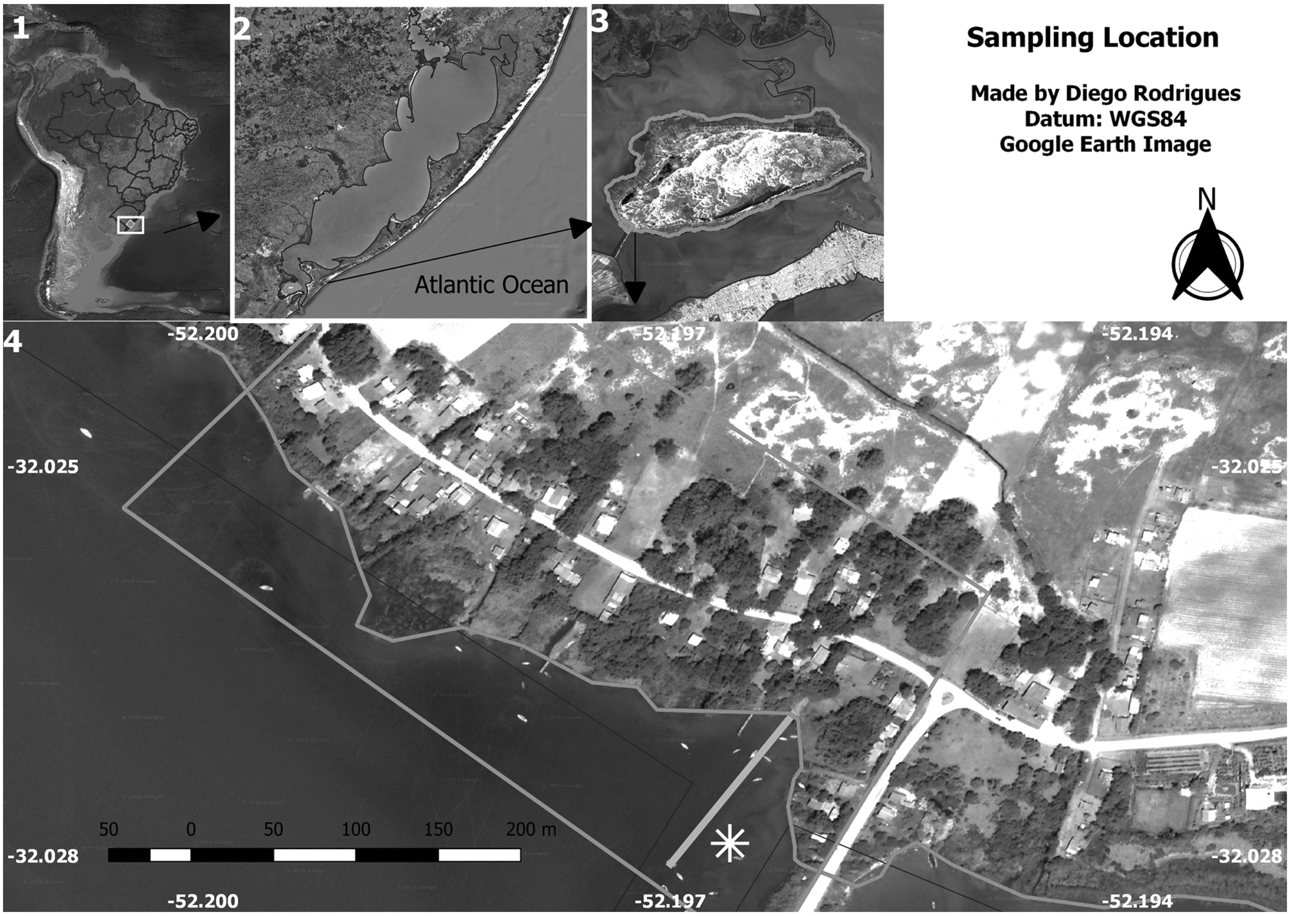

Figure 1. Sampling site located (star) in the estuarine region of the Patos Lagoon, southern Brazil. (**1**) South America; (**2**) Patos Lagoon; (**3**) Ilha dos Marinheiros; (**4**) sampling site.

A mesh (7 cm aperture) was used to cover the sampler to prevent the entrance of large animals. Samplers were submerged (1 m deep), attached to a pier by nylon ropes, and laid five meters away from each other along this pier. Every two weeks samplers were emptied by washing the shells in a mesh. All sediment washed from the samplers was put in plastic bags and taken to the laboratory for sorting. The location was chosen based on the fact that it represented a habitat with low anthropogenic impact with regard to pollution and substrate modification. This sampling was part of a broader design to compare abundances of *R. harrisii* in three locations in the estuarine region.

Laboratory analyses

Samples taken to the laboratory were washed and specimens of *R. harrisii* were sorted, sexed, measured and weighed. Species identification was based on Melo (1999) and Williams (1984). The size was measured as carapace width (CW, in mm) between the lateral spines, using a digital calliper (to nearest 0.1 mm). Weight was measured in grams. Sex was determined using a stereoscopic microscope.

Individual growth

Considering the small monthly sample sizes, some compromise had to be made to estimate the individual growth. Therefore, sexes were combined and animals caught were pooled by season (Summer, Dec–Feb; Autumn, Mar–May; Winter, Jun–Aug; Spring, Sept–Nov). The first pooled sample (Winter/2015) was considered time zero. Subsequently, Spring/2015, Summer/2015, Autumn/2016, Summer/2016 and Summer/2017 were utilized for modal progression analysis (MPA). Due to the small sample sizes, Winter/2016 (n = 17) and Spring/2016 (n = 17) were not utilized for the MPA.

Modal groups were determined on CW frequency distributions (1 mm bins) using the software PeakFit (SPSS Inc.). Gaussian peaks were then fitted to carapace width frequency distributions by an automated least-squares fitting procedure. Modal values determined in each CW frequency distribution were tentatively linked to visualize the modal progression. Growth curves, based on the von Bertalanffy growth function (VBGF), were estimated for the determined cohorts. Fitting was performed by least-squares minimization. Thereafter, a pooled VBGF was estimated. Maximum longevity (T_{max}) was calculated by the inverted von Bertalanffy equation, using 99 % of the asymptotic size as recommended by D'Incao and Fonseca (2000), and recently supported by investigations on brachyurans (Miazaki *et al.*, 2019; Gonçalves *et al.*, 2020). Average maximum longevity was estimated by 95 % of the largest animals (Taylor, 1965).

Mortality

To estimate the mortality rate, parameters of individual growth estimated for this population were utilized to convert length to age (*t*). Instantaneous rate of total mortality (Z) was estimated by a size-converted catch curve — $\ln(N/\Delta t) = a+bt'$ — where the slope of regression (*b*) is the estimate of Z, N is the number of individuals in a given size class, Δt is the time for the individuals growth through that size class and *t* is the mean age of the individual in that size class (Pauly, 1990). Least-squares regression was utilized, and the significance of the regression assessed by an F-test.

To assess the estimate of the instantaneous rate of total mortality (Z) for *R. harrisii*, information regarding von Bertalanffy growth parameters *k* and Z were compiled for 15 species of brachyurans inhabiting estuarine and coastal areas. With this information, a linear regression — least-squares minimization — was fitted to predict Z in relation to *k*.

RESULTS

A total of 1,082 animals were caught, 619 females and 463 males. Size range was 2.4 to 14.3 mm for females and 2.5 to 17.9 mm for males. Average CW of males and females was 8.41 ± 0.16 and 7.00 ± 0.10 mm, respectively. On average, females were lighter (0.16 ± 0.007 g) than males (0.35 ± 0.016 g).

Individual growth

Two cohorts were followed for the period of study (Fig. 2), and the pooled growth curve (Fig. 3) resulted in estimates of $CW_\infty = 16.92$ mm and $k = 1.28$ year^{-1}. This curve exhibited a 12.22 mm and 15.61 mm CW for 1 and 2 year old crabs, respectively. Based on the growth parameters estimated for this pooled growth curve, maximum longevity was estimated as 43 months (approximately 3.5 years). This value could only be reached by a male, as no female is as large as this. For a female, considering the maximum size observed, the maximum longevity estimated is 18 months. Average maximum longevity (pooled data) was estimated at 20 months.

Mortality

The instantaneous rate of total mortality was 0.181 month^{-1} (95% confidence limit, 0.155 – 0.206), which is equivalent to 2.17 ± 0.30 year^{-1}. The regression fitted was significant ($F_{calc} = 239.81 > F_{crit.\ 0.05\ 1,11} = 4.84$) (Fig. 4).

The regression fitted to the compilation data was also significant ($F_{calc} = 103.33 > F_{crit.\ 0.05\ 1,29} = 4.19$), but the intercept was not different from zero (95 % confidence limits, -0.66 to 1.05, $p = 0.65$). Therefore, a regression through the origin was fitted, which was also significant ($F_{calc} = 105.90 > F_{crit.\ 0.05\ 1,30} = 4.17$) (Fig. 5). Using this regression, the regression slope was 2.24 ± 0.22, and the estimate of Z for *R. harrisii* was 2.89 ± 0.29 year^{-1}.

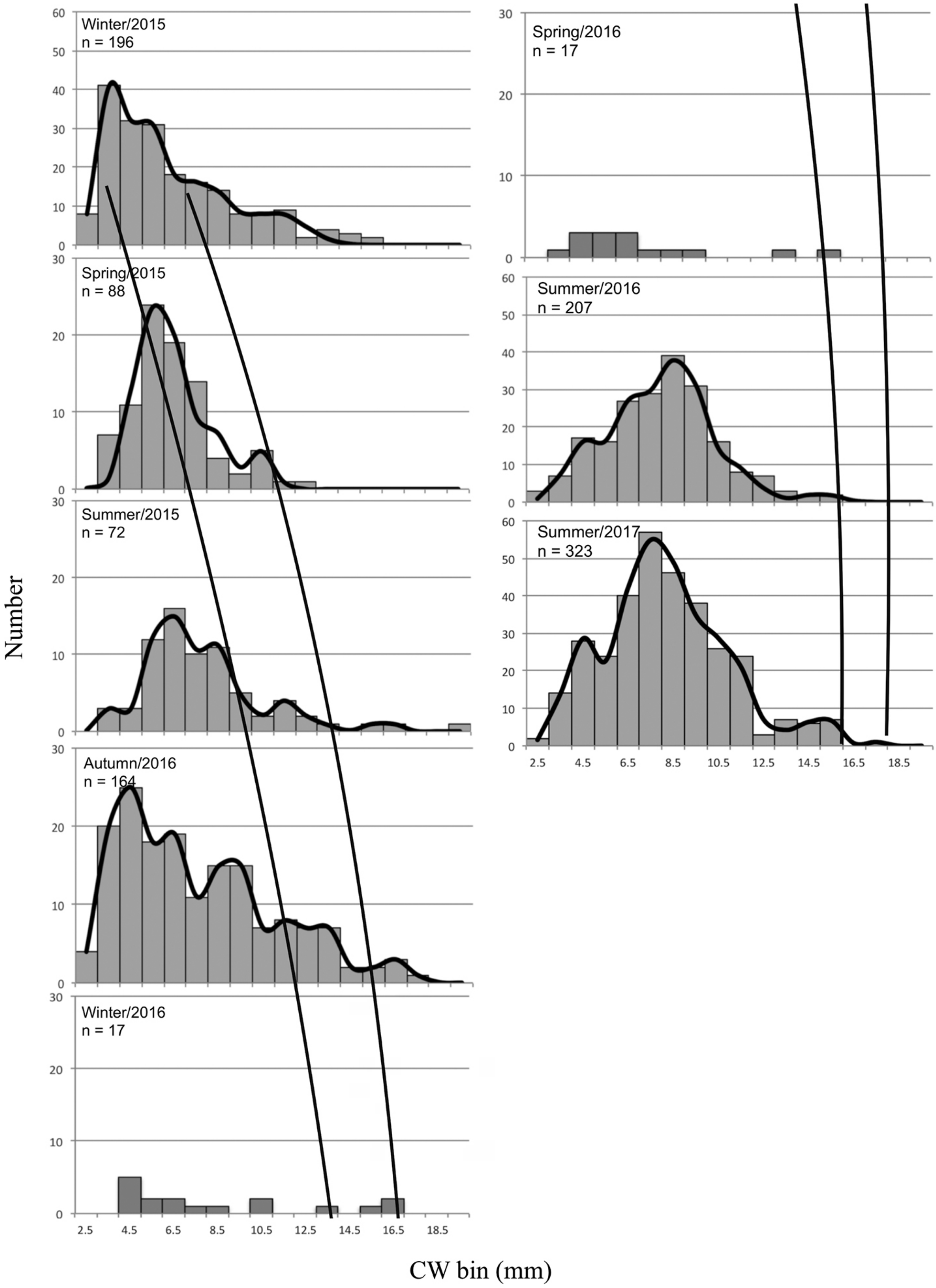

Figure 2. Carapace width frequency histograms, and cohorts overlaid. Data seasonally pooled.

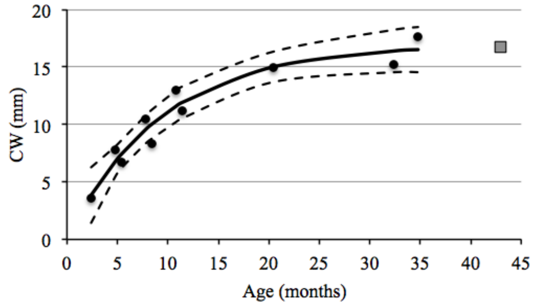

Figure 3. Growth curve — von Bertalanffy growth model — and 95% confidence limits. $CW_t = 16.92\ [1\text{-}e^{1.28(t\text{-}0.01)}]$. Significant fit ($F_{calc.} = 54.31 > F_{crit.\ 0.05\ 2,7} = 4.74$; $R^2 = 0.91$). Grey square is the estimated T_{max}.

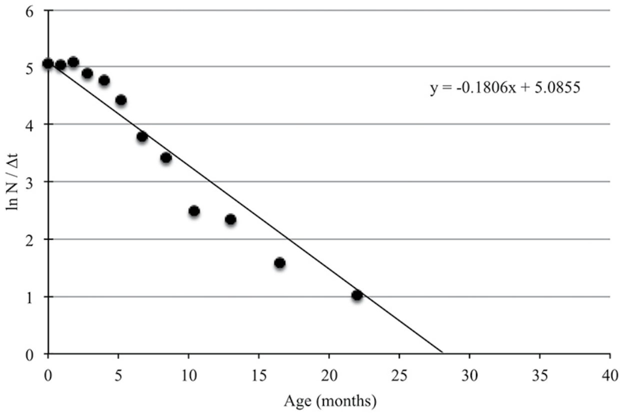

Figure 4. Size-converted catch curve. Significant fit ($F_{calc.} = 239.81 > F_{crit.\ 0.05\ 1,11} = 4.84$; $R^2 = 0.95$).

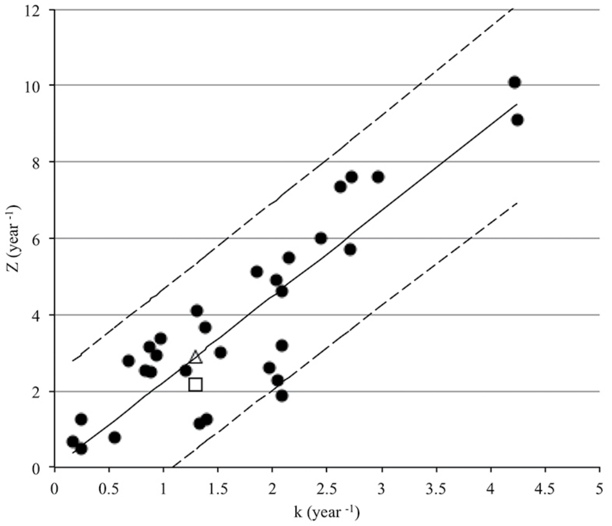

Figure 5. Relationship between von Bertalanffy *k* and total mortality Z. Significant fit ($F_{calc.} = 105.90 > F_{crit.\ 0.05\ 1,30} = 4.17$; $R^2 = 0.77$). Data from 15 species: Sukumaran and Neelakantan (1996); Lee and Hsu (2003); Kock *et al.* (2005); Fisher and Wolf (2006); Keunecke *et al.* (2007; 2008); Mokhtari *et al.* (2008); Diele and Kock (2010); Costa and Soares Gomes (2011); Sara (2011); Klaoudatos *et al.* (2013); Hamid and Wardiatno (2015); Sara *et al.* (2017); Vidhya *et al.* (2018). Square symbol represents Z estimated by the length-converted catch curve; triangle represents Z estimated using the relationship found.

DISCUSSION

Maximum longevity was estimated at 3.5 years. At first, this estimate could be considered high as larger brachyurans living in the same estuary have lower maximum longevities (*Neohelice granulata* (Dana, 1851), 2 years, maximum CW 38 and 27.2 mm for males and females); *Callinectes sapidus* Rathbun, 1896, 3 years, maximum CW 136.30 and 132.70 mm for males and females) (D'Incao *et al.*, 1993; Rodrigues and D'Incao, 2008). The average lifespan of brachyurans was estimated at 5.6 years, with a general trend of the largest species having the longest life spans, while the smallest species have lifespans between one and two years (Vogt, 2019), which suggests *R. harrisii* has indeed a longer maximum longevity than expected.

While the estimate of maximum longevity is related to the maximum size, this estimate is also quite dependent on the von Bertalanffy growth rate (*k*). This happens when the growth curve is estimated by size-based methods — which is the situation in most studies of crustacean populations in the wild — and so the von Bertalanffy *k* shows how fast this growth curve will reach the asymptotic size. Therefore, any bias in von Bertalanffy *k* estimation directly affects the estimate of maximum longevity.

We have estimated a slower growth rate than what has been reported for *R. harrisii* reared in laboratory conditions. For instance, Morgan *et al.* (1983) found that it takes two months to reach 8.0 mm CW, at 25 ºC. Based on the growth curve estimated in the present investigation, six months are needed for a crab to reach this size in the wild. In another study with animals kept in the laboratory (Turoboyski, 1973), but with temperature regimes simulating natural conditions (highest temperature 22.8 ºC; lowest, 0.9 ºC), a 5.5 mm CW is reached at around three months, while in our population this size is reached in five months.

As a size-based method was utilized to study individual growth, the maximum longevity estimate is related to the largest animal found. In the present investigation, the largest animal found measured 17.9 mm CW, and the average CW of the 1% largest animals was 16.50 ± 0.18 mm. Our approach was to use 99 % of the estimated asymptotic CW (16.92 × 0.99 = 16.75 mm) — proposed by D'Incao and Fonseca (2000) —

as the size for T_{max} estimation, as this figure should be somewhat similar to the 1 % largest animals caught, which was the case. Therefore, it seems plausible the use of this CW to estimate T_{max}.

Considering the evolutionary theory of ageing, a high longevity could possibly be explained by low predation (Kirkwood and Austad, 2000). A relationship between mortality rate and longevity has been shown elsewhere in a classic paper for teleosts (Beverton and Holt, 1959). The total mortality of a population can be split into natural mortality processes, such as old age and diseases. Alien species can be resistant to local diseases, and spread them, as is the case for *R. harrisii* and the white spot baculovirus (Hayes and Sliwa, 2003), and therefore this alien species acts as a disease carrier, without being affected by them (Hulme, 2014).

Moreover, total mortality is related to extrinsic mortality, which is typically linked to predation. Fish species have been cited as the main predators of *R. harrisii,* such as catfish, eel and flounder (Kujawa, 1965; Turoboyski, 1973; Williams, 1984). The ichthyofauna of the estuarine region of Patos Lagoon has approximately 110 species (Calliari *et al.*, 1997: 123), including estuarine resident catfish (*Genidens genidens* (Cuvier, 1829)). Other catfish, such as *Netuma barba* Lacepède, 1803 and *Netuma planifrons* Higuchi, Reis and Araújo, 1982 are anadromous species that migrate to the estuarine region to reproduce. The marine flounder *Paralichthys orbygnianus* Valenciennes, 1839 spawns in the sea but has sub-adult life-cycle stages found in these estuarine regions. Anguiliforms (eels) are occasional visitors to the estuarine region. Lastly, *Micropogonias furnieri* Desmarest, 1823 is a very abundant marine species that uses estuarine waters as a nursery ground.

There are no reports of natural predators for *R. harrisii*. For example, a study regarding the natural diet of the white croaker (*M. furnieri*), one of the most abundant fish species in the estuary, did not report the occurrence of *R. harrisii* in the stomach contents (Figueiredo and Vieira, 2005). While it can be said that *M. furnieri* is not a crab eater, as tanaids are the main item in the stomach contents, it is important to point out that other studies have reported a high frequency of occurrence of decapods in stomach contents of this species, including *Cyrtograpsus angulatus* Dana, 1851, *N. granulata*, and *C. sapidus*. At Chuí Stream — Brazil-Uruguay border — 16% of the occurrence was decapods in the gut contents of *M. furnieri* (Mendoza-Carranza and Vieira, 2008) and around 40% of occurrence was *Cy. angulatus* at Rocha Lagoon, Uruguay (Olsson, 2013). Therefore, the absence of *R. harrisii* in the stomach contents of *M. furnieri,* reported for the estuarine region of the Patos Lagoon (Figueiredo and Vieira, 2005; Mendoza-Carranza and Vieira, 2008), is noteworthy.

Among the catfish, *N. barba* is one the species for which diet has been studied. Pereiopods of *Callinectes* Stimpson, 1860, and polychaetes were found in the stomach contents of juveniles and it is reported that the diet of adults is composed of molluscs and polychaetes (Araujo, 1984, *op. cit.* in Calliari *et al.*, 1997: 133). The swimming crab *C. sapidus* is a very abundant brachyuran which uses estuarine regions as nursery grounds. Studies on the natural diet of *C. sapidus* did not mention *R. harrisii* (Kapusta and Bemvenuti, 1998; Oliveira *et al.*, 2006).

Therefore, it seems plausible to assume that *R. harrisii* is under a low predation impact and this would explain the high longevity found, as this species has been caught in the estuarine region since 1982 and no reports of its presence in the diet of fish or crabs are published. While we have to acknowledge it does not provide irrefutable proof of a low predation impact, this hypothesis cannot be ruled out.

Rhithropanopeus harrisii is an established species in the estuarine region of the Patos Lagoon. Another study in the Patos Lagoon (Rodrigues and D'Incao, 2015) reported a larger maximum size for males (20.4 mm) and a smaller maximum size for females (12.7 mm) than those observed in our study. For marine and estuarine invertebrates it has been suggested that invasions are related to an increase in body size (Grosholz and Ruiz, 2003). For *R. harrisii* in the native distribution range (*i.e.*, Cheasapeake Bay, USA), the maximum size of males and females is 21.3 mm and 16 mm, respectively (Williams, 1984). European non-native populations show larger sizes for males (26.1 mm) and females (19.0 mm) (Turoboyski, 1973). Sizes of 22.9 mm (males) and 19.8 mm (females) were reported in Polish estuarine regions (Czerniejewski, 2009). Such a predicted increase in body size has not been observed in Patos Lagoon populations. The reasons why this suggested pattern was not observed are not understood, but it is important to discuss some reasoning.

Grosholz and Ruiz (2003) proposed two biological explanations for this increase in body size in invasive species. One is that resource increases in the new environment lead to a faster growth and therefore larger size. The second is that the absence of natural enemies (*e.g*, predators or parasites) results in larger body sizes. Here we argue against both explanations. It has been previously shown (Beverton and Holt, 1959) that faster growth rates are typically related (intra and interspecifically) to smaller maximum sizes, not larger. Regarding the second possibility, another interpretation is that the absence of natural enemies could ease the 'need' for faster growth, as animals will not be under pressure to grow fast to reach sexual maturity (Stearns, 1992). In this case, a low natural mortality could be related to a slower growth rate.

Natural mortality is difficult to observe in populations in the wild, and in the absence of age information it is hard to estimate it (Vetter, 1988; Zheng, 2005). In an attempt to circumvent this, several empirical relationships have been proposed (reviewed in Kenchington, 2013). However, a difficulty is that these relationships have not been based on data from crustaceans, and most of them are based on teleosts.

For deep-water brachyurans from the Mediterranean, one study (Company and Sardà, 2000) has reported a data compilation of von Bertalanffy growth parameters, but no information regarding Z is found. Another compilation (Zheng, 2005) reports data for temperate deep-water crabs, in which the attempt to fit Hoenig's relationship (Hoenig, 1983) to crab data yields a determination coefficient of 0.30, leading to the conclusion that "a meaningful relationship between M estimates and maximum ages is difficult to be established" (Zheng, 2005).

Considering *R. harrisii* is not subject to fishery, the total mortality found ($Z = 2.17$ year^{-1}) can be considered an estimate of the natural mortality. In the present investigation a promising significant relationship was found between estimates of Z and von Bertalanffy's *k*. We are not aware of any similar relationship — for estuarine-coastal brachyurans — in the available literature. The application of this relationship resulted in a predicted instantaneous total mortality ($Z = 2.89$ year^{-1}) which is 25 % higher than that found in the catch-curve analysis. However, considering the upper confidence limit of the catch-curve estimate ($2.17 + 0.30 = 2.47$), and the lower confidence limit of this estimate ($2.89 - 0.29 = 2.60$), the estimates are different by only 5 %. Therefore, in light of the information published in the literature, the instantaneous total mortality estimated by size-converted catch curve can be considered quite robust.

A weakness of the study is that no estimation of growth and mortality has been done for the sexes separately. In fact, providing enough animals are caught monthly for a modal progression analysis, it is better to estimate growth curves separately, as differences in size at sexual maturity could affect growth rates. For example, females of *C. sapidus* were observed to stop growing after maturation (Smith and Chang, 2007). However, we have not been able to analyze the sexes separately, as the small sample sizes did not permit it. While aware of these limitations, it is important to note that we found no indication in the literature of possible differences in growth rate or mortality between sexes. In fact, a comprehensive study on *R. harrisii* (see Turoboyski, 1973) has pointed out that no differences in post-moult body growth were seen between the sexes.

The growth and mortality parameters estimated in the present investigation have important consequences for the understanding of the population dynamics of *R. harrisii* in the estuarine region of the Patos Lagoon. Considering that this species has been found in this region for at least 30 years, this first account of growth and mortality of a population of *R. harrisii* is important to provide a starting point to assess differences between populations found around this estuarine region; as well as a reference point to study new populations which may be found in the future in other estuarine regions of the South American coastline.

In short, the present investigation has shown, for the first time, the growth curve for an invasive population of *R. harrisii*. Maximum longevity was estimated at 3.5 years, and from this it is suggested that this species is subject to weak natural predation. The instantaneous mortality rate estimated fits an empirical relationship found for estuarine and coastal brachyurans very well.

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