Article

Moving northwards: Invasive Green Crab (*Carcinus* spp.) Expands into the Southwestern Atlantic

Micaela Müller Baigorria [1,2*], Maite Narvarte [3], Nicolás Bonel [1] and Leandro Hünicken [4]

[1] Genética y Ecología Evolutiva, CERZOS, CONICET-UNS, Camino La Carrindanga Km 7, Bahía Blanca, Argentina.
[2] Facultad de Ciencias Marinas, Universidad Nacional del Comahue, San Martin 224,8520, San Antonio Oeste, Rio Negro, Argentina.
[3] Centro de Investigación Aplicada y Transferencia Tecnológica en Recursos Marinos (CIMAS, CONICET-UNCo), Güemes 1030, 8520, San Antonio Oeste, Rio Negro, Argentina.
[4] Sede Atlántica, Universidad Nacional de Río Negro, Ruta Provincial N°1 y Rotonda Cooperación, R8500FAL, Viedma, Río Negro, Argentina
* Correspondence: micaela.muller431@gmail.com

Simple Summary: Green crabs are invasive species that threaten coastal ecosystems around the world by competing with native animals and damaging habitats. Recently, a population of green crabs was discovered in the San Matías Gulf in Argentina, marking the furthest north this species has been found in the Southwestern Atlantic. We studied this population to understand its characteristics and how it might grow and spread in the future. We found that male crabs were more abundant and larger than females, and the overall population density was relatively low, which suggests that the population is still becoming established. Interestingly, the size of the crabs in this area is more similar to a related, less common species of green crab, which has also been reported in the Southwestern Atlantic, than to the more widely studied species. Since these two species are nearly identical in appearance, they are often misidentified, making it important to study their genetic makeup. Female crabs carrying eggs were found throughout most of the year, showing that this population can adapt well to local conditions and reproduce for extended periods. These findings suggest that the population could expand further and have serious impacts on native species and ecosystems. Monitoring this population over time will help scientists and policymakers better manage the spread of this invasive crab.

Abstract: The invasive European green crab (*Carcinus* spp.) has become a significant ecological concern due to its rapid global spread and impact on coastal ecosystems. In the Southwestern Atlantic, the northernmost population was recently recorded in the San Matías Gulf, providing an opportunity to study its demographic and life-history traits at the leading edge of its range. We conducted a comprehensive analysis of this population, assessing sex ratio, population density, size distribution, and the size at which 50% of females were ovigerous (SM_{50}). Our findings revealed a pronounced male-biased sex ratio (1.50 males per female) and a relatively low population density (0.52 crabs.m^{-2}), suggesting early-stage population establishment. The size range of individuals aligned more closely with *Carcinus aestuarii* than *C. maenas*, raising the possibility of hybridization or misidentification. Ovigerous females were present throughout most of the year, highlighting an extended reproductive period and adaptability to local environmental conditions. These traits, combined with rapid range expansion, underscore the invasive potential of *Carcinus* spp. and its ecological implications for the San Matías Gulf. Long-term monitoring and genetic analyses are essential to clarify species composition and inform management strategies to mitigate further spread and impacts of this invasive population.

Keywords: *Carcinus maenas*, *Carcinus aestuarii*, life history traits, sex ratio, population density, ovigerous females, newly established population, expansion range.

1. Introduction

The distribution and spread of invasive species depend on a complex interplay of factors, including the invader's traits, the initial introduction's size and timing **[1]**, and the frequency, intensity, and success of subsequent arrivals. These dynamics are particularly pronounced in marine ecosystems, where disturbances and increased resource availability can significantly enhance the establishment success of invasive species **[2]**. Furthermore, both biotic and abiotic characteristics of the receiving ecosystem **[3]**, along with the invader's tolerance to environmental stressors, play a critical role in determining the success of the invasion. The interaction of these factors not only influences the initial establishment but also shapes the progression of subsequent invasion stages.

During range expansion into new areas, invasive species often benefit from reduced conspecific density and increased space, conditions that promote population growth below carrying capacity **[4,5]**. In such expanding ranges, populations frequently exhibit reproductive traits indicative of high reproductive effort, including extended reproductive periods and a reduction in age and size at first reproduction **[4]**. These traits, combined with shifts in life-history strategies at low densities, such as shorter generation times, further accelerate population growth **[6]**. Understanding population characteristics during these early stages of an invasion is crucial for unraveling the mechanisms that drive invasion dynamics and predicting future expansion patterns.

Crustaceans are among the most successful aquatic alien invaders, often occupying complex trophic roles, leading to cascading effects throughout invaded ecosystems across the globe **[7]**. These species can alter key ecosystem functions, disrupting energy flow and nutrient cycles, which, in turn, affect critical services such as biodiversity, fisheries yields, and water quality **[8]**. In aquatic environments, invasive crustaceans threaten local biodiversity, outcompete native species for resources, and may introduce new parasites, impacting both native and invasive hosts (**[9]** and references therein).

The invasive European green crab, *Carcinus maenas* (commonly known as the shore crab), is native to northwest Europe and the western Mediterranean **[10].** Widely recognized as a dominant intertidal decapod crustacean in its native range **[11]**, *C. maenas* has exhibited remarkable adaptability to diverse environmental conditions, facilitating its establishment as a globally invasive species with significant ecological impacts **[12–14].** Its ability to outcompete and displace native crab populations has earned it a place on the International Union for Conservation of Nature's (IUCN) list of the world's 100 worst invasive species **[15].**

The species was first recorded outside its native range along the mid-Atlantic coast of the United States in 1817, and it has since expanded globally, facilitated by international trade and ballast water transport **[16]**. Established populations now exist in South Africa, Australia, and Argentina, among other regions (references in **[11]**). However, recent studies suggest that the so-called *C. maenas* populations in some areas may also include its sister species, *C. aestuarii*, or even hybrids between the two **[17–19]**. *Carcinus aestuarii*, native to the Mediterranean Sea, is morphologically similar to *C. maenas*, making differentiation challenging without molecular tools **[20,21]**. This indistinguishability has likely led to an underestimation of *C. aestuarii*'s invasive range.

In the Southwestern Atlantic, *C. maenas* was first reported in 2001 in Bahía Camarones, Chubut province, Argentina **[22,23]**. It has steadily expanded its range along the coast, reaching Puerto Madryn by 2015 **[24]**. In 2019, Malvé et al. **[25]** documented an individual in Puerto Lobos, suggesting a potential incursion into the San Matías Gulf. By 2021, a population was confirmed in the northern region of the Gulf **[26]** (Figure 1), marking the northernmost distribution of *C. maenas* in the Southern West Atlantic. However, recent molecular evidence detected *C. aestuarii* sequences in Nuevo Gulf populations, raising the possibility that the San Matías Gulf population might also include *C. aestuarii* **[18,19]**. These findings underscore the need for molecular

tools to accurately identify and re-evaluate the distribution and ecological impacts attributed to *Carcinus spp.* in the region.

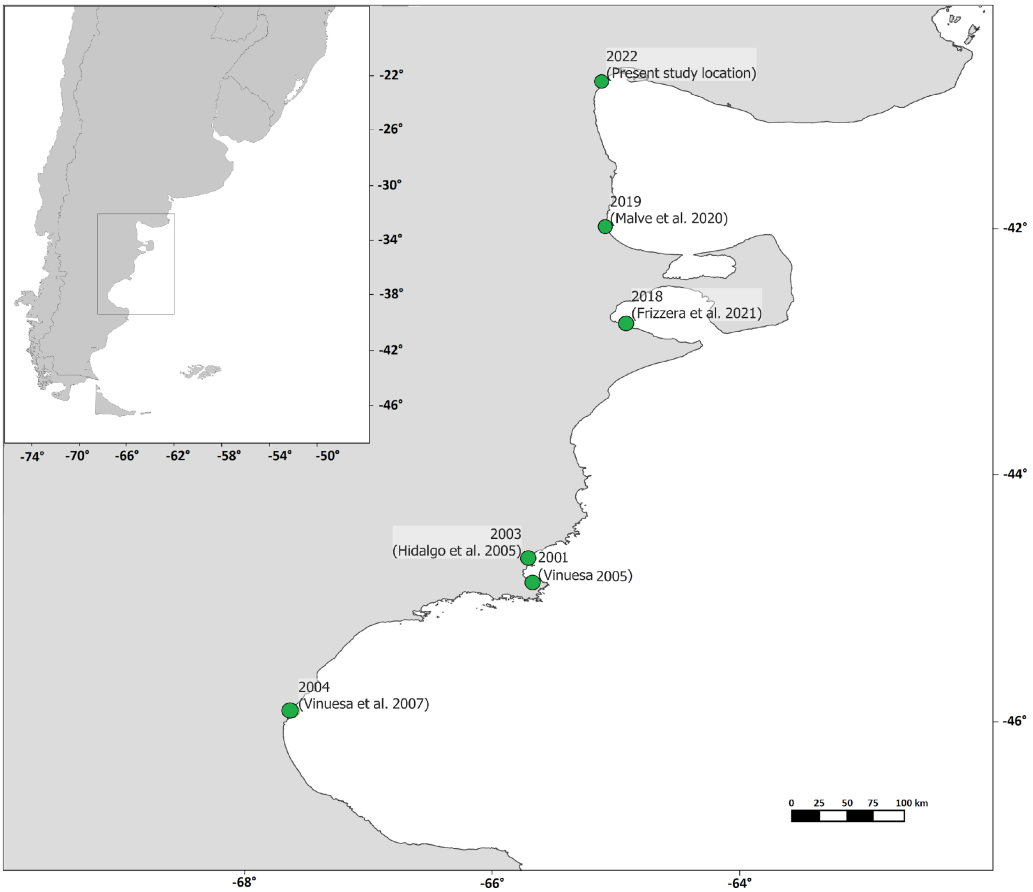

Figure 1. Distribution of *Carcinus* spp. along the southwestern Atlantic coast. Green dots represent previously documented populations, with the year of observation and corresponding citation indicated.

This progressive northward expansion in the Southwestern Atlantic could threaten the integrity of coastal ecosystems in southern South America and jeopardize the livelihoods of shellfish-based fisheries, since this crab primarily preys upon mollusks and crustaceans in coastal ecosystems **[27]**. Despite the ecological and economic implications, there remains limited knowledge about the demographic and biological traits of *Carcinus spp.* at the northernmost distribution in the southwestern Atlantic. Understanding the demographic and life history characteristics of these crabs, including the potential contribution of *C. aestuarii*, is critical for unraveling the mechanisms behind their range expansion.

Here, we investigate the demographic and life history characteristics of the newly established *Carcinus spp.* population in the San Matías Gulf. Specifically, we assess key population parameters, including sex ratio, population density, size distribution, and the proportion of ovigerous females. By comparing these traits to those reported for other *Carcinus spp.* populations at varying stages of establishment, this study aims to provide valuable insights into how invasive species establish and modify their life history traits across invaded environments.

2. Materials and Methods

2.1. Study area

The present study was conducted in the rocky intertidal zone of northern San Matías Gulf, Río Negro province, Argentina (40°49.88′ S, 65°6.46′ W). The intertidal zone extends for over 200 meters across the tidal gradient. Its topography is characterized by a gently sloping ramp on the seaward side, influenced by a semidiurnal macro-tidal regime with up to 9 meters of amplitude and significant seasonal variation **[28]**. Close to the mean high tide level, the upper intertidal area is dominated by macroalgae and tide pools.

During low tide, these upper areas experience high desiccation and fluctuations in temperature and salinity, as the tide takes approximately 12 hours to cover them **[28]**. Low-lying areas near the seaward edge are characterized by dense populations of the mytilids *Brachidontes rodriguezii* and *Perumitylus purpuratus*, as well as barnacles. The tidal cycle exposes organisms to extreme yet predictable changes in abiotic conditions at least twice daily, likely influencing their vertical distribution and zonation patterns. Consequently, the intertidal zone can be characterized into two distinct, but spatially adjacent, areas.

2.2. Field sampling, density, and individual size

We conducted monthly sampling of the invasive crab *Carcinus spp.* from August 2022 to July 2023 in the intertidal zone of San Matías Gulf. Sampling efforts focused on both the upper and lower intertidal areas, with a simple random sampling design used to allocate quadrats within each area. During low tide, we laid out four 25 m^2 quadrats per area to obtain a representative sample and estimate population density.

To estimate individual size, we collected crabs from each quadrat and measured carapace width (CW) to the nearest 0.1 mm using a digital caliper. Crabs were sexed through visual inspection of the abdomen (Figure A1), small individuals that could not be sexed were categorized as *juveniles*, and we recorded the presence of ovigerous females. After measurements and observations, all crabs were released back into their natural habitat.

2.3. SM_{50}

To estimate the size at which 50% of female crabs are ovigerous (SM_{50}), we grouped female individuals into carapace width (CW) intervals of 5.3 mm, determined using Sturges' formula for class intervals **[29]**. We then applied a weighted logistic regression (see below for more details).

2.4. Statistical analyses

All statistical analyses were conducted using *R* version 4.3.1. Linear mixed models (LMMs) for Gaussian continuous variables (density and size) were fitted using the *lme4* package, while generalized linear models (GLMs) for binomial variables (SM_{50}) were implemented using base R functions.

For the linear mixed models, the fixed effect of *Sex* (Male and Female) was included, with *Site* (Upper and Lower) and *Month* (sampling dates from August 2022 to July 2023) treated as random effects to account for spatial and temporal variability in the data. Fixed effects were assessed using likelihood ratio tests (LRT), comparing the model with the factor of interest against a model without that factor, while retaining all random effects. Random effects were tested using LRT, following the corrections outlined by **[30]**.

To estimate the SM_{50}, we applied a weighted logistic regression using a generalized linear model (GLM) with a binomial error distribution and a logit link function. The binomial response variable was defined by the presence and absence of ovigerous females, with carapace width (CW) as the independent variable. We applied weights corresponding to the total number of individuals in each size class to adjust for differences in sample sizes across classes, ensuring that size classes with larger sample sizes contributed proportionally more to the model.

3. Results

We found that males outnumbered females, yielding a sex ratio of 1.50 (709 males and 472 females). This sex ratio was consistent with the observed density differences, where males exhibited, on average, a 40% higher density than females (Table 1, Figure 2). The overall density of *Carcinus* spp. in the San Matías Gulf (0.52 ± 0.05 ind.m^{-2}), with males showing significantly higher densities compared to females (Table 1). The lowest density for both sexes was observed in August, in the winter season, followed by a sustained increase in density during the warmer months from December to February (Figure A2).

Table 1. Summary of means (±SE) and statistical significance of sex effect on density (ind.m^{-2}) and size (carapace width, mm) in response to sex difference of the invasive crab *Carcinus spp.* from the intertidal area of the San Matías Gulf, Argentina. Number of observations are indicated between parentheses. Significant values of each effect are shown in bold.

Variables	Sex Females (F)	 Males (M)	Sex effect	Sex comparison	Effect size
Density	0.20 ± 0.10 (96)	0.33 ± 0.14 (96)	X^2_1 = 14.65; **P <0.001**	F vs. M	-3.90***
Size	37.1 ± 1.0 (472)	40.0 ± 1.1 (709)	X^2_1 = 21.41; **P <0.001**	F vs. M	-4.65***

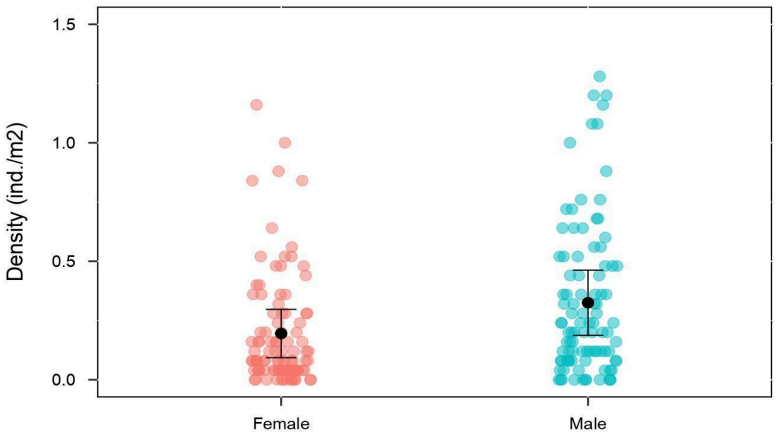

Figure 2. Difference in density (individuals per square meter) between male and female individuals of the invasive crab *Carcinus spp*. The red and blue points represent the estimated density for each sampling point across the upper and lower intertidal zones of the San Matías Gulf, Argentina, between August 2022 and July 2023. The black points indicate the mean density for each sex (± SE.)

We also found a significant difference in size (carapace width, CW) between male and female individuals. On average, males (40.0 mm) were 7% larger than females (37.1 mm; Table 1, Figure 3 and Figure A3). CW range was 16.4–64 mm for females and 11.0–72.1 mm for males. Juveniles showed, on average, a CW = 12.4 ± 0.4 mm (4.5–18.9 mm; Figure A3).

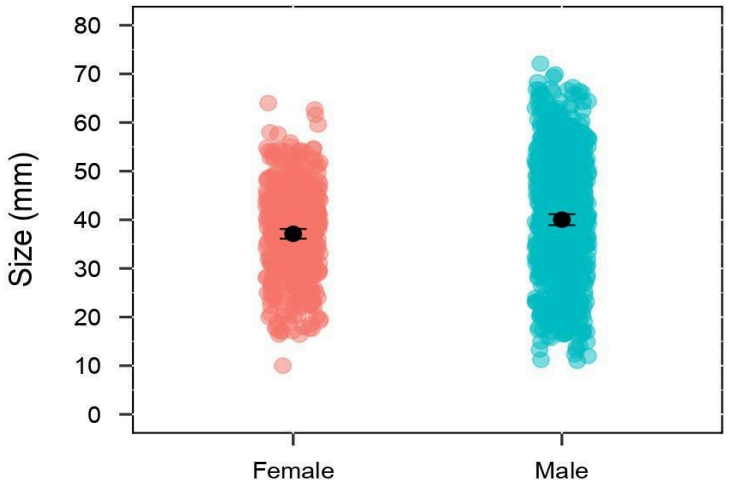

Figure 3. Difference in carapace width (size) between male and female individuals of the invasive crab *Carcinus spp*. The plot shows individual crab measurements sampled from August 2022 to July 2023, across the upper and lower intertidal zones of the San Matías Gulf, Argentina. The black bars represent the mean size (± SE.)

A total of 472 female *Carcinus spp.* individuals, ranging in carapace width (CW) from 16.4 to 64 mm, were sampled between August 2022 and July 2023 in the intertidal zone of the San Matías Gulf, Argentina. The weighted logistic regression model revealed a significant relationship between the proportion of mature female crabs and CW (GLM, z = 31.44, $P < 0.001$). The carapace width at which 50% of female crabs were ovigerous (SM_{50}) was estimated to be 61.48 mm (Figure 4). Ovigerous females were present in the intertidal zone throughout nearly the entire year, underscoring the species' prolonged reproductive activity in this region. The proportion of ovigerous females exhibited, however, a pronounced seasonal pattern, with the highest values observed between May and July 2023, peaking in July, and the lowest proportions recorded from January to March 2023 (Figure A4).

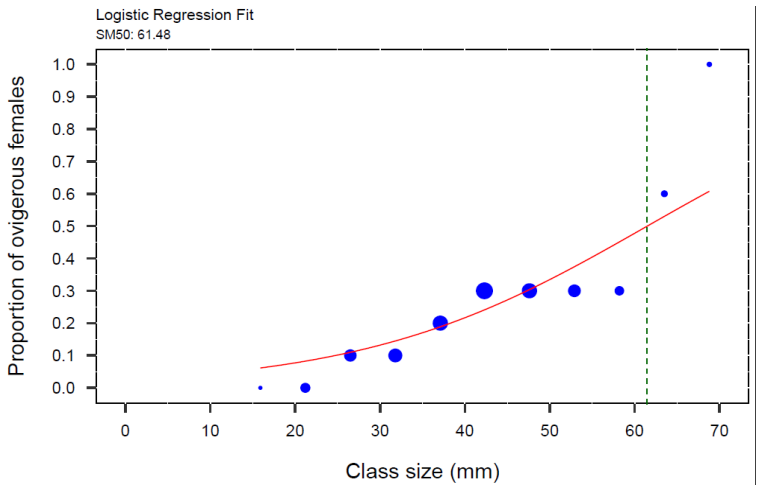

Figure 4. Weighted logistic regression of proportion of ovigerous females to carapace width (CW). SM_{50} for female crabs was estimated at the inflection point of the curve, which corresponds to 61.48 mm CW (N = 472) indicated by the green dotted line. The blue circles represent the proportional size of the points, scaled by the total number of individuals in each size class, grouped in 5.3-mm size-class intervals.

4. Discussion

This study provides the first comprehensive analysis of the invasive crab (*Carcinus spp.*) population in the San Matías Gulf, representing the northernmost record of this species in the SW Atlantic. Our results revealed a pronounced male-biased sex ratio, with males exhibiting 40% higher density than females and attaining significantly larger sizes. Additionally, we provide the first estimate, for this region, of the size at which 50% of females were ovigerous. Ovigerous females were observed in the intertidal zone throughout most of the year, despite a distinct seasonal reproductive pattern, indicating the species' extended reproductive activity and its remarkable adaptability to local environmental conditions. These traits highlight the potential for further population expansion and underscore the ecological risks posed by this invasive species in the San Matías Gulf.

4.1 Sex Ratio

Our results revealed a strongly male-biased sex ratio (1.50 males per female), a pattern consistent with numerous studies on *C. maenas* and *C. aestuarii* populations worldwide (Table 2). This bias is often attributed to differences in habitat use, behavior, and physiological requirements between sexes. Females, for instance, may migrate to subtidal zones during the breeding season to release larvae in more stable conditions, resulting in reduced numbers in intertidal areas during low tide sampling periods **[31,32]**. Alternatively, the male bias could reflect sampling bias or behavioral differences, as males are generally more active and exploratory, increasing their likelihood of being captured **[33].**

Interestingly, sex ratio patterns in *Carcinus* spp. populations appear to vary geographically, with some studies reporting female-biased or balanced ratios (Table 2), suggesting that local environmental factors and sampling methods may influence observed patterns. For instance, while male-biased populations dominate at higher latitudes, female-biased ratios have been documented in lower latitudes, possibly due to environmental and reproductive constraints (reviewed by **[11]**). Our findings align with the hypothesis that latitude and local environmental factors shape sex ratio dynamics, although the specific drivers in the San Matías Gulf warrant further study.

Table 2 -Morphometric and population parameters of European green crabs (*Carcinus maenas* and *C. aestuarii*) obtained through bibliographic review. Data are presented as mean ± SD (n) and range (min-max) in parentheses. The complete dataset is available in Table S1.

Species	**Sex**	**Maximum carapace width**	**Sex ratio (M:F)**	**Density (crabs.m^{-2})**	**SM_{50}**
Carcinus aestuarii	Female	56.4 ± 16.8 (9) (37.2-92.0)	1.5 ± 1.5 (8) (0.5-5.3)	0.4 ± 0.2 (3) (0.2-0.5)	33.7 ± 15.7 (5) (23.0-29.65)
	Male	65.7 ± 11.6 (8) (53.0-85.5)			
Carcinus maenas	Female	72.9 ± 11.4 (42) (52.0-93.0)	1.8 ± 1.6 (36) (0.4-8.2)	19.4 ± 33.2 (18) (0.1-101.2)	38.3 ± 14.0 (6) (28.9-49.96)
	Male	82.7 ± 11.5 (62) (57.0-114.0)			

4.2 Population Density

The overall density of *Carcinus* spp. in the San Matías Gulf (0.51 ind./m²) falls within the lower range reported for invasive populations globally (Table 2). Seasonal fluctuations in density were evident, with the lowest values recorded during winter and a steady increase observed during the warmer months. These trends align with seasonal reproductive and molting cycles documented in other *Carcinus* spp. populations **[34]**. By comparison, established populations of *Carcinus maenas* have reported a mean density of 19.4 ± 33.2 crabs.m^{-2} based on 18 studies, while *Carcinus aestuarii* exhibits a much lower mean density of 0.4 ± 0.2 crabs.m^{-2} based on only three studies. The stark difference in reported densities, coupled with the smaller number of studies on *C. aestuarii*, may result from the challenges in distinguishing the two morphologically similar species, potentially leading to the underreporting of *C. aestuarii*. Additionally, *C. aestuarii* may have a more limited geographical distribution compared to *C. maenas*, which could further explain the disparity in density estimates. These factors highlight the importance of molecular identification in regions like the San Matías Gulf to clarify species composition and better understand population dynamics.

However, direct comparisons across studies are challenging due to methodological differences and biases in population assessments. For instance, direct counting is limited to intertidal zones, diving is impractical in complex habitats, trap-based methods selectively capture actively foraging individuals, and mark-recapture techniques may be compromised by tag loss during molting **[11]**. These inherent limitations emphasize the need for standardized methodologies to facilitate more meaningful comparisons. Despite these constraints, our findings provide valuable baseline data for this population, first detected in 2022 **[26]**. The relatively low density observed in this study likely reflects the early stage of population establishment, during which densities often remain below carrying capacity due to abundant resources and minimal competition. Combined with the species' rapid expansion into the Southwestern Atlantic **[35]**, this highlights the urgent need for long-term monitoring of density trends. Such monitoring is essential for understanding the population dynamics of this invasive species and assessing its ecological impacts on local ecosystems.

4.3 Size

In line with global patterns for *Carcinus spp.*, males in the San Matías Gulf attained significantly larger carapace widths than females (mean: 40.0 mm vs. 37.1 mm; Table 2, Figure 5). Interestingly, the size range for both sexes aligns more closely with reported

measurements for *Carcinus aestuarii* than for *Carcinus maenas*. This observation can be explained by several non-exclusive hypotheses.

The alignment with *C. aestuarii* size ranges may, in part, result from the broader confidence intervals reported for this species. The limited number of studies on *C. aestuarii* compared to *C. maenas* contributes to greater variability in size estimates, potentially making our findings appear more similar to *C. aestuarii*. However, the mean sizes observed in our study remain smaller than those typically reported for *C. maenas*, suggesting additional factors may be at play.

Our sampling methodology, which focused on the intertidal zone, likely contributed to the observed size distribution. Larger individuals of *Carcinus* spp. often migrate to subtidal areas, particularly during certain life stages or environmental conditions, while smaller individuals predominate in intertidal habitats **[36].** This highlights the importance of standardizing sampling methods across habitats to obtain more accurate estimates of population size structure and density.

Hybridization between *C. maenas* and *C. aestuarii*, documented in regions such as Japan where both species co-occur **[17],** could explain the intermediate size ranges observed in our study. Hybridization has the potential to produce phenotypes that exhibit traits from both parent species **[37–39],** potentially influencing growth patterns and size distributions. Considering recent molecular evidence indicating the presence of *C. aestuarii* in the nearby Nuevo Gulf, the possibility of hybrids in the San Matías Gulf warrants further genetic investigation.

The relatively smaller sizes observed in this study could reflect traits characteristic of newly established populations, shaped by strong *r*-selection pressures. At the leading edge of a species' range or during early population establishment, selective forces may favor traits that optimize rapid population growth and survival under favorable conditions. These traits include reduced age of maturity, increased growth rates, and greater allocation of energy to reproduction **[4,6,40-42]**. Faster-growing individuals can reach reproductive sizes sooner, shortening generation times and accelerating population growth **[43,44]**. These life-history strategies are particularly advantageous for invasive species, facilitating both primary invasion and secondary spread **[45,46]**.

Regardless of the underlying cause, our findings raise important questions about the potential presence of *C. aestuarii* or hybrids in the San Matías Gulf. Recent molecular evidence from the nearby Nuevo Gulf supports this possibility, emphasizing the need for genetic analyses to confirm the species composition in the region. Further research is crucial to understanding the ecological and evolutionary processes shaping size distribution and other life-history traits in this invasive population.

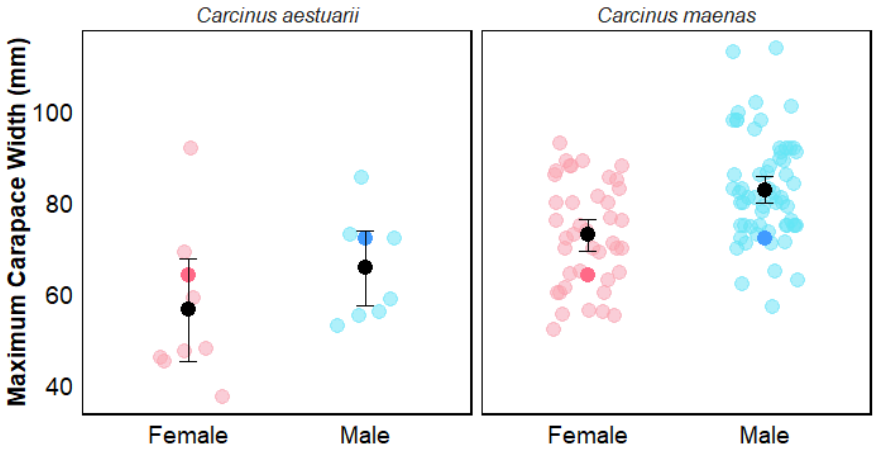

Figure 5. Maximum carapace width (mm) of *Carcinus aestuarii* and *C. maenas* by sex, including data from both bibliographic sources (pale dots) and this study (bold dots). Black dots with error bars represent mean ± 95% confidence interval.

4.4 SM_{50} and ovigerous females

The size at which 50% of females were ovigerous (SM_{50}) in the present study is larger compared to the SM_{50} reported for *C. maenas* and *C. aestuarii* populations (Table 2). This discrepancy can be attributed to differences in methodology. While previous studies primarily relied on macroscopical and histological techniques to determine gonadal and physiological maturity (Table 2), our study estimated SM_{50} based on the proportion of females observed in the ovigerous condition. As a result, it is likely that the size at which 50% of females achieve physiological maturity is smaller than the SM_{50} estimate reported here.

In the Southwestern Atlantic, the presence of ovigerous females has typically been observed between May and September **[47].** However, in the San Matías Gulf, ovigerous females were present in the intertidal zone throughout nearly the entire year. This extended reproductive period highlights the reproductive flexibility of *Carcinus* spp. in adapting to local environmental conditions. Such prolonged reproductive activity likely enhances recruitment success, facilitating population growth and expansion in this recently established population.

5. Conclusions

This study provides the first comprehensive assessment of the invasive crab (*Carcinus* spp.) population in the San Matías Gulf, marking the northernmost record of this species in the Southwestern Atlantic. Our results highlight key population traits that shed light on its ecological and invasive dynamics. The pronounced male-biased sex ratio, higher densities of males compared to females, and significant differences in size distributions align with patterns observed in other *Carcinus* populations. The relatively low population density and smaller sizes observed in this study suggest that the population is in the early stages of establishment, shaped by *r*-selection pressures that favor traits optimizing rapid growth and reproduction. This is further evidenced by the presence of ovigerous females throughout most of the year, indicating an extended reproductive period that enhances recruitment success and promotes population expansion.

These findings underscore the potential for *Carcinus* spp. to continue expanding its range in the Southwestern Atlantic, posing significant ecological implications to local biodiversity and coastal ecosystems. Long-term monitoring of population density, size structure, and reproductive patterns will be crucial for understanding the dynamics of this invasive population and informing management strategies to mitigate its impacts.

Author Contributions: Conceptualization, M.B.M., M.N., L.H.; methodology, M.B.M., M.N. N.B., L.H.; software, M.B.M., L.H..; formal analysis, M.B.M., N.B., L.H.; investigation, M.B.M., M.N., L.H.; resources, M.N., L.H.; data curation, M.B.M., N.B., L.H.; writing—original draft preparation, M.B.M., M.N., L.H.; writing—review and editing, M.B.M., N.B., L.H.; supervision, M.N., L.H.; project administration, M.B.M., M.N., L.H.; funding acquisition, M.B.M., L.H. All authors have read and agreed to the published version of the manuscript.

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Appendix A

Table A1. Detailed results of the linear models on density (ind.m^{-2}) and size (carapace width, mm) in response to sex difference of the invasive green crab *Carcinus* spp. from the intertidal area of the San Matías Gulf, Argentina. In both cases, we fitted a statistical model with a Gaussian distribution. Significant values of each effect are indicated in bold.

	Fixed Effect			Random Effect	Number of observations
Variable	**Sex**	**Month**	**Site**	**Site | quadrat**	
Density	$X^2_1 = 14.65$ *P* **<0.001**	variance = 0.01 *P* **<0.001**	variance = 0.02 *P* **<0.001**		192
Size	$X^2_1 = 21.41$ *P* **<0.001**	variance = 8.51 *P* **<0.001**	variance = 1.06 *P* = 0.124	var. quadrat = 0.01 var. Site*quadrat = 1.4 *P* = 0.09	1181

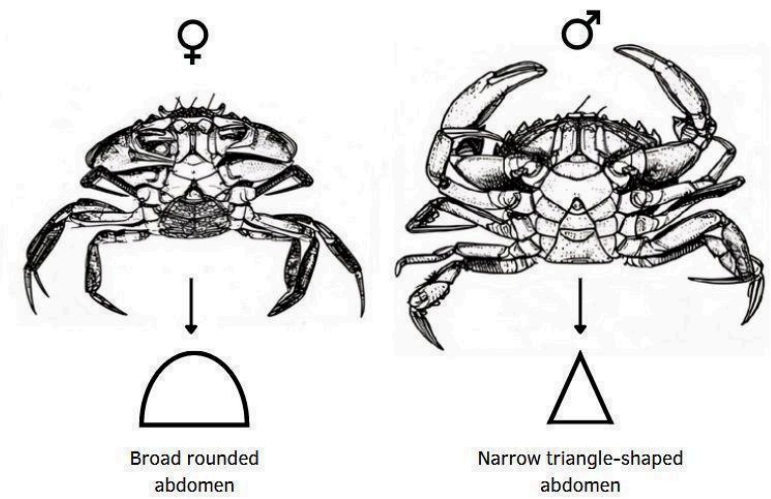

Figure A1. Diagram of the ventral view of a female and male crab (*Carcinus* spp.), highlighting differences in abdominal morphology.

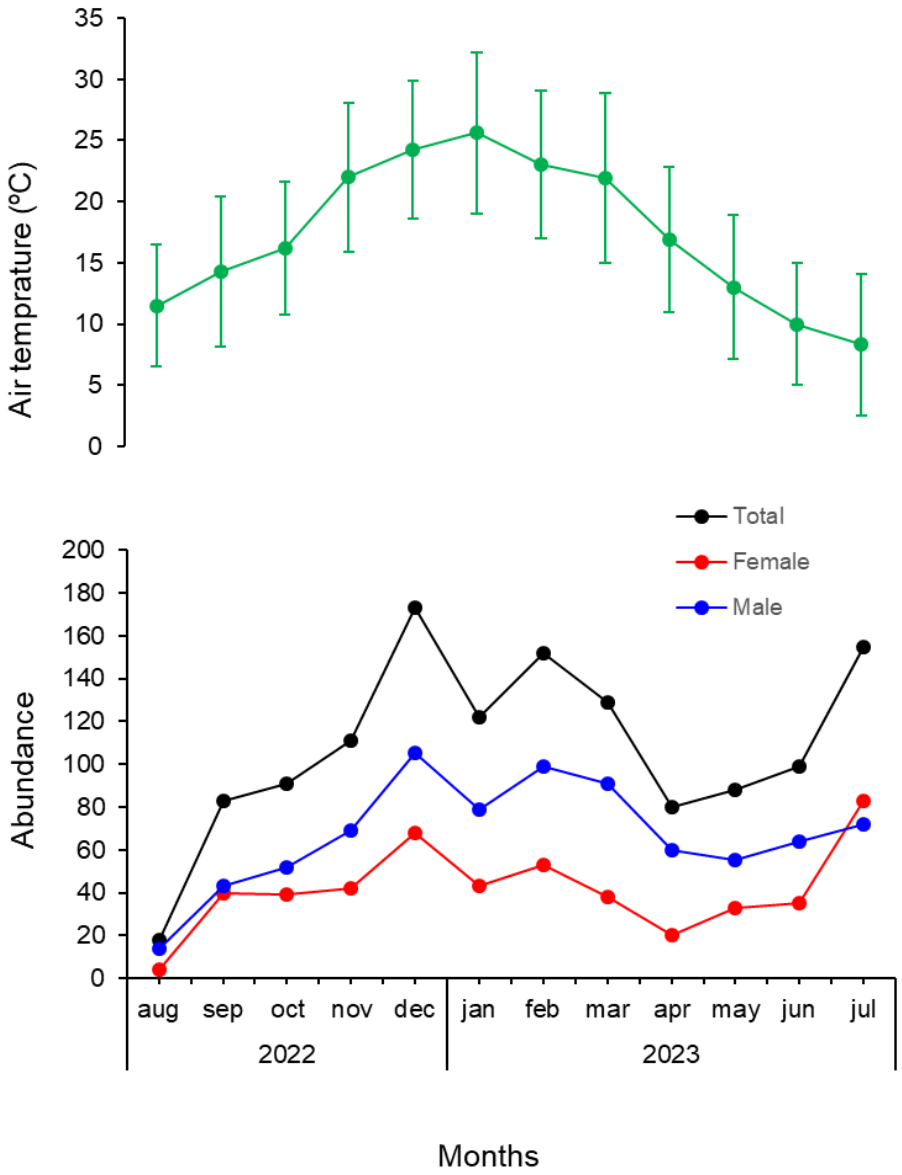

Figure A2. Monthly variation in the abundance of the invasive crab *Carcinus* spp. in the intertidal zone of the San Matías Gulf, Argentina, from August 2022 to July 2023. Data represent pooled observations from sampling quadrats (25 m² each) placed in the upper and lower intertidal zones. The black line shows total abundance, while the red and blue lines indicate the abundance of females and males, respectively.

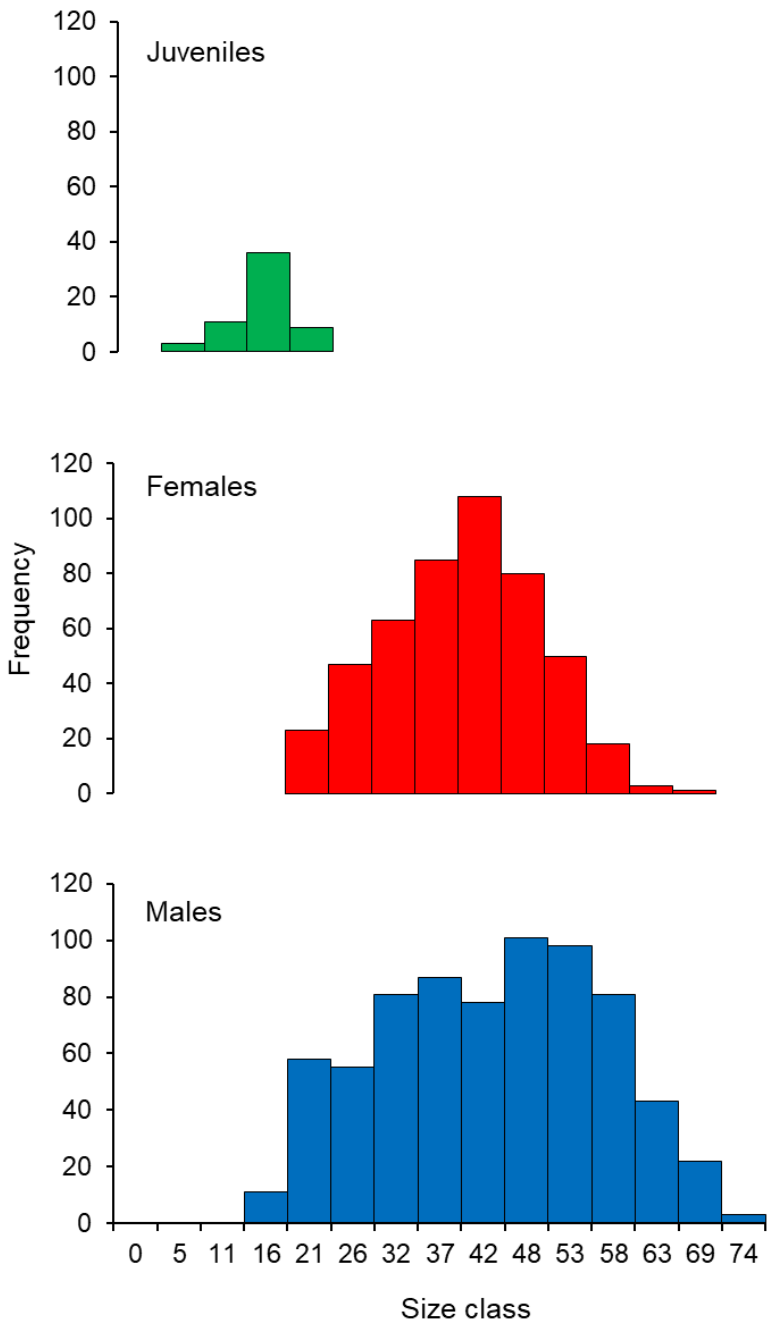

Figure A3. Size-class frequency distribution of the invasive green crab (Carcinus spp.) in the intertidal zone of the San Matías Gulf, Argentina. The histograms show the frequency of individuals within 5.3-mm size-class intervals for juveniles (n = 59), females (n = 472), and males (n = 709). Data were collected from pooled months and sites across the upper and lower intertidal zones between August 2022 and July 2023.

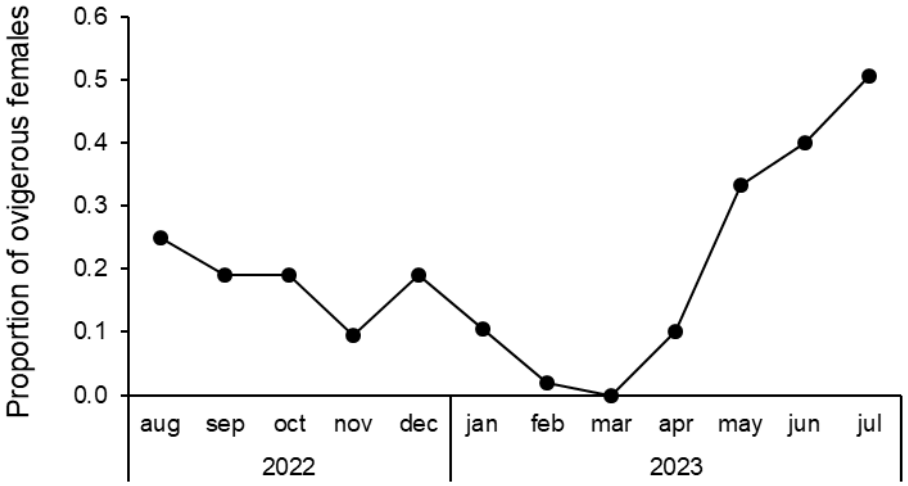

Figure A4. Seasonal variation in the proportion of ovigerous females of the invasive green crab (*Carcinus* spp.) in the intertidal zone of the San Matías Gulf, Argentina, from August 2022 to July 2023. Data represent pooled observations from both upper and lower intertidal zones across multiple sampling sites.

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