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The population dynamics of *Carcinus maenas* (Crustacea: Portunoidea) in a coastal lagoon (Portugal, SW)

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Summary: The green crab (*Carcinus maenas*) population was investigated in a coastal lagoon (Santo André) located on the southwest coast of Portugal. This study assessed the spatial-temporal variability of green crab abundance in the lagoon and its relationship with environmental variables. Experimental fishing was used to collect data on abundance, size structure and other demographic characteristics. Sampling was conducted monthly in 2019 at five sites, using fyke nets. From a total of 15063 individuals collected, 3898 were analysed. The highest catches were obtained in winter and at sites closer to the sea. The population was male-biased (58.70% of males and 41.30% of females), with an average carapace width of 48.81 mm for males and 40.79 mm for females. Ovigerous females were most abundant in December and January, and 50% were sexually mature at 45.11 mm. Based on data from the experimental fishing and fishermen's logbooks, the estimated annual catch of green crab ranged from 1873 to 3354 kg/ha, confirming the potential value of its fishery in the lagoon. This resource can be exploited for multiple purposes, including its meat or shell waste, thus contributing to the circular economy. Considering that green crab is a bycatch of the eel fishery, fishing regulations need to be modified to safeguard the stocks of both species.

Keywords: green crab; population dynamics; artisanal fishing; sustainable fisheries; lagoon fishery; coastal lagoons.

Dinámica poblacional de *Carcinus maenas* (Crustacea: Portunoidea) en una laguna costera (Portugal, SO)

Resumen: La población de cangrejo verde (*Carcinus maenas*) fue investigada en una laguna costera (Santo André) situada en la costa suroeste de Portugal. Este estudio evaluó la variabilidad espacio-temporal de la abundancia del cangrejo verde en la laguna y su relación con las variables ambientales. Se utilizó la pesca experimental para recolectar datos sobre abundancia, estructura de tallas y otras características demográficas. El muestreo se realizó mensualmente en 2019 en 5 sitios, utilizando redes de pesca. De un total de 15063 individuos recogidos, se analizaron 3898. Las mayores capturas se obtuvieron en invierno y en los sitios más cercanos al mar. La población presenta un predominio de machos (58,70% de machos y 41,30% de hembras), con una anchura media del caparazón de 48,81 mm para los machos y 40,79 mm para las hembras. Las hembras ovígeras son más abundantes en diciembre y enero, y el 50% son sexualmente maduras con 45,11 mm. A partir de los datos de la pesca experimental y de los cuadernos de pesca de los pescadores, la captura anual estimada de cangrejo verde osciló entre 1873 y 3354 kg/ha, lo que confirma el valor potencial de su pesca en la laguna. Este recurso puede ser explotado para múltiples fines, incluyendo su carne o sus desechos, contribuyendo así a la economía circular. Teniendo en cuenta que el cangrejo verde es una captura accesoria de la pesquería de anguila, es necesario modificar la normativa pesquera para salvaguardar las poblaciones de ambas especies.

Palabras clave: cangrejo verde; dinámica poblacional; pesca artesanal; pesca sostenible; pesca en lagunas; lagunas costeras.

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INTRODUCTION

The green crab, *Carcinus maenas* (Linnaeus 1758), has a wide native distribution on the Atlantic coast, extending from Europe to North Africa (Crothers 1968). It is also distributed worldwide due to several successful introductions and spreading episodes arising from anthropogenic activities (Carlton and Cohen 2003). This crab inhabits intertidal and subtidal areas such as rocky shores, estuaries, salt marshes and coastal lagoons, which demonstrates its tolerance to large fluctuations in salinity, temperature and oxygen (Crothers 1967, Amaral et al. 2009). Despite this plasticity in habitat use, when environmental conditions change, the distribution of this species can also change (Almeida et al. 2008), as it actively moves in search of better-quality habitats (Ameyaw-Akumfi and Naylor 1987). The species plays an important role in trophic food webs (Baeta et al. 2006), where it can be a prey for several fish species (Hampel et al. 2005, Avignon et al. 2017) and also an active benthic predator on shellfish, crustacea and polychaetes (Chaves et al. 2010), acting as an energy carrier in all systems (Glamuzina et al. 2017). Although the species can reach a carapace width of 86 mm (Crothers 1967), in high-density populations the crabs tend to be smaller due to intraspecific competition and cannibalism (Moksnes 2004). Females can achieve sexual maturity at a carapace width of between 15 and 30 mm, and breeding can occur during the entire year (Crothers 1967). Despite the existence of specimens in all life cycle stages throughout the year (Baeta et al. 2005), the abundance of ovigerous females is higher in late winter and spring, in deeper saline waters (Crothers 1967, Queiroga et al. 1994).

One of the aquatic systems inhabited by the green crab is that of coastal lagoons, which are among the most productive ecosystems in the world (Kennish and Paerl 2010). Coastal lagoons are shallow water bodies exposed to conspicuous significant environmental fluctuations and are in most cases very productive systems, where wind and bottom topography have an important effect on water mixing (Kjerfve 1994, Kennish and Paerl 2010, Pérez-Ruzafa et al. 2011). These systems are usually separated from the sea, and the connection is made by one or more restricted inlets (Kjerfve 1994). However, coastal lagoons that remain isolated from the sea for long periods are quite rare (Cancela da Fonseca et al. 1989) and become more vulnerable to eutrophication processes (Kjerfve 1994). Despite their fragile environmental balance, coastal lagoons are of great ecological importance, which, combined with their calm and easily predictable conditions, makes them important in regional socio-economic activities related to professional and recreational fisheries (Pérez-Ruzafa et al. 2011). In Santo André Coastal Lagoon, fisheries are socially and economically important and mostly directed towards the European eel, *Anguilla anguilla* (Correia et al. 2019). In some cases, the great abundance of green crab can lead to economic losses for fishermen, mainly due to the damage they cause to fyke nets, and to the fish caught. To overcome this problem, in 2019, the fisheries management authority included the green crab in the local fisheries regulation, but this should be supported in sound knowledge about the population dynamics.

To promote future sustainability of the fishery and improve gains for the fishermen's community, it is urgent to collect population parameters for a baseline assessment of green crab in the lagoon. This information is fundamental for establishing suitable management practices that ensure the correct management of the resource and avoid its waste. Hence, this study aims to characterize the green crab population in the Santo André Lagoon by analysing population attributes such as abundance, spatial-temporal variability, size structure, sex ratio and reproductive potential, and to estimate the annual catch of green crab in the lagoon.

MATERIALS AND METHODS

Study area

Santo André Lagoon is a coastal lagoon in the northeastern Atlantic located in the southwest of mainland Portugal (38°05'47.57''N; 8°47'23.69''W, see Fig. 1). This lagoon is part of the Natural Reserve of Lagoa de Santo André and Sancha and it is under the protection of the Ramsar Convention on Wetlands and Natura 2000 (Birds Directive - Special Protection Area and Habitats Directive - Site of Community Importance). The lagoon has an area of 150 ha (Cancela da Fonseca et al. 2001), with an average annual depth of 1.8 m (Cancela da Fonseca et al. 1989). The high nutrient levels and shallow depth of this coastal lagoon provide ideal conditions for high rates of primary production (Duarte et al. 2002).

A sand bar separates the water body from the ocean during most of the year. The connection to the sea is artificially established, usually in March, through a man-made channel that typically remains open for a few weeks to a month (Cancela da Fonseca et al. 1989). Outside this period, the lagoon may sporadically be in contact with the sea, especially when waves surpass the dunes, usually in autumn and winter (Félix et al. 2015). Water renewal occurs when the communication between the lagoon and the sea is re-established, which is essential to maintain the functioning and productivity of the system. In addition to preventing eutrophication processes, this connection also allows the recruitment to the lagoon of several marine animals and their larval stages, as well as plant species (Costa et al. 1985, Bernardo et al. 1988, Félix et al. 2015). The lagoon can be colonized by both marine and freshwater species, but in most cases the species survive only for short periods due to the lagoon's highly fluctuating environment (Cancela da Fonseca et al. 1989, Garside et al. 2014).

The lagoon fauna is dominated by macroinvertebrates, fish species and aquatic birds (Cancela da Fonseca et al. 2001), some of which are exploited by the fishing community and have high economic value. The European eel supports the most important fishery in the lagoon, with an estimated 4 to 8 t of this species being harvested annually (Correia et al. 2019).

Field sampling and laboratory work

Sampling (experimental fishing) was conducted monthly at five locations from January to December 2019. To cover the habitat diversity, the five sampling sites were selected on the basis of the distance between them and the substrate type. Sediments were then grouped as Mud <63 µm; 0.063 mm ≤Muddy sand/Sandy mud <0.2 mm; 0.2 mm ≤Sand <2 mm; 2 mm ≤Gravel, following the classification system adopted in the sediment charts of the Portuguese Navy Hydrographic Institute (Moita 1985). Site A is the closest to the sea and has a sandy bottom; site B is located in the middle of the lagoon, with mud and sand; site C is the upstream area, with a muddy and sandy bottom; site D in the southern area has a sandy bottom and is an even more closed water body inside the lagoon; and site E, in the northern area, has a muddy bottom and is an important fishery area (Fig. 1).

At each location, four unbaited winged fyke nets with the same dimensions as those used by fishermen (2 m bag length, 5 m wing length, 1.5 m wing height and 18 mm mesh size in cod-end) were set during the afternoon and removed the next morning. On each sampling occasion, four environmental variables (Table 1) were measured using a multiparametric probe (YSI II Water Quality Sonde).

For each fyke net, the total number of crabs caught were counted and weighed. A random subsample of 20 individuals per fyke net was retained and transported to the laboratory and frozen until processing, to collect individual data: carapace width, measured between the tips of their fifth anterior lateral spines (±1 mm accuracy); weight (precision±0.01 g); sex, determined by analysis of the abdomen (V-shaped abdomen in males and wider and U-shaped abdomen in females); and ovigerous females, depending on whether visible eggs were present.

Data on crab catches from the artisanal fishery were obtained from three volunteer fishermen (≈8% of the total number of fishermen with a fishing licence) during the 2019 fishing season, which was divided into two fishing periods. The first fishing period ran from 1 January to 17 March and the second from 16 July to 30 September. Logbooks were distributed to fishermen who volunteered to record the number and/or total weight of crabs caught per day, as well as the number of fyke nets used daily.

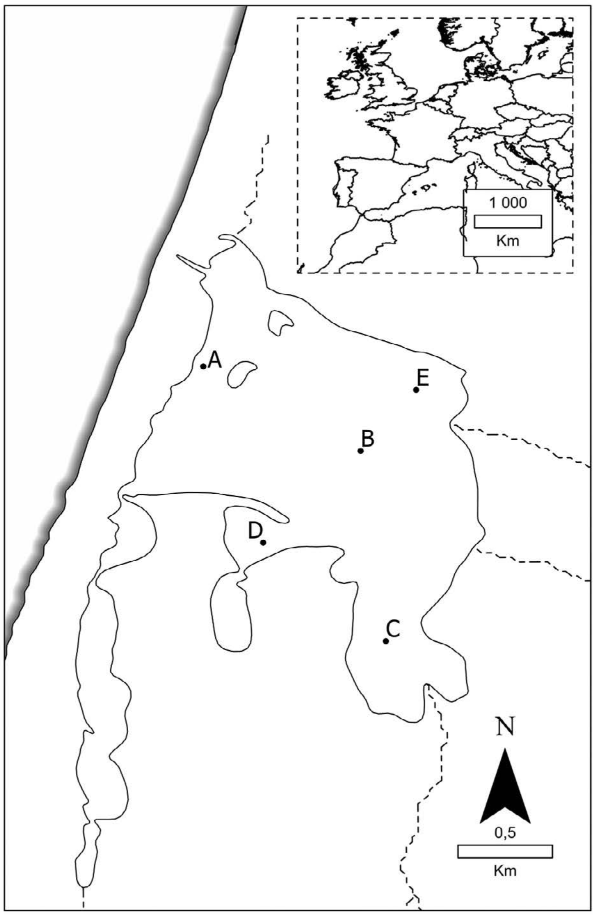

Fig. 1. – Location of Santo André Lagoon (Portugal) and the five sites (A-E) that were sampled in this study.

Statistical analysis

Spatial-temporal variability of green crab abundance was assessed using a permutational analysis of variance (PERMANOVA) (Anderson et al. 2008), in which a two-way fixed-effect crossed design was performed (factors: sampling month and sampling

Table 1. – The range of environmental variables measured monthly at each sampling site in Santo André Lagoon (Portugal) from January to December 2019.

Variable	Units	Range [minimum – maximum]					Mean
		Site A	Site B	Site C	Site D	Site E	
Water temperature	°C	[9.57 - 25.08]	[9.57 - 25.86]	[10.35 - 26.24]	[10.51 - 25.82]	[9.58 - 25.81]	18.92
Depth	m	[1.17 - 3.06]	[0.88 - 1.84]	[0.77 - 1.76]	[0.52 - 1.45]	[0.93 - 1.98]	1.49
Total dissolved solids	g/L	[17.10 - 24.85]	[17.05 - 24.66]	[16.42 - 23.82]	[16.88 - 24.62]	[17.09 - 24.66]	20.39
Salinity		[16.10 - 24.31]	[16.09 - 24.10]	[15.44 - 23.25]	[15.87 - 24.08]	[16.09 - 24.11]	19.57

site). A square root transformation was applied to the variables, and the Bray-Curtis similarity coefficient was used as a resemblance measure. A posteriori pairwise tests were conducted when significant interactions between factors were identified. These procedures were performed using PRIMER® v6 (Clarke and Gorley 2006).

The influence of environmental factors on the abundance of green crab (response variable) was assessed with a generalized linear model (GLM, McCullagh and Nelder 1989) performed in R environment (R Core Team 2021) using the "MASS" software package (Venables and Ripley 2002). In addition to the environmental variables measured on each sampling occasion (Table 1), the remaining explanatory variables included in the analysis were sampling month (January-December), sediment type and total organic matter content (%) (unpublished data). Before modelling, a Spearman correlation test was performed between the predictors, and a high correlation coefficient (ρ>0.7, Dormann et al. 2013) was identified between total dissolved solids and salinity. Thus, to avoid redundancy, total dissolved solids was removed from subsequent analysis. The Akaike information criterion (Sakamoto et al. 1986) was chosen for the selection of the best model. Subsequently, an ANOVA was performed with the chi-squared (χ^2) test to verify the significance of the variables in the model.

Laboratory data were used for the biological characterization of the green crab population. Regarding carapace width, after verifying the normality and homoscedasticity of the dataset, a two-way ANOVA was conducted to examine the effect of sampling month and sampling site on carapace width. A Tukey HSD post hoc test was performed for multiple comparisons between effects. The statistical tests were conducted in IBM® SPSS® Statistics 26 (IBM Corp. Released 2019).

The gender data of the individuals were analysed by sampling month and by sampling site using a χ^2 test. Data on ovigerous and non-ovigerous females were also analysed by sampling month and by sampling site using a χ^2 test. These statistical tests were conducted using IBM® SPSS® Statistics 26 (IBM Corp. Released 2019). To estimate the size at which 50% of the green crab females were sexually mature in the lagoon, a logistic regression model was used, and the maturity ogive was calculated using the "sizeMat" software package (Torrejon-Magallanes 2020) in R environment (R Core Team 2021).

Data from fishing logbooks and experimental fishing were used to estimate the total weight of green crabs harvested annually (kg/ha/year). The catch per unit effort (CPUE), was determined as the average ± standard deviation of the estimated CPUE for each fisherman and the average obtained from the experimental fishery, expressed as kg of green crabs per fyke net per fishing day. The total annual green crab catch in the Santo André Lagoon was estimated by multiplying the average CPUE obtained by the total number of fishing days, by the total number of fishermen with a fishing licence, and by the number of fyke nets they used in each fishing period.

RESULTS

Abundance and distribution

A total of 15063 green crabs were collected over the study period: 6740 at site A, 1995 at site B, 904 at site C, 3123 at site D and 2301 at site E (Fig. 2). The highest number (1944 crabs) were collected at site A in January and the lowest number (14 crabs) at site C in February. January and December were the months with the highest catches (2819 and 2116, respectively) and October was the month with the lowest (326 crabs) (Fig. 2). The highest catches were at site A from January to May plus December and at site D from July to September.

Regarding the spatial-temporal variability, PERMANOVA tests showed that the abundance of green crab was significantly different for both factors, sampling month (F=6.0738, df=11, ρ<0.05) and sampling site (F=15.4270, df=4, ρ<0.05), and for the interaction between factors (F=2.3634, df=44, ρ<0.05). Pairwise tests revealed significant differences between October and all months, except for February and March (Supplementary material Table S1). Pairwise tests for each pair of sampling sites revealed significant differences between all sampling sites, except for site E, which did not differ from sites B and D (Supplementary material Table S2).

The GLM developed to understand the relationship between abundance and environmental factors showed a predictive performance of 37.18%. The variables that best explained the species abundance inside the lagoon

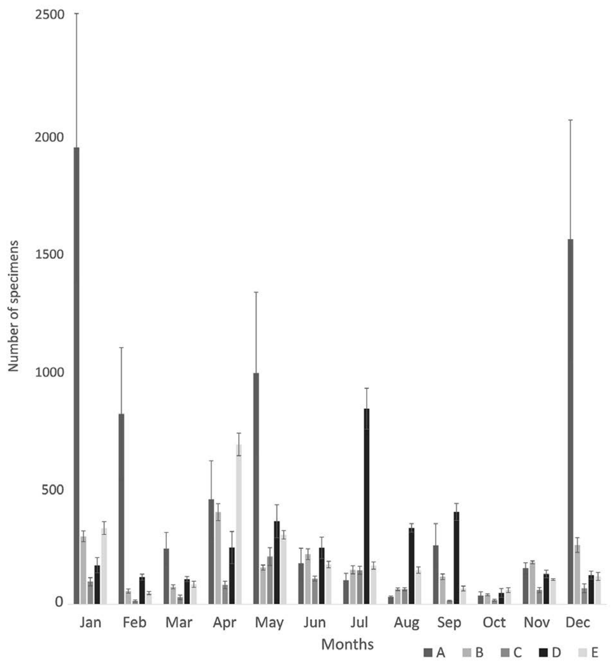

Fig. 2. – The number of green crab, *Carcinus maenas*, caught monthly at each sampling site during the sampling period (January to December 2019) in Santo André Lagoon (Portugal). The bars display standard deviation (n=15063).

Table 2. – Summary of the GLM coefficients.

Variable	Estimate	Std. error	z value	Pr (>lzl)
(Intercept)	7.04	0.08	85.25	< 0.05
Sediment type (muddy)	- 0.92	0.04	- 23.24	< 0.05
Sediment type (muddy sand)	- 0.14	0.03	- 4.42	< 0.05
Sediment type (sand)	0.71	0.02	29.90	< 0.05
Temperature	- 0.05	0.00	- 31.29	< 0.05
Salinity	- 0.05	0.00	- 16.47	< 0.05
Depth	0.14	0.01	11.05	< 0.05

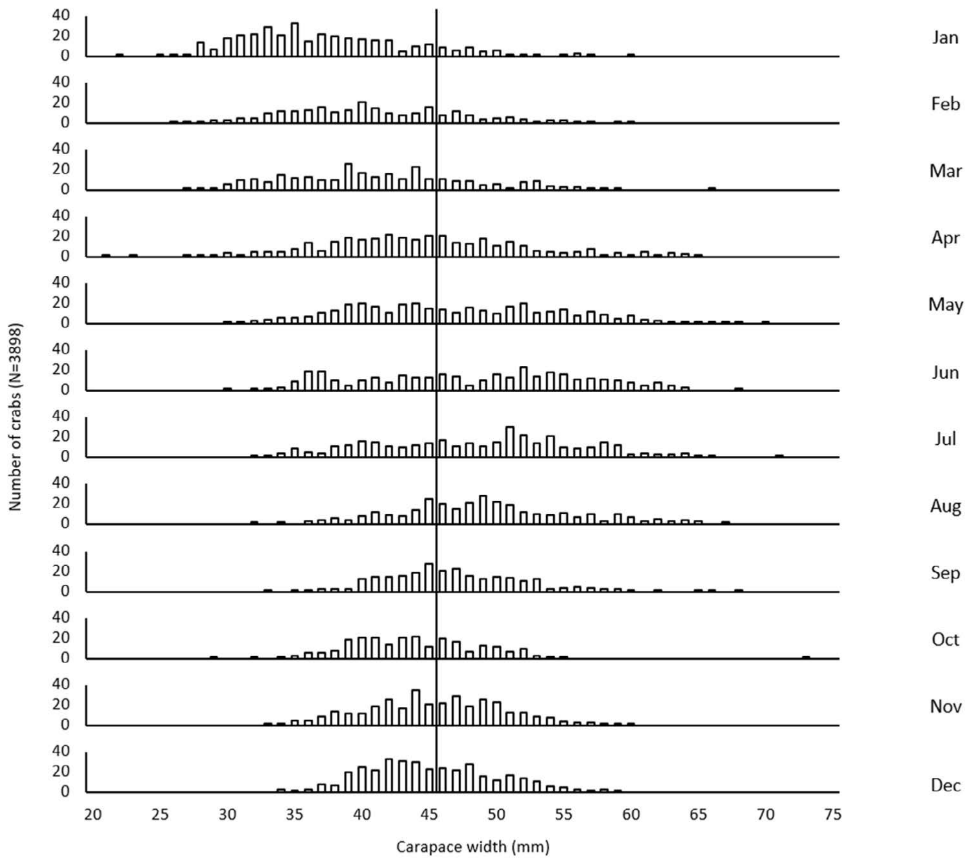

Fig. 3. – Monthly frequency distribution of carapace width of green crab, *Carcinus maenas*, in Santo André Lagoon (Portugal) throughout the sampling period (January to December 2019). The average carapace width of the population is represented by a vertical line (45.50 mm).

were sediment type (27.26%), temperature (6.15%), salinity (3.06%) and depth (0.71%). The abundance increased in deeper sandy areas and decreased in the remaining sediment types and with higher water temperature and salinity. The summary of the model coefficients is presented in Table 2.

Size and sex structure

Of the 3898 specimens analysed in the laboratory over the study period, 2288 (58.70%) were males and 1610 (41.30%) were females. The carapace width of the largest green crab measured was 73.60 mm and that of the smallest 21.24 mm. The carapace width of males ranged from 21.24 to 71.46 mm and that of females from 26.68 to 73.60 mm. The average carapace width of the whole green crab population was 45.50 mm (Figs 3 and 4), with 40.79 mm for females and 48.81 mm for males (Fig. 5). The largest green crabs were predominant in the summer months (Fig. 3). The results of the ANOVA showed that there were statistically significant differences in carapace width between sampling months ($F=90.07$, $df=11$, $\rho<0.05$) and between sampling sites ($F=18.00$, $df=4$, $\rho<0.05$) and a statistically significant interaction between the effects of both factors ($F=4.66$, $df=44$, $\rho<0.05$). The Tukey HSD post hoc test revealed that the smaller carapace width of green crabs caught in January was significantly different ($\rho<0.05$) when compared with the measures obtained for the remaining months (Fig. 3). Regarding sampling sites, the Tukey

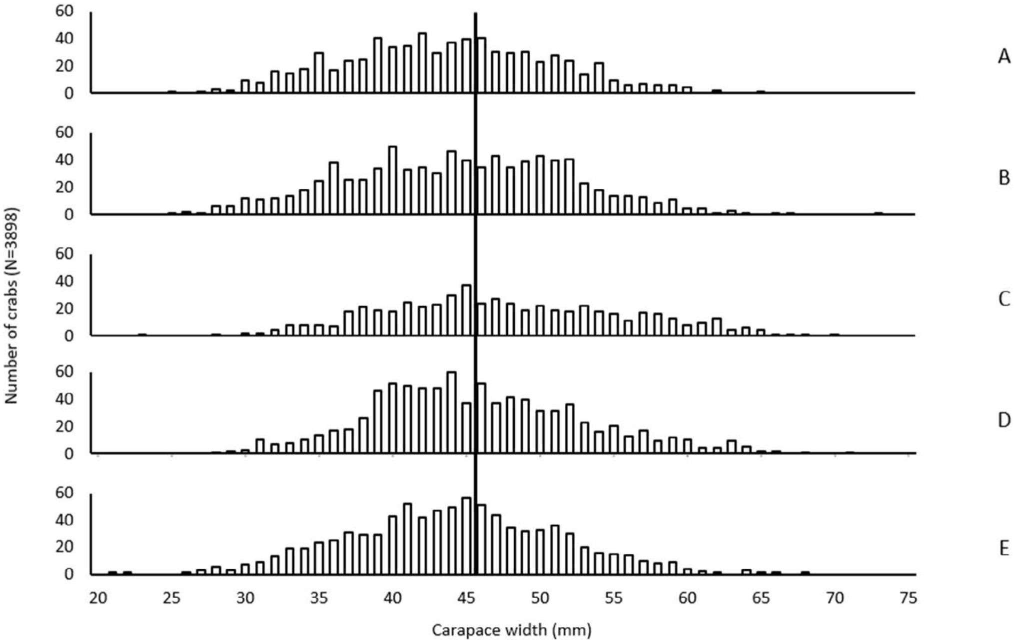

Fig. 4. – Frequency distribution of green crab, *Carcinus maenas*, carapace width by sampling site. The average carapace width of the population is represented by a vertical line (45.50 mm).

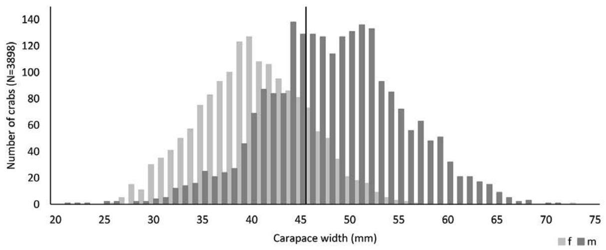

Fig. 5. – Carapace width frequency distribution for males “m” (n=2288) and females “f” (n=1610) of green crab, *Carcinus maenas*, in Santo André Lagoon (Portugal). The average carapace width of the population (45.50 mm) is represented by a vertical line.

HSD test showed that the carapace width was significantly different between site C and the other sampling sites (ρ<0.05) and between site D and the other sampling sites (ρ<0.05). There was no statistically significant difference in carapace width between sites A and B (ρ=0.10), A and E (ρ=0.54) or B and E (ρ=0.87).

The population sex ratio varied significantly, in relation to both the sampling month (χ^2=752.06, df=11, ρ<0.05), and the sampling sites (χ^2=37.36, df=4, ρ<0.05). The highest female-biased sex ratios occurred in January and December, with respectively 79.13% and 80.05%, followed by February, with 63.16%. From March to November, catches were dominated by males, with August standing out with the highest proportion of males (92.79%), while March was the month closest to a balanced distribution between sexes, with 45.51% females and 54.48% males (Fig. 6). Overall, the sex ratio

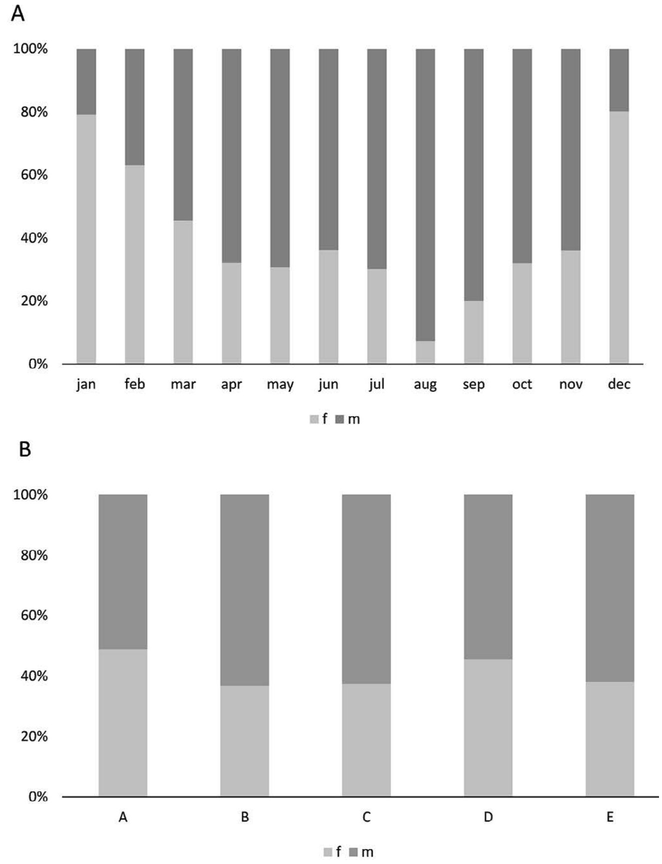

Fig. 6. – The sex ratio of green crab, *Carcinus maenas*, by sampling month (A) and sampling site (B) during the sampling period (January to December 2019). Males “m” (n=2288) and females “f” (n=1610).

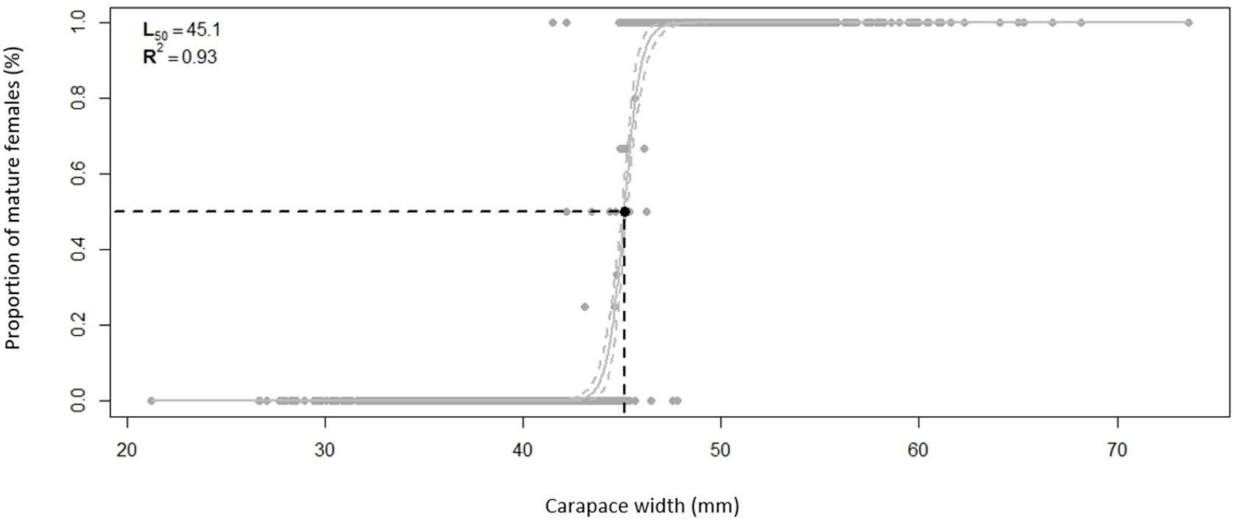

Fig. 7. – Fitted logistic regression for the proportion of females of green crab, *Carcinus maenas*, by carapace width (mm) with L_{50} and R^2 shown. The grey lines show the expected probability of maturity, and the grey dots indicate the observed proportion of ovigerous females (sample size=173). The equation is Y=1/1+exp-(A + B*X), where median bootstrap of A=107.3665 and B=2.3807.

was biased towards males at all sampling sites except site A, where the sex ratio was closer to a 1:1 balance (48.75% females; 51.25% males) (Fig. 6).

The ratio between ovigerous and non-ovigerous females varied significantly with the sampling month (χ^2=143.13, df=11, ρ<0.05) but not with the sampling site (χ^2=7.19, df=4, ρ=0.13). Non-ovigerous females (n=1430; 88.82%) predominated over ovigerous females (n=180; 11.18%) in all months and sites sampled. The highest catches of ovigerous females occurred in January and December (23.29% and 22.74%, respectively), whereas in June, August and September no ovigerous females were caught. All sampling sites followed the same pattern, with an average of 11.59% ovigerous females per site.

Over the study period, the size of ovigerous females varied between 26.68 and 56.22 mm (mean, 41.07 mm) and that of non-ovigerous females between 27.05 and 73.60 mm (mean, 40.75 mm). In Santo André Lagoon, 50% of females attained sexual maturity when they reached an average carapace width of 45.11 mm (Fig. 7).

Estimation of annual catches

In 2019, for the first fishing period, each fisherman caught on average 2.92±3.23 kg/fyke net/fishing day, ranging from 0.14 kg/fyke net/fishing day in February to 12.86 kg/fyke net/fishing day in January. In the second fishing period, each fisherman caught on average 1.60±0.39 kg/fyke net/fishing day, ranging from 0.16 kg/fyke net/fishing day in September to 2.75 kg/fyke net/fishing day in August (Fig. 8).

The average obtained with experimental fishing throughout the entire year, using the same gear as the fishermen, was 1.24±1.44 kg/fyke net/fishing day, ranging from 0.04 kg/fyke net/fishing day in February to 6.97 kg/fyke net/fishing day in December (Fig. 8).

The average daily catch from the two commercial fishing periods and the average daily catch from the experimental fishing were used to estimate the total amount of green crab harvested in the lagoon in 2019. Considering the whole fishing period allowed (155 days), the entire fishing community (39 licensed fishermen) and the area of the lagoon (150 ha), the total green crab catches in 2019 was estimated to range between 281 and 503 t. As there is no catch limit imposed by the legislation, these values suggest that fishermen can harvest 1.87 to 3.35 t/ha (1873 to 3354 kg/ha) of green crab annually.

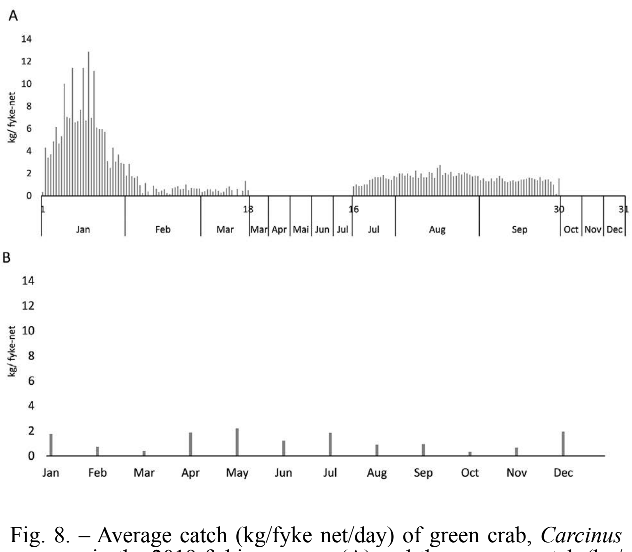

Fig. 8. – Average catch (kg/fyke net/day) of green crab, *Carcinus maenas*, in the 2019 fishing season (A) and the average catch (kg/fyke net/day) in the experimental fishing (B). Fishing periods: 1 January to 17 March and 16 July to 30 September.

DISCUSSION

This study analysed the population dynamics of green crab and explored its potential importance as a fishery resource in Portugal. The distribution and abundance of green crab in the Santo André Lagoon are highly variable in time and space (Fig. 2), displaying active habitat selection during the life cycle, similar to the results of other authors elsewhere (Baeta et al. 2005, Almeida et al. 2008). The species is present throughout the lagoon, but the highest catches were obtained at site A (the closest to the sea and with a sandy bottom), mostly in winter and spring and at site D (the second closest to the sea and with a sandy bottom), with particularly high catches in summer. These two sampling sites seem to be the preferential areas for the species in the lagoon, which can be attributed to their greater proximity to the sea or to the type of bottom sediment (sand), as confirmed by the GLM and previously verified by Cancela da Fonseca and Luís (1992). Despite the past (Cancela da Fonseca and Luís 1992) and current habitat preference observed in this lagoon, the species seems to benefit from other habitats like shellfish beds or vegetation areas (Almeida et al. 2008, Amaral et al. 2009, Almeida et al. 2011). The assessment of habitat quality and species preferences is very important as it allows the implementation of more accurate policies, management or conservation measures or strategies (Amaral et al. 2009).

The green crab carapace width is within the size range reported for the species (Crothers 1967, Baeta et al. 2005). The male-biased sex ratio was observed for almost the whole year, in line with that of other green crab populations on the Atlantic coast (Lyons et al. 2012, Ladeira 2016). Lyons et al. (2012) reported larger specimens in spring/summer in southwest Ireland which were also mature adults of the population. Thus, the relative size of individuals from both sexes might be related to the breeding season, as males must be larger than females (Reid et al. 1997) and the mating process is estimated to occur in late summer (Crothers 1967).

The reproduction was not inhibited by the salinity of the lagoon, as this species can reproduce at salinities above 10 (Crothers 1967). Ovigerous females were more abundant in this lagoon in the winter period, which has also been reported for other areas of the Portuguese Atlantic coast (Baeta et al. 2005, Queiroga et al. 1994). The estimated carapace width of females at maturity was 45.11 mm, which is lower than the sizes reported for North Wales or southwest Ireland (Reid et al. 1997, Lyons et al. 2012) and lower than the sizes reported for other Portuguese brackish water systems except the Sado estuary (Monteiro et al. 2022).

The current estimate of the annual catch of green crab in Santo André Lagoon is higher than that obtained in a previous study conducted in 1985/1986 (1873 to 3354 kg/ha vs 130 kg/ ha, respectively) (Cancela da Fonseca and Luís 1992). The exploitation of this aquatic resource could increase sustainability of fisheries, as pressure on other vulnerable species (e.g. European eel) would be reduced. Although green crab currently has no commercial value in Portugal, in the second half of the 20th century it had some importance in European landings (Portugal, Spain, France, England, Italy), especially in the Venice lagoon in Italy (Cohen et al. 1995, Libralato et al. 2004). Future studies should therefore assess the potential of using this resource to develop high-value by-products that can improve benefits and returns to fishermen.

The considerable biomass of green crab available in the Santo André Lagoon could be used to produce crab flour (Fulton and Fairchild 2013), fish bait (Morris et al. 2007) and food for shrimp aquaculture (Cancela da Fonseca and Luís 1992). Beyond these uses, green crab is also appropriate for human consumption (Morris et al. 2007), as it provides a nutritious source of protein (Cancela da Fonseca and Luís 1992, Naczk et al. 2004; Fulton and Fairchild 2013), with similar nutritional values to and lower cholesterol levels than other harvested crabs (Skonberg and Perkins 2002). By-products of this resource, such as shell powder, could also be transformed into innovative biofertilizers for agriculture (Nekvapil et al. 2021), supplements to improve eggshell quality in the poultry industry (Lichovnikova 2007), or fine filler material in concrete for construction purposes (Mo et al. 2018), thus contributing to the circular economy (Nekvapil et al. 2021).

In conclusion, despite all the advantages of exploiting this resource, the green crab fishing is intrinsically dependent on eel fishing. The European eel is the most valuable resource in the lagoon (Correia et al. 2019), while green crab is currently considered a bycatch. Non-targeted crab fishing has been carried out (and the crabs have been discarded) with the same fishing gears and in the same fishing periods, jeopardizing compliance with the minimum allowed green crab size and the possibility of closing the crab fishery in subsequent years. The continued study of population dynamics will also help to identify and measure changes in the ecosystem, which can be used as an alternative approach in the absence of other elements to evaluate the system (Glamuzina et al. 2017). The future management of this resource should be included in an integrated science-based strategy in which the lagoon is evaluated as a whole and treated in conformity with its socio-economic importance.

CRediT authorship contribution statement

Teresa Portela: Formal analysis, Methodology, Writing - Original Draft; Dénnis Cruz: Data collection; Writing - Review and Editing; Rui Monteiro: Formal analysis, Methodology; Writing - Review and Editing; Maria João Correia: Formal analysis; Writing - Review and Editing; José Lino Costa: Conceptualization, Writing - Review and Editing; Isabel Domingos: Supervision, Conceptualization, Writing - Review and Editing, Project administration, Funding acquisition.

Declaration of competing interests

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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SUPPLEMENTARY MATERIAL

Table S1. – Pairwise tests for the factor “sampling month”.

Groups	t	P(perm)	Unique perms	Groups	t	P(perm)	Unique perms
Jan, Feb	3.7116	0.001	998	Apr, Aug	3.0969	0.002	999
Jan, Mar	3.9287	0.002	997	Apr, Sep	2.3225	0.013	999
Jan, Apr	0.47135	0.885	998	Apr, Oct	3.9262	0.001	999
Jan, May	0.45667	0.824	998	Apr, Nov	2.67	0.005	999
Jan, Jun	1.9069	0.038	998	Apr, Dec	1.1568	0.221	998
Jan, Jul	1.2023	0.229	999	May, Jun	1.7448	0.081	999
Jan, Aug	4.0878	0.001	998	May, Jul	1.1674	0.255	999
Jan, Sep	3.0979	0.002	999	May, Aug	3.8685	0.001	999
Jan, Oct	4.8765	0.001	999	May, Sep	3.0733	0.001	998
Jan, Nov	3.3763	0.001	999	May, Oct	4.7643	0.001	996
Jan, Dec	1.5284	0.1	999	May, Nov	3.0702	0.003	999
Feb, Mar	0.91513	0.429	997	May, Dec	1.5584	0.093	999
Feb, Apr	3.051	0.003	998	Jun, Jul	0.80699	0.465	998
Feb, May	3.7335	0.001	998	Jun, Aug	1.8481	0.046	998
Feb, Jun	2.5543	0.004	999	Jun, Sep	1.594	0.096	999
Feb, Jul	2.9059	0.003	999	Jun, Oct	3.2024	0.002	999
Feb, Aug	1.7451	0.067	999	Jun, Nov	1.0645	0.296	999
Feb, Sep	1.3744	0.143	999	Jun, Dec	0.67788	0.618	999
Feb, Oct	0.7272	0.605	999	Jul, Aug	2.729	0.004	999
Feb, Nov	2.5979	0.004	999	Jul, Sep	2.0069	0.029	999
Feb, Dec	2.2828	0.009	999	Jul, Oct	3.8378	0.001	999
Mar, Apr	3.1779	0.001	999	Jul, Nov	2.0802	0.026	998
Mar, May	3.8398	0.002	998	Jul, Dec	0.57233	0.738	999
Mar, Jun	2.2571	0.023	999	Aug, Sep	1.1555	0.264	999
Mar, Jul	2.8711	0.006	997	Aug, Oct	2.1846	0.025	999
Mar, Aug	0.99599	0.354	999	Aug, Nov	1.591	0.097	999
Mar, Sep	1.1927	0.231	999	Aug, Dec	1.8447	0.036	999
Mar, Oct	0.90361	0.475	999	Sep, Oct	2.0573	0.03	999
Mar, Nov	2.0552	0.031	999	Sep, Nov	1.9222	0.032	998
Mar, Dec	2.1511	0.015	999	Sep, Dec	1.3002	0.188	999
Apr, May	0.74987	0.585	999	Oct, Nov	3.2271	0.002	999
Apr, Jun	1.5525	0.094	998	Oct, Dec	2.9851	0.004	999
Apr, Jul	0.88335	0.429	998	Nov, Dec	1.5218	0.095	999

Table S2. – Pairwise tests for the factor “sampling site”.

Groups	t	P(perm)	Unique perms
A, B	2.5533	0.001	999
A, C	3.7155	0.001	998
A, D	2.0883	0.007	999
A, E	2.2993	0.009	999
B, C	6.2873	0.001	999
B, D	2.29	0.015	999
B, E	0.62797	0.63	999
C, D	6.6606	0.001	997
C, E	6.267	0.001	999
D, E	1.8042	0.052	999