UNIVERSIDADE D
COIMBRA

João Nuno Gomes Monteiro

EFFECT OF EXTREME CLIMATIC EVENTS ON *CARCINUS MAENAS* POPULATION IN THE MONDEGO ESTUARY

Dissertação no âmbito do Mestrado em Ecologia orientada pelo Doutor Filipe Miguel Duarte Martinho e pelo Professor Doutor Miguel Ângelo do Carmo Pardal e apresentada ao Departamento de Ciências da Vida da Universidade de Coimbra.

Junho de 2019

Departamento de Ciências da Vida da Faculdade de Ciências e Tecnologia
da Universidade de Coimbra

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Contents

Resumo

Eventos climáticos extremos têm vindo a aumentar a sua frequência e intensidade nas últimas décadas. Deste modo, é importante compreender como estes afetam as espécies e habitats. O objetivo deste estudo foi analisar a variação temporal e espacial na dinâmica populacional de *Carcinus maenas* no estuário do Mondego, e os efeitos dos eventos climáticos extremos (secas e cheias) nesta população. As amostragens foram realizadas mensalmente durante os anos de 2003 a 2018 (exceto 2012 e 2013), durante a noite com o auxílio de uma rede de arrasto de vara de 2 metros. As densidades de *C. maenas* foram padronizadas em indivíduos por $1000m^2$.

Analisando as densidades de juvenis observou-se a existência de um padrão de recrutamento contínuo ao longo de todo o estudo, com picos de recrutamento em anos de secas, além disso, é observável que os juvenis se encontram maioritariamente em zonas mais a montante do estuário. A população é constituída essencialmente pelo morfótipo verde, encontrando-se os indivíduos com morfótipos laranjas e vermelhos em zonas mais a jusante do estuário. O ratio sexual (machos/fêmeas) foi diferente conforme as classes de tamanho, apresentando valores superiores a 1 nas primeiras classes de tamanho, mostrando posteriormente, um equilíbrio do número de machos e fêmeas. A produção secundária (P) estimada para *C. maenas* foi diferente durante todos os anos do estudo, tendo valores superiores em anos de secas. Os diagramas de ordenação (RDA) mostraram as diferenças espaciais, temporais e ambientais de *Carcinus maenas* no estuário do Mondego. Através da análise das somas acumulativas (CUSUM) verificou-se uma correlação entre a maioria das características biológicas de C. *maenas* e as variáveis ambientais e o índice de oscilação norte atlântico (índice NAO).

Avaliando as diferentes populações de caranguejo verde no planeta, observaram-se claras diferenças no período de recrutamento, no tamanho máximo dos indivíduos e na esperança média de vida. As populações do Sul da Europa apresentam menores tamanhos máximos e um maior período de recrutamento. Com o aumento da latitude, observa-se populações com maiores tamanhos máximos e com um menor período de recrutamento.

A existência de eventos climáticos extremos leva à alteração da dinâmica populacional de *Carcinus maenas*, sendo que as maiores diferenças são observáveis durante secas extremas, onde devido à diminuição do caudal do rio e ao aumento da salinidade, irá existir um maior recrutamento de juvenis, levando assim a um aumento da densidade populacional.

PALAVRAS-CHAVE: Secas, Cheias, Alterações climáticas, *Carcinus maenas*, Recrutamento.

Abstract

Extreme climate events have been increasing in frequency and intensity in the last decades. So, it is important to understand how these affect species and habitats. The objective of this study was to analyse the temporal and spatial variation in the population dynamics of *Carcinus maenas* in the Mondego estuary and the effect of extreme climate events (droughts and floods) on this population. Samplings were performed monthly during the years 2003 to 2018 (except 2012 and 2013), with a 2-meter beam trawl during the night. The densities of *C. maenas* were standardized in individuals per 1000m^2.

Analysing juvenile densities, a continuous recruitment pattern was observed throughout the study, with recruitment peaks in years of droughts, in addition, it was observable that juveniles are found mainly in upstream areas of the estuary. The population consists essentially on the green morphotype, being the orange and red morphotypes present in more downstream areas of estuary. The sex ratio (males/females) was different according to the size classes, being much higher than 1 in the first size classes, showing afterwards, in older individuals a value close to 1. The secondary production (P) estimated for *C. maenas* was different during all the period, having higher values in droughts years. The ordering diagrams (RDA) showed spatial, temporal and environmental differences of *Carcinus maenas* in the Mondego estuary. A correlation between *Carcinus maenas* biological features and the environmental variables and the North-Atlantic Oscillation index (NAO index) was verified through the cumulative sums analysis (CUSUM).

The different populations of the green crab on the planet, showed clear differences in the recruitment period, the maximum size of the individuals and the life span. Southern European populations have lower maximum carapace width and a longer recruitment period. With the increase of latitude, populations with larger maximum carapace width and with a shorter recruitment period were observed.

The existence of extreme climate events causes leads to an adjustment on the population dynamics of *Carcinus maenas*. Bigger differences are present during extreme droughts, where due to the low river flow and an increase in the salinity, there will be a more intense recruitment of juveniles, leading to an increase in population density.

KEYWORDS: Droughts, Floods, Climate change, *Carcinus maenas*, Recruitment.

1. Introduction

1.1 Estuarine ecosystem and its major threats

Estuaries and coastal zones are areas of high importance for coastal hydrology processes, geochemical and biological cycles (Robins et al., 2016), presenting a biological productivity similar to tropical forests and coral reefs (Cai, 2011). In addition, estuaries are also considered dynamic and heterogeneous ecotones, where several hydrographic variations influence the species, their trophic network and the cycling of organic material (Yagi et al., 2011; Kaiser et al., 2005). As a transition area between rivers and the sea, estuaries are also characterized by a high daily variation in water temperature, water circulation, salinity, and oxygen conditions (Zhang et al., 2018).

Many species of fish and invertebrates use estuaries as nursery grounds in the early stages of the life-cycle (Beck et al. 2001; Lamberth and Turpie, 2003; Martinho et al, 2007; Martinho et al, 2009). Estuaries contribute substantially to successful recruitment in fish and macroinvertebrates, increasing juvenile growth and survival (Yagi et al., 2011), due to the high availability of food and protection (Cardoso et al., 2004; Martinho et al., 2007). Not only marine species benefit from estuaries, they have also a great importance to terrestrial populations, providing feeding and breeding areas to birds (Sharps et al., 2015). At the physico-chemical level, estuaries are also of great importance for coastal protection, erosion control, water purification and nutrient cycling (Barbier et al., 2011). These also provide cultural, recreational and educational services for humans.

Although estuaries are among the most important socio-economic and ecological ecosystems, they are constantly subject to anthropogenic and environmental stress. With increasing development on the XX and XXI centuries, there was an increase in anthropogenic impacts on these ecosystems, such as the increase in the number of contaminants released (Dafforn et al., 2012), increase in physical disturbances caused by ships and dredging near ports (Hedge et al., 2009), construction of barriers (Führböter et al., 2015), introduction of exotic species and increased eutrophication (Verdelhos et al., 2005; Golubkov and Alimov, 2010). In addition to anthropogenic factors, estuaries are also subject to high environmental variability as a consequence of climate change (Hein et al., 2018) and the increase in frequency and intensity of extreme climatic events (floods, droughts, heat and cold waves), which can lead to changes throughout the estuarine community, biodiversity and reproduction periods (Cardoso et al., 2007, Bessa et al., 2010).

One of the major scientific challenges is to understand how human activities and climate change affect ecosystems and their communities. The responses of marine communities will be distinct, changing species distribution and abundance according to their thermal tolerance and adaptability (Fields et al., 1993), in addition, the effects of waves and freshwater inputs will lead to consequences in benthic processes. Climate change will affect individuals, populations and communities through the individuals' physiological and behavioural responses to environmental change. Species that are near the edge of their tolerance to another stressor may have a lower threshold. Thus, intact communities may be more resilient to climatic disturbances and the risk of population collapses and biodiversity loss due to climate change may minimize (Hewitt et al., 2016). Changes in the abundance of key species will lead to major consequences, as these species can perform diverse functions (Roessig et al., 2004). Thus, it is necessary to understand the mechanisms by which species respond to these disturbances and better understand the dynamics of these habitats.

1.2 The Mondego estuary

1.2.1 Description and geographic localization

The Mondego River, the largest river with an exclusively Portuguese course, has its source in Corgo das Mós, in Serra da Estrela at 1547m (Rodrigues, 1997, Acabado, 1998) and run for 227 km until it flows into the Atlantic Ocean (Pardal, 2002). It drains a hydrological basin of approximately 6670 km^2, of which 1715 km^2 belongs to the lower Mondego valley with only 40 km long (Ribeiro, 2001; Marques et al., 2003), and an annual mean rainfall between 1000 and 1200 mm (Duarte et al., 2001).

The Mondego estuary, located on the Atlantic coast of Portugal near the city of Figueira da Foz (40º8'48 "N, 8º51'24" W), is a temperate coastal system (Ribeiro, 2001). In the upstream zone of the estuary, approximately at 7 km from the mouth, the estuary is divided in two arms (North and South) joining again near the mouth, thus creating a small island, the Murraceira Island (Figure 1).

The two arms of the estuary are quite distinct in hydrodynamics, morphology and sedimentation patterns, which allows classifying these as two subsystems (Reis & Duarte, 1990; Veríssimo et al., 2016; Neves et al., 2018). The north arm receives most of the freshwater inflow from the Mondego River (Duarte et al., 2001; Cruzeiro et al., 2016), and it is deeper, reaching 5 to 10 m deep during high tide, with a tidal amplitude of 2 to 3 m (Cunha et al., 1997; Teixeira et al, 2008; Veríssimo et al., 2016). In addition, the north arm is predominantly sandy and has been intensively dredged to make the Figueira da Foz port more functional (Cunha et al., 1997; Personal observation). In turn, the south arm is shallow, having between 2 to 4 m deep during high tide, with a tidal amplitude of 1 to 2 m (Teixeira et al, 2008). This arm is almost silted in the upstream area (Cunha et al., 1997; Duarte et al., 2001) and is characterized by large intertidal areas that become exposed during the low tide (Nyitrai et al., 2013; Veríssimo et al., 2016). The hydraulic circulation in the south arm depends on the tides and on the freshwater discharge of a small tributary, the Pranto River that is controlled artificially by a sluice located 3 km from the confluence with the south arm (Teixeira et al., 2008; Nyitrai et al., 2013). Water from this small tributary presents a high concentration of nutrients (from agricultural and rice fields), which enter the south arm. This input of nutrients along with the increase of disturbances caused by aquaculture and agricultural activities lead to eutrophication problems in the south arm (Dolbeth et al., 2003; Verdelhos et al., 2005; Dolbeth et al., 2010).

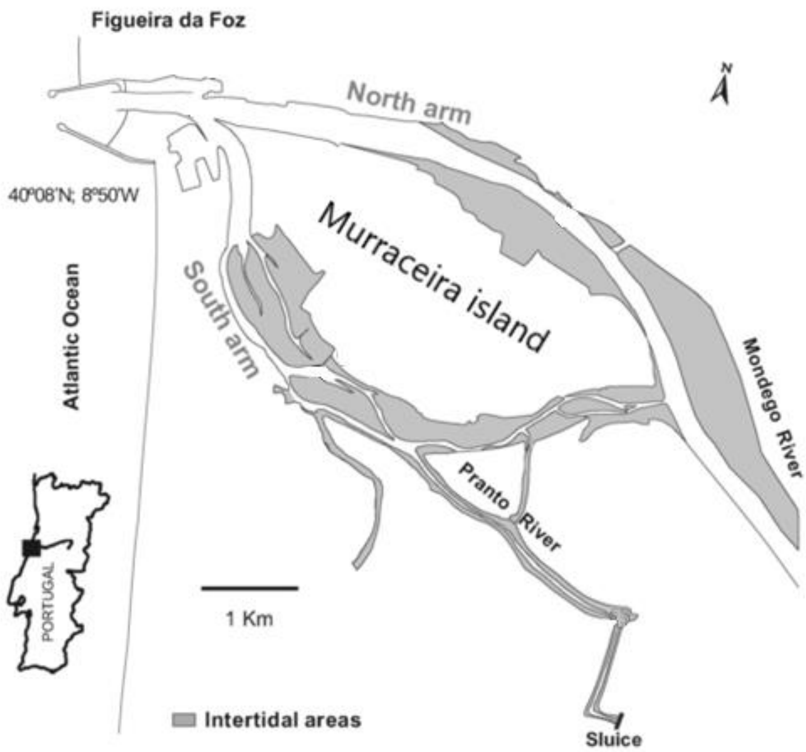

Figure 1 - Geographic localization and representation of the Mondego estuary.

1.2.2 Main impacts

Over the last few decades, the Mondego estuary has been severely disturbed. The anthropogenic activities carried out in the estuary led to changes in some specific physical characteristics (water residence time, hydrodynamics and depth). These disturbances led to a decrease in the environmental quality of the estuary, which in turn led to a decrease in the biodiversity (Baptista et al., 2015; Crespo et al., 2015).

The increase in the navigation in the commercial port of Figueira da Foz implies regular dredging of the north arm. These regular dredging contributed to a severe disturbance of the bottom of this subsystem, leading to a decrease of the benthic species present in the north arm (Baeta et al., 2005).

In addition to dredging, there are other anthropogenic impacts, such as exploitation of economically valuable living resources, like fish and invertebrates (Baeta et al., 2005). Morphological modifications of the estuary and the adjacent coastal strip, mainly as a result of the construction of jetties near the port and of coastal protection works (Cunha et al., 1997) leading to an alteration of the sedimentary dynamics. Moreover, urban and industrial growth over the estuarine and dune fields contribute to the destruction of dune vegetation. The development of aquaculture and rice cultivation, with a parallel decline in salt production and traditional agricultural crops (Ribeiro, 2001). Chemical impact resulting from the discharges of domestic effluents, nutrients derived from fertilizers and other chemical products coming from the agricultural crops of lower Mondego.

Many of the implications mentioned above, but especially the latter, contribute to the fact that, as in most estuaries around the world (Flindt et al., 1999; Marques et al., 2003), there has been an increase in eutrophication in the Mondego estuary since the 80s. Eutrophication, defined as excessive input of organic carbon associated with nutrient enrichment, from coastal waters, is now widely recognized as a major global threat (Raffaelli et al., 1991; Verdelhos et al., 2005; Dolbeth et al., 2010).

The major impacts of eutrophication on the estuary were found in the southern arm, where the *Zostera noltii* beds, which represent a habitat rich in biodiversity with higher productivity (Cardoso et al., 2004; Pardal et al., 2004; Verdelhos et al. al., 2005), were drastically reduced and replaced by macroalgae blooms, mainly constituted by *Enteromorpha* spp. This increase in green macroalgae blooms are due to the high availability of nutrients (Verdelhos et al., 2005). Since the 1980s, the *Zostera noltii* beds were drastically reduced from an area of approximately 15 hectares to less than 300 m^2 in 1997 (Cardoso et al., 2004; Pardal et al., 2004; Verdelhos et al. al., 2005), leading to severe alterations in the estuarine benthic community, and in the long term may originate a new trophic network configuration (Marques et al., 2003).

1.3 *Carcinus maenas* – General concepts

Carcinus maenas (Linnaeus, 1758) (Figure 2), commonly referred to as the European green crab, is a small decapod belonging to the family Portunidae, native to the coasts and estuaries of the Northeast Atlantic, from Mauritania to Norway, including Iceland (Crothers, 1967; Carlton & Cohen, 2003; Rewitz et al., 2004; Young et al., 2017). In the last two centuries, this species has spread its geographic distribution and settled in five major regions of the globe (Northeast, Northwest and Southwest of the Pacific Ocean, and Northwest and Southeast Atlantic Ocean) (Thresher et al., 2000). *Carcinus maenas* is considered an invader, being included in the top 100 of the most invasive species by the IUCN (Leignel et al., 2014), mainly due to their high phenotypic plasticity and high tolerance to both salinity and temperature variations. This large distribution of the green crab demonstrates its high tolerance to variations of different environmental conditions (Cosham et al., 2016; Young et al., 2017). This species presents a wide omnivore diet (Roman & Palumbi, 2004; Macdonald et al., 2018).

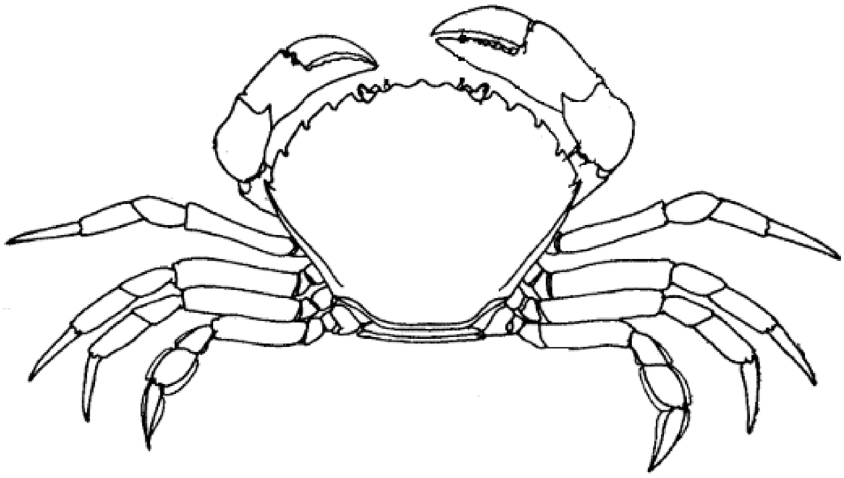

Figure *2*- Representation of the European green crab, *Carcinus maenas* (Linnaeus, 1758) (Adapted from Crothes, 1967).

Carcinus maenas presents two distinct phases in its life cycle, a larval stage and a benthic stage. The larval stage, like in most estuarine crustacean decapods, occurs in coastal waters and lasts around two months (Amaral et al., 2007), and consists of four zoeae stages and a larval megalopae stage (Rice & Ingle, 1975). Zoeaes are planktonic organisms, which feed and grow in the pelagic realm and remain in this environment for 18 to 42 days, depending on the water temperature (Berrill, 1982; Dawirs, 1985; Young & Elliott, 2018). Afterwards, in the megalopae stage, larvae leave the planktonic life and recruit on the benthos, thus passing into a benthic life inside estuaries. This stage takes between 9 and 16 days, also varying according to the water temperature (Crothers, 1967; Queiroga et al., 1997). The megalopae stage, presents two types of locomotion, being able to swim or to walk on the substrate. This type of mixed locomotion is typical to transition stages between the pelagic and benthic part of the lifecycle. The final settlement of the megalopae occurs in the upstream areas of the estuary (Baeta et al., 2005), in areas that offer good feeding and growth conditions (Klein-Breteler, 1975). To move to the nursery areas, the larvae use the tides as a means of transport (Queiroga et al., 1994; Moksnes et al., 2014). In the case of the Mondego estuary, the main nursery areas for this species are located near the Pranto River (Baeta et al., 2005) (Figure 3).

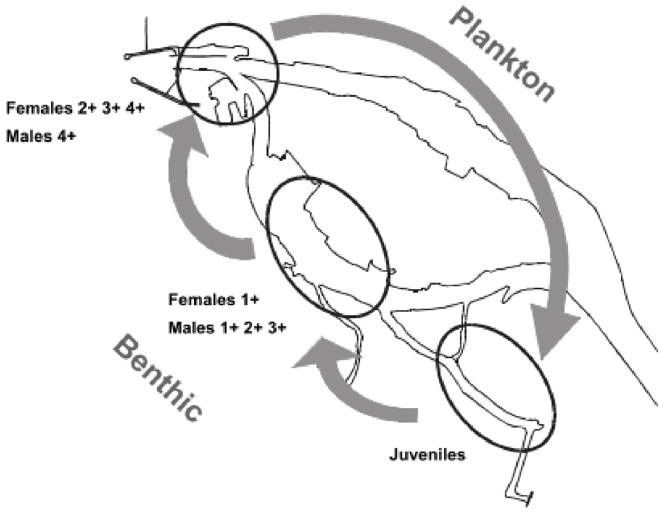

Figure 3- The *Carcinus maenas* life cycle in the Mondego estuary (Adapted from Baeta et al., 2005)

After the larval stages, at the beginning of benthic development, there will be a development of sexual characteristics throughout growth. The abdomen of the females will broaden and round, and in turn the males' abdomen will narrow into a triangular shape and will merge the 3rd, 4th and 5th segments (Figure 4) (Demeusy, 1958). Male chelae also become wider, and males will exhibit more aggressive behaviour (Crothers, 1967).

Since it is a crustacean, the growth in *Carcinus maenas* is discontinuous, being carried out through moult. The moult consists on the formation of a new exoskeleton under the old exoskeleton, with the exposure of the old exoskeleton and the consolidation of the new one with the deposition of calcium salts (Crothers, 1967; Reid et al., 1997).

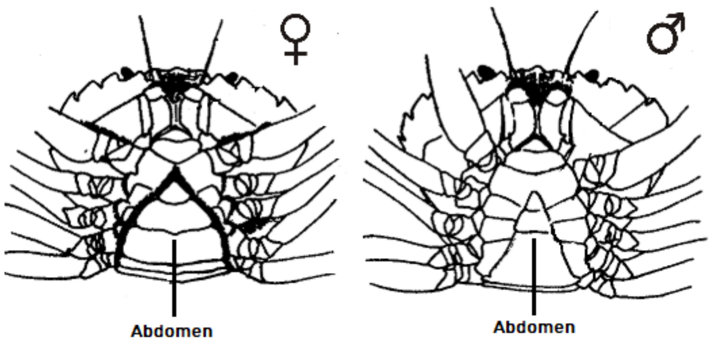

Figure *4*- Sexual dimorphism, broad and round abdomen in females and narrow and triangular in males (Adapted from Crothes., 1967).

Juveniles will remain in nursery areas, where they have a high abundance of food resources and protection against predators until they become adults. During their ontogenic development, *C. maenas* carry out many carapace moults, allowing them to grow. This growth depends directly on the environmental conditions. Although the green crab is an eurythermal species (Broekhuysen, 1936; Klassen & Locke, 2007), *C. maenas* will not be able to carry out moult at temperatures below 10ºC, which will prevent it from growing (Berrill, 1982). *Carcinus maenas* is also an euryhaline species, tolerating a wide salinity range between 4 and 54 ‰ (Broekhuysen, 1936; Crothers, 1967). Variations in salinity and temperature influence the development of their eggs, as the lower limit of salinity for the development of the eggs is 20 ‰ at 16ºC and 26 ‰ at 10ºC, thus increasing the limit with the decrease of the temperature (Dawirs, 1985). It is necessary to consider the synergistic effects of temperature and salinity, because due to unfavourable stress values of one of the variables, can influence a reduction in survival and changes in the population abundance of *C. maenas* even if the other variable presents optimal values (Young & Elliott, 2018).

The green crab reaches sexual maturity at different sizes according to the geographic location. In the Mondego estuary, sexual maturity is reached with a carapace width (CW) of approximately 30 mm for females (Baeta et al., 2005). Mating in this species can only occur immediately after the moulting of the females while the exoskeleton is not completely calcified, while in turn, males are able to mate with the fully consolidated exoskeleton (Crothers, 1967; Reid & Naylor, 1994). Males can recognize a female that is in moult, through pheromones released before moulting by the female (Eales, 1974; Klassen & Locke, 2007). Due these pheromones the male is always close to the female before and during the moulting, and after the copula to secure the female from other males (Young & Elliott, 2018). After the copula, the female lays the eggs that will be transported during some months, depending on the physical-chemical characteristics in which it is found (Broekhuysen, 1936).

The European green crab presents a variation in its morphotype: although it is called "green crab" it exhibits a range of carapace colours from green to red. It is important to point out that after the moult, the crabs present a green carapace, and that in physiological terms this tends to obtain a red colour, due to the photo-denaturation of the pigment astaxanthin (pigment present in the carapace), that when denaturated it obtains a red colour (Lee, 1977; Styrishave et al., 2004). The difference in coloration is indicative of the duration of intermoult time (individuals with a longer intermoult time present a red morphotype) (Reid et al., 1997; Costa et al., 2013).

In addition to variations in carapace colour, it is possible to observe that in individuals of the same size, those with a red morphotype, have a thicker carapace and a stronger and heavier chelae, which confers an advantage during mating and foraging, compared to crabs with green morphotype (Reid et al., 1997). Nevertheless, red crabs are less tolerant to environmental variations and osmotic extremes, thus being restricted to subtidal areas near the downstream section of rivers. According to Styrishave et al., (2004), two steps are present on the *C. maenas* life-cycle. The male juveniles tend to perform several moults and thus grow quite fast, but when reaching sexual maturation tend to increase the time of interchange in order to be able to have a greater capacity of mating.

Migrations of *C. maenas* occur within the estuaries, being most juveniles found in the upstream areas, in the case of the Mondego river, near the Pranto River, since the juveniles present low tolerance to high salinities. With the increase of size and over the years, they will migrate to downstream, near the mouth (Baeta et al, 2005). In addition to these migrations, intertidal migrations are also performed, presenting different responses and behaviours, according to sex, size and morphotype (Hunter & Naylor, 1993; Cosham et al., 2016). These features of the *C. maenas* behaviour allow them to be present along the estuary, and according to its state of development, will have a greater capacity to resist the environmental variation (Bessa et al., 2010).

Carcinus maenas is an opportunistic omnivore that feeds on a wide variety of prey (Cohen et al., 1995; Mcdonald et al., 2001). In several estuarine areas, it can be considered a benthic top predator (Baeta et al., 2006; Amaral et al., 2009; McGaw et al., 2011), having a high impact on the structure of the estuarine benthic communities (Grosholz et al., 2000; Macdonald et al., 2018).

There is a continuing need for long-term data-sets (LTDs), since they allow to evaluate the impact of extreme climatic events on species and to help in the management of water resources (Wood & Armitage, 2004). In addition, LTDs help to make wise decisions on habitat management and conservation. Through LTDs analysis it is possible to check environmental trends and responses of biodiversity. This represents an important contribution to understanding how ecosystems respond to natural and anthropogenic processes, and how this knowledge should be applied to develop better strategies to improve environmental quality (Holmes, 2006).

1.4 Objectives

Over the last few years, extreme climate events led to changes in the macrobenthic structure of the Mondego estuary and to an increased pressure in the species presents in this ecosystem. *Carcinus maenas* is considered a key species in this estuarine ecosystem, so it is important to have a comprehensive view on the long-term effects of extreme climate events on this species. Therefore, the main objectives of the present study were:

1. To describe the population dynamics of *Carcinus maenas* in the Mondego estuary in the period 2003-2018 (except 2011 and 2012) in terms of:

- Temporal and spatial abundance patterns;
- Population structure and sex ratio;
- Morphological characteristics;
- Secondary production;

2. To evaluate the impact of extreme climatic events (drought and floods) on the *C. maenas* population dynamics.

3. To compare the morphological and reproductive characteristics of the green crab populations throughout several latitudes (native and non-native populations).

2. Material and methods

2.1 Sampling programme

The population of *Carcinus maenas* was sampled monthly in the Mondego estuary (Figure 5) from June 2003 to December 2018, at four stations (Mouth, South arm, Pranto River, and North arm). Data between August 2010 and April 2013 were not available for this study, and hence were not considered.

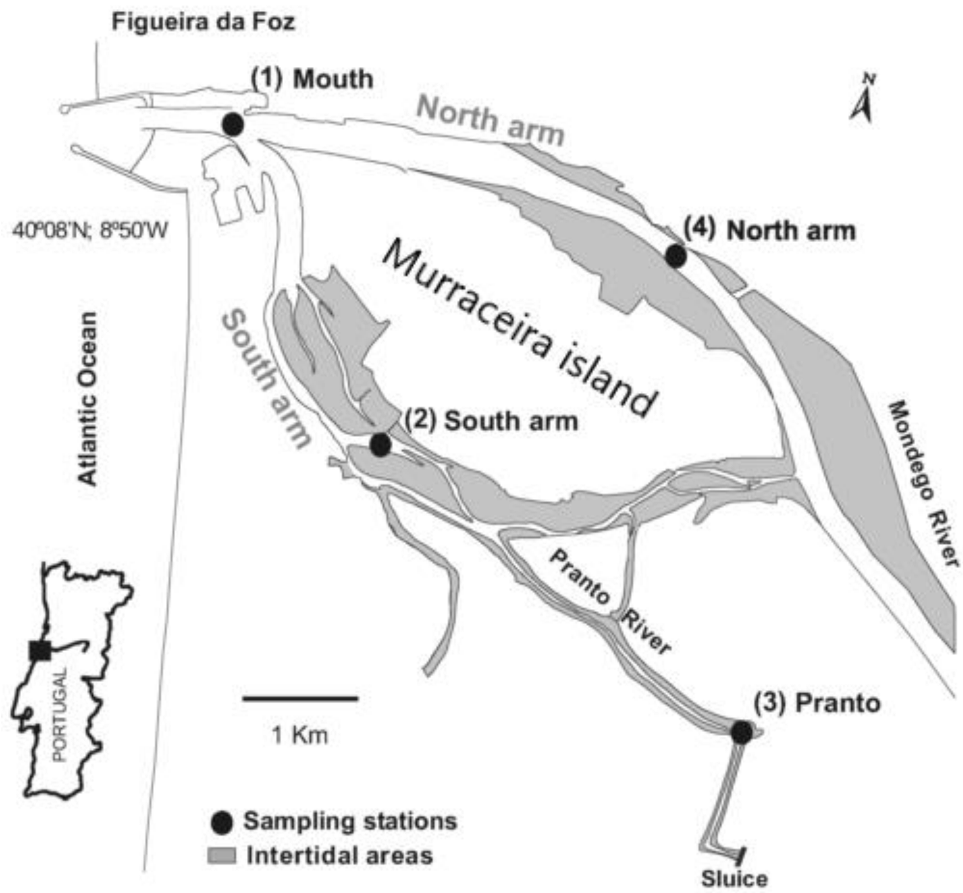

Figure 5- Geographical location of the Mondego estuary and the 4 local sampling sites, Mouth, South arm, Pranto River and North arm.

Sampling of *Carcinus maenas* was performed during the night, at high water of spring tides, using a 2 m beam trawl with one tickler chain and 5 mm mesh size in the cod end. At each station, three hauls were towed for an average of 5 min each, covering at least an area of 500 m^2, the distance travelled in each trawl was determined using a GPS. Still in the boat, the crabs were separated from the remaining sample and placed in iceboxes. At each sampling station, after fishing took place, the bottom water was analysed for temperature, salinity, dissolved oxygen and pH. Upon arriving at the laboratory, the crab samples were frozen until further analysis.

2.2 Laboratory procedures

In the laboratory, all captured crabs were counted and measured (maximum width of cephalothorax, LC, with a calliper with 0.1 mm precision, sexed (observing the presence/absence of the copulatory pleopods), the reproductive condition (occurrence of female carrying eggs), presence of parasites, the state of hardness and the carapace morphotype ("Green", "Orange" and "Red) recorded. The juveniles were analysed with a binocular loupe with ruler, to verify the width of the cephalothorax and to observe the presence or absence of the copulatory pleopods. In total, 79959 crabs were analysed, being 50732 males and 29227 females.

The density (ind/1000m^{-2}) and biomass (g AFDW/1000m^{-2}) of *Carcinus maenas* were determined for each sampling site. Biomass was calculated using the regression equations for this species from the Mondego estuary (equations 1 and 2; Baeta et al. 2005). The biomass was then calculated using the following equations for both males and females, which relate the cephalothorax width (LC), and the biomass (W) expressed in g.m^{-2} ash-free dry weight (AFDW):

$$\mathrm{W} = 0.00005 * \mathrm{LC}^{2.885} \quad (\mathrm{Males}) \qquad \text{equation 1}$$

$$\mathrm{W} = 0.00005 * \mathrm{LC}^{2.8586} \quad (\mathrm{Females}) \qquad \text{equation 2}$$

Environmental data, including total precipitation (monthly, seasonal and annual) and the occurrence of weather extremes (e.g. heat waves) were obtained from the Instituto Português do Mar e da Atmosfera (IPMA, I.P.; http://www.ipma.pt/pt/oclima/boletins/). Monthly runoff values for the Mondego river were obtained from the "Açude de Coimbra 12G/01A" station of the Sistema Nacional de Informação de Recusos Hidricos (SNIRH; https://snirh.apambiente.pt/). Monthly records of the North Atlantic Oscillation index (NAO) were provided by the University Corporation for Atmospheric Research (https://climatedataguide.ucar.edu/climate-data/hurrell-north-atlantic-oscillation-not-index-pc-based).

2.3 Data analysis

2.3.1 Analysis of population structure

The population structure of *C. maenas* was defined by size-frequency distribution across 76 classes of cephalothorax width. Each class size is 1 mm width and were studied through analysis on successive sample dates between 2003 and 2018 (data between August 2010 and April 2013 were not available for this study), at four sampling stations (Mouth, South arm, Pranto River and North arm). The density, biomass, sex ratio, number of juveniles and morphotypes of the population were analysed through graphs, where were represented as an average in each date and its standard derivation. Subsequently, these values were compared with climatic characteristics (dry, regular and rainy years), to purchase the significance of the results obtained, 1-way ANOVAs were performed using STATISTICA 7 software. A significance level of 0.05 was considered in this analyse.

To observe differences in the sex ratio throughout the life cycle, size classes were created with a scale of 15 mm (0-15 mm, 15-30 mm, 30-45 mm, 45-60 mm, 60-76 mm). After the classes were created, the percentage of males in the population (males / females) was calculated for each sampling date. Finally, to purchase the significance of the results obtained, 1-way ANOVAs were performed.

2.3.2 Secondary production

Annual average secondary production in the Mondego estuary was estimated according to the size-frequency method modified by Benke (1979) for the 15-year study period:

$$P = \mathrm{a}\left[\sum_{\mathrm{j}=1}^{\mathrm{a}-1}(\overline{\mathrm{N}}_{\mathrm{j}} - \overline{\mathrm{N}}_{\mathrm{j}\,+\,1}) \times \sqrt{(\overline{\mathrm{W}}_{\mathrm{j}} \times \overline{\mathrm{W}}_{\mathrm{j}\,+\,1})}\right]\frac{365}{\mathrm{CPI}}$$

- a → Number of size classes;
- $\overline{N}$ j → Mean density (ind * $1000m^{-2}$) in size class j;
- $\overline{N}$ j+1 → Mean density (ind * $1000m^{-2}$) in size class j+1;
- $\overline{W}$ j → Mean individual weight (g AFDW) in size class j;
- $\overline{W}$ j+1 → Mean individual weight (g AFDW) in size class j+1;
- j and j+1→ Consecutive size classes (j = 1, 2, …, a);
- CPI → Production interval between classes, development time is from hatching to death of the largest size category (average life expectancy of the species in days).

After calculating the secondary productivity value, the $P/\overline{B}$ ratio value was calculated using productivity and average biomass values.

2.3.3 Spatial distribution

The spatial distribution of the population was evaluated in relation to the environmental variables. For this step, a multivariate analysis was performed, being used a redundancy analysis (RDA) because the data were linear ($SD < 3$), it was performed with the software Canoco (version 4.5) (Ter Braak and Smilauer, 1988). The biological data were separated by size classes, morphotypes and sex. The abiotic parameters used in this analysis were temperature, salinity and precipitation. This analysis was performed for both biomass and density values. The density and biomass data were averaged by sampling stations (Mouth, South arm, Pranto River and North arm) and years. Subsequently, different years were classified as dry, normal or rainy, according to information from the Instituto Português do Mar e da Atmosfera (IPMA, I.P.; http://www.ipma.pt/pt/oclima/boletins/).

2.3.4 CUSUM analysis

To detect points of change in the population and in the hydro-climatic parameters, the cumulative sum (CUSUM) of the mean deviations were calculated from the reference period from 2003 to 2018. The interpretation was based on the sign and slope of the line that reflects the deviation of a certain period in relation to the average value of the time series (Ibañez et al., 1993; Marques et al., 2014). Afterwards, to understand the main processes that may have triggered these changes, were identified the multiple abiotic factors that were responsible for the biological variations, Pearson correlation analyses were performed using STATISTICA 7 software, a significance level of 0.05 was considered in this analyse.

3. Results

3.1 Characterisation of the sampling areas

During the 16 years of study, considerable variations were observed in the precipitation and in the flow of the freshwater. Some of these variations were caused by the existence of extreme climate events leading on variations of runoff. One of the greatest extreme climatic events in Portugal occurred in 2004/2005, when the country was under an extreme drought scenario. This was caused by a lower precipitation in comparison to the normal climatological in this period, which caused a significant reduction in river runoff (Figure 6). In addition, the years 2007, 2008, 2015 and 2017 were also classified as dry years by IPMA. In contrast, 2010, 2014 and 2016 were considered as very rainy years, with high precipitation and consequently a higher river flow (Figure 6). Due to extreme climate events and changes in the freshwater flow to the estuary, the physical-chemical parameters also underwent major changes. For example, in the case of floods, there was a decrease in salinity, and the opposite was observed during drought periods (Table 1).

It was also possible to observe the existence of a typical estuarine gradient (Table 1), where salinity and dissolved oxygen increase, and the water temperature decrease from upstream to downstream areas. The mean salinity registered at Mouth, South arm, Pranto River and North arm was 30.5, 30.5, 23.4 and 18.8, respectively.

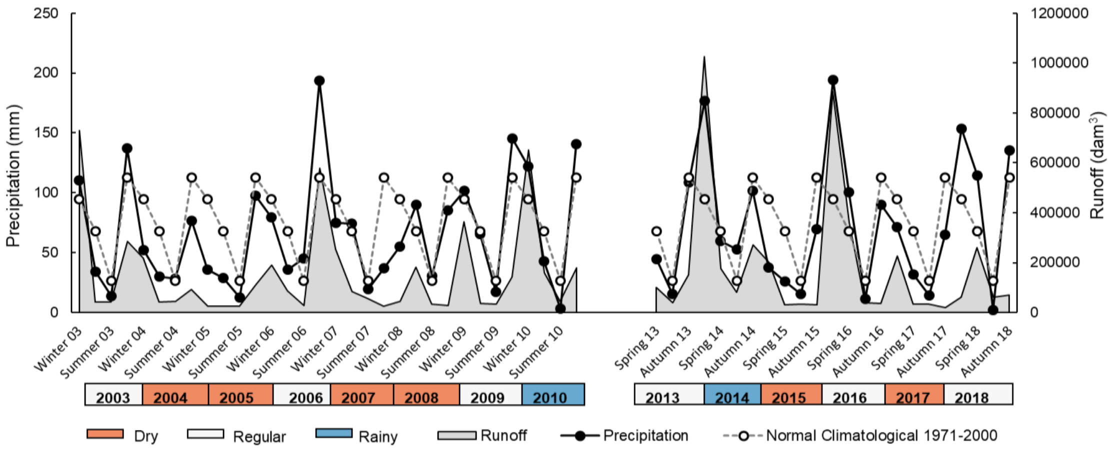

Figure 6 - Seasonal precipitation and river runoff values from Winter 2003 to Autumn 2018 plotted against the normal climatological average precipitation values from 1971 to 2000. The black line represents the seasonal precipitation (mm), the grey line represents the normal climatological in each season (mm), the area in grey represents the average river flow (dam^3); orange represents the dry years, the white the regular years and the blue the rainy years.

Table 1- Mean environmental characteristics ± standard deviation of the sampling areas through the fourteen years study (2003 to 2018, except 2011 and 2012).

Year	Mouth			South arm			Pranto River			North arm		
	Temperature (Cº)	Salinity	Dissolved oxygen (mg/L)	Temperature (Cº)	Salinity	Dissolved oxygen (mg/L)	Temperature (Cº)	Salinity	Dissolved oxygen (mg/L)	Temperature (Cº)	Salinity	Dissolved oxygen (mg/L)
2003	16.9 ± 2.3	30.8 ± 3.0	9.7 ± 1.6	18.1 ± 3.1	28.5 ± 4.9	8.8 ± 1.5	19.5 ± 4.8	23.2 ± 4.8	7.3 ± 1.4	18.2 ± 3.3	19.2 ± 7.6	8.2 ± 1.6
2004	14.7 ± 1.7	31.4 ± 3.5	9.9 ± 1.2	15.8 ± 2.0	30.1 ± 3.4	9.5 ± 0.8	17.3 ± 4.6	23.5 ± 4.3	8.6 ± 1.6	16.0 ± 3.1	21.5 ± 5.4	9.4 ± 1.0
2005	15.1 ± 2.8	32.5 ± 2.1	10.2 ± 1.3	15.3 ± 3.3	32.2 ± 4.1	9.5 ± 1.1	17.7 ± 5.4	29.4 ± 4.4	8.0 ± 1.5	15.9 ± 3.9	24.6 ± 6.1	9.0 ± 1.1
2006	15.2 ± 3.4	25.5 ± 9.8	9.5 ± 0.7	15.8 ± 3.0	28.5 ± 8.0	9.4 ± 0.9	18.4 ± 5.3	21.9 ± 6.3	7.8 ± 1.5	16.2 ± 4.1	17.4 ± 10.8	8.8 ± 1.0
2007	14.8 ± 1.0	33.9 ± 2.4	9.2 ± 1.0	15.3 ± 1.7	32.0 ± 2.8	9.3 ± 0.7	18.6 ± 3.3	27.4 ± 4.3	8.4 ± 1.7	15.3 ± 1.6	30.3 ± 5.1	8.6 ± 0.6
2008	15.9 ± 1.8	35.2 ± 0.7	8.9 ± 1.3	18.5 ± 5.1	34.1 ± 1.1	8.2 ± 1.2	19.7 ± 4.5	29.5 ± 2.1	7.1 ± 1.1	16.3 ± 2.4	30.8 ± 2.1	8.2 ± 1.0
2009	14.6 ± 2.3	30.4 ± 6.5	9.5 ± 0.9	15.1 ± 2.0	32.1 ± 3.6	9.1 ± 1.0	18.6 ± 4.8	26.0 ± 5.1	7.7 ± 1.4	15.3 ± 2.7	27.9 ± 5.7	9.2 ± 1.0
2010	15.2 ± 2.3	27.3 ± 5.5	9.1 ± 1.5	15.5 ± 1.5	32.0 ± 2.5	9.1 ± 0.9	20.1 ± 4.8	19.5 ± 7.6	8.3 ± 1.6	15.7 ± 3.1	20.5 ± 8.5	8.9 ± 1.5
2013	15.9 ± 1.6	31.2 ± 2.2	9.7 ± 1.2	16.3 ± 1.6	32.6 ± 0.6	9.8 ± 0.7	22.0 ± 4.6	25.9 ± 2.7	8.7 ± 1.2	19.1 ± 3.5	14.0 ± 6.9	9.0 ± 1.3
2014	15.9 ± 2.6	23.0 ± 12.6	7.5 ± 2.4	16.2 ± 2.8	27.6 ± 10.0	7.6 ± 2.1	20.4 ± 5.3	13.5 ± 9.9	6.7 ± 2.3	17.3 ± 3.7	7.1 ± 9.5	7.8 ± 2.4
2015	15.5 ± 1.5	33.2 ± 0.9	7.4 ± 0.6	16.1 ± 1.6	32.9 ± 1.5	8.7 ± 0.9	19.0 ± 4.4	25.1 ± 5.1	7.5 ± 2.0	17.5 ± 4.4	12.1 ± 6.7	6.8 ± 1.0
2016	15.4 ± 1.4	28.1 ± 7.2	7.7 ± 0.6	15.8 ± 2.2	26.8 ± 7.4	7.6 ± 1.3	19.4 ± 5.5	19.2 ± 6.7	6.5 ± 1.8	17.8 ± 4.1	9.3 ± 9.8	7.6 ± 1.0
2017	14.7 ± 1.3	31.4 ± 4.6	9.0 ± 0.8	16.4 ± 1.6	31.9 ± 1.5	9.2 ± 0.5	21.7 ± 4.3	23.4 ± 6.4	8.3 ± 0.4	16.4 ± 3.9	14.1 ± 10.3	8.6 ± 1.0
2018	15.1 ± 2.1	33.2 ± 1.0	8.7 ± 0.6	15.3 ± 2.4	28.6 ± 5.7	9.4 ± 0.8	18.7 ± 4.6	18.9 ± 8.6	7.9 ± 1.0	16.2 ± 3.5	15.7 ± 10.1	8.8 ± 1.2

3.2 Characterization of *C. maenas* population

3.2.1 Juveniles

While the presence of juveniles (LC < 15 mm) in the Mondego estuary was observed throughout the year, recruitment peaks were mainly detected in the spring, due to the breeding season in the winter. Most juveniles were found in the Pranto River (Figure 7) throughout the study. In addition, it was possible to observe a high peak in juvenile density in spring 2009.

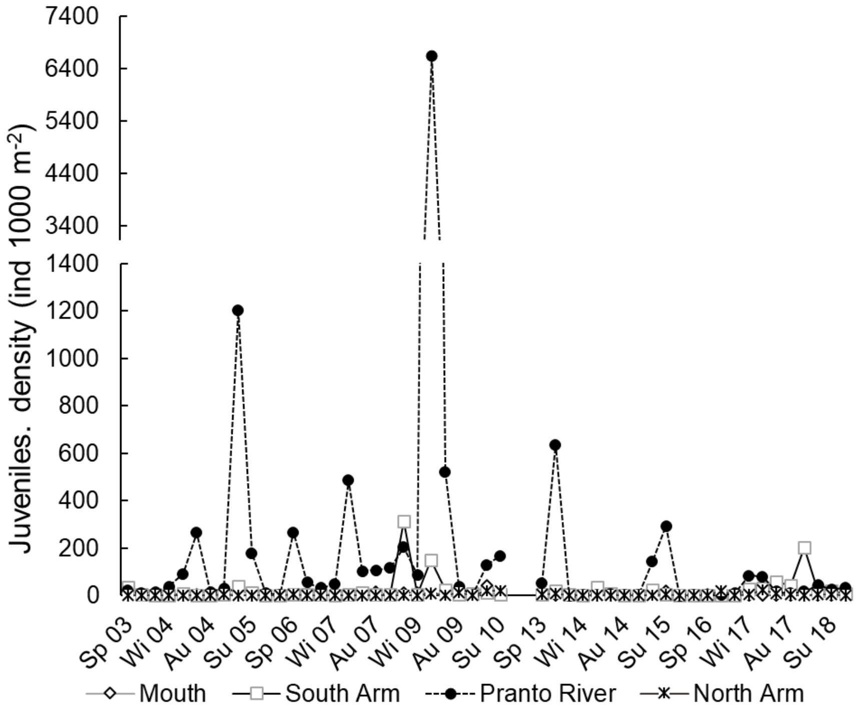

Figure 7- *Carcinus maenas*. Seasonal variation in the density of juveniles less than 15 mm (LC) between Spring 2003 and Autumn 2018, except for the period between Summer 2010 and Winter 2013.

Annually it was observed that most juveniles were present in the Pranto River station, and that during the dry years (2004, 2005, 2007, 2008) there was a higher density and biomass of juveniles in the estuary (Figure 8A, C).

Due to the higher abundance of juveniles, these were analysed in 3 size classes (less than 5 mm, between 5 - 10 mm and between 10 - 15 mm). By the analysis of juveniles present in the Pranto River, it was observed that there is a higher density of the two smaller classes. In the dry years there is a higher juveniles' density compared to the regular and rainy years (Figure 8B). The same pattern is observed when evaluated biomass (Figure 8D)

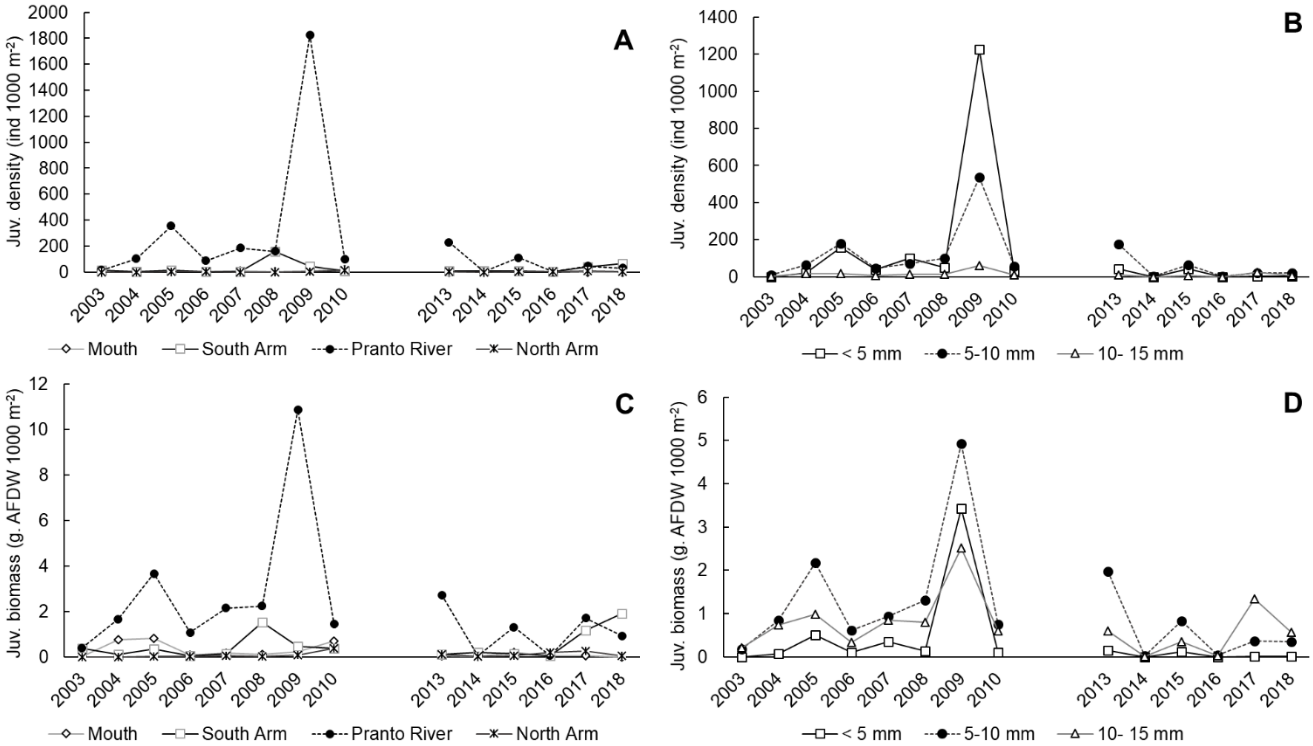

Figure 8- *Carcinus maenas*. Annual variation of juveniles with less than 15 mm (LC) between 2003 and 2018, except for 2011 and 2012.Variation of density (A) and biomass (C) of juveniles at all sampling stations; Variation of density (B) and biomass (D) of juveniles in the Pranto River station divided into three size classes, < 5 mm, between 5 and 10 mm and 10 to 15 mm.

3.2.2 Total population

The highest population density was observed in the Pranto River, with higher densities observed in the dry years: 2004, 2005, 2007, 2008 and 2017 (Fig. 9A). The highest mean annual density was obtained in 2009, with an average density of 2500 individuals/1000 m^2. Notably, most of these individuals were juveniles, as previously observed (see Figure 8). The mean density over the entire sampling period was 521 individuals/1000 m^2.

When observing the biomass variation (Figure 9B) the results were more homogeneous, not showing great differences between the stations. There was a large biomass in the Pranto River station, due to the high juveniles' density, in turn, in the south arm and north arm stations the biomass is similar to the Pranto River, because in these stations the individuals were larger. As mentioned above in dry years, the biomass is higher.

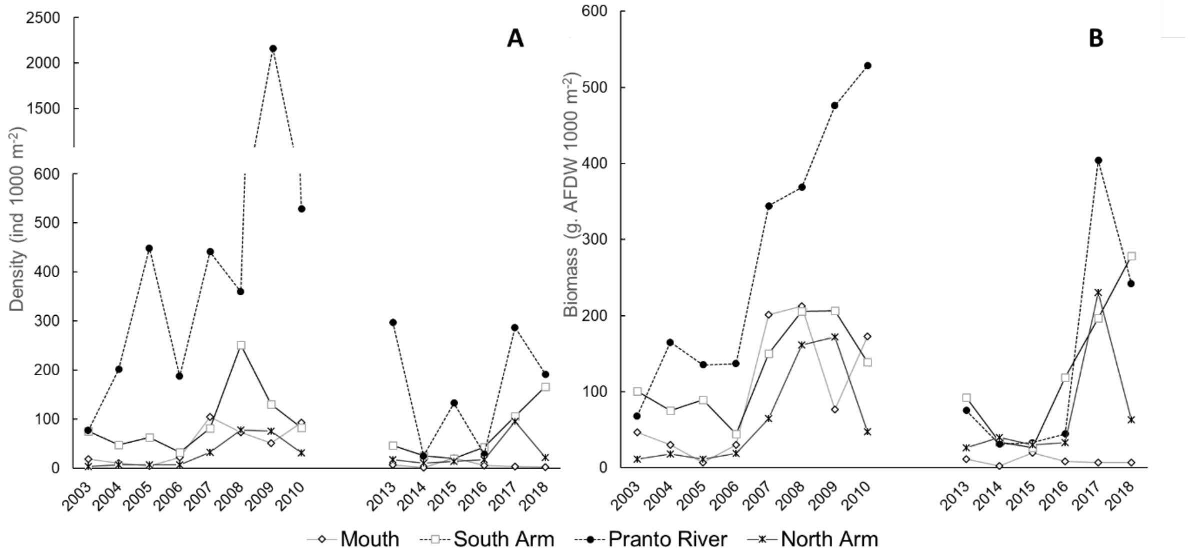

Figure 9- *Carcinus maenas.* Annual variation of density (A) and total biomass (B) along the estuary with the 4 sampling stations represented.

Analysing the 3 morphotypes of *Carcinus maenas*, it is possible to verify differences between them ($F = 899.204$; $p = 0.00$). there is a large percentage of individuals with the green morphotype in both sexes and higher percentage of individuals with orange and red morphotypes in females when compared to males (Figure 10A). Nevertheless, no differences were observed in the variations of the morphology in relation to the various climat characteristics ($p = 0.60$) (Figure 10B).

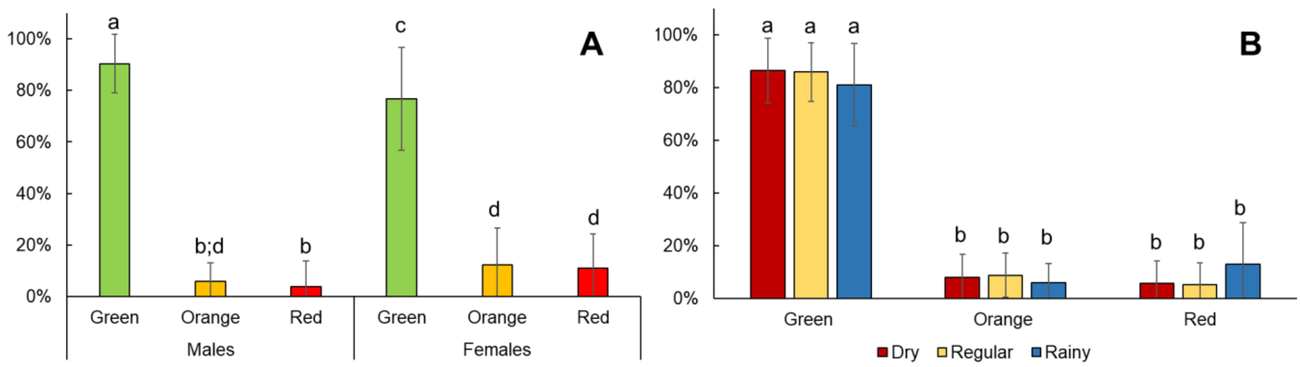

Figure 10- *Carcinus maenas*. Variation of the percentage of the three types of morphotypes (green, orange and red); According to sex (A); and according to the climate characteristics (B); a, b, c and d show the significant differences.

The percentage of males in the population (indicative of the sex ratio) was evaluated in different size classes ([0 - 15[mm, [15 - 30[mm, [30 - 45[mm, [45 - 60[mm, [60 - 80] mm). It was possible to observe the existence of significant differences according to the size class (F = 51.606; p = 0.00), with a large percentage of males being present in a first class of juveniles. Then there was a decrease in the percentage of males and approximation of a sex ratio of 1:1, and finally in the larger classes there was, once more, an increase in the percentage of males in the population (Figure 11A).

No significant differences were observed, analysing possible changes in the percentages of males in the different classes as a consequence of the different climate characteristics (F = 4.579; p = 0.000021) (Figure 11B)

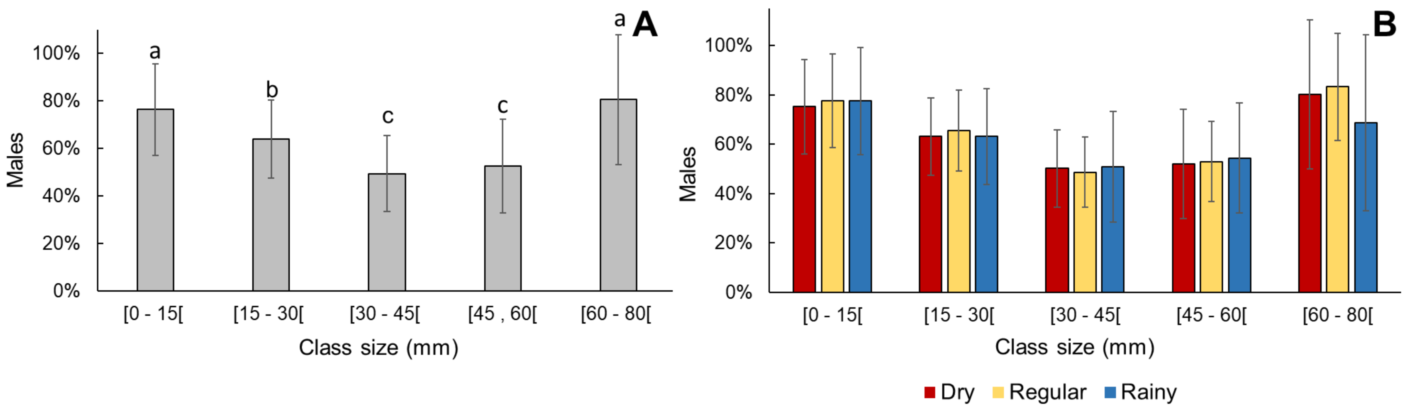

Figure 11- *Carcinus maenas*. Variation of the percentage of males along the growth, divided into 5 size classes ([0 - 15[mm, [15 - 30[mm, [30 - 45[mm, [45 - 60[mm, [60 - 80] mm); Throughout the study (A); and according to the climate characteristics (B); a, b and c show the significant differences.

3.2.3 Secondary Production

The average annual growth production (P) of the *Carcinus maenas* population variated between 67.07 g.1000m^{-2}.year^{-1} AFDW in 2013/2014 and 7032.12 g.1000m^{-2}.year^{-1} AFDW in 2008/2009 (Table 2). The secondary production and biomass varied according to the years, presenting lower values in rainy years, and contrastingly higher values in dry years, P/$\overline{\mathrm{B}}$ ratios varied between 2.08 in 2003/2004 and 32.21 in 2008/2009.

Table 2- *Carcinus maenas*. Production estimates between 2003 and 2018, except for 2011 and 2012, in the Mondego estuary.

Year	Production (g AFDW.1000m^{-2}. year^{-1})	Biomass (g AFDW. 1000m^{-2})	P/$\overline{\mathrm{B}}$ ratio
2003/2004	82.57	39.75	2.08
2004/2005	337.62	60.29	5.60
2005/2006	463.56	55.29	8.38
2006/2007	575.80	114.94	5.01
2007/2008	1415.68	227.09	6.23
2008/2009	7032.12	218.32	32.21
2009/2010	1701.05	222.61	7.64
2013/2014	296.93	40.66	7.30
2014/2015	67.07	31.84	2.11
2015/2016	135.80	35.67	3.81
2016/2017	992.46	148.00	6.71
2017/2018	933.46	164.85	5.66

3.3 Spatial distribution

The ordination diagram in Figure 12A depicts the spatial and temporal variations in the density of *Carcinus maenas* in the Mondego estuary, as well as the dominant environmental factors. This analysis was performed using the density data of the various size classes of the juveniles, the 3 types of morphotypes and both sexes according to the different sampling stations and the different years, where the environmental variables explain 33.1% of the variation. The first two axes of the redundancy analysis (RDA) explained for 98.2% and 1.5% of the total variation, respectively, and the Monte Carlo test indicated significance of the results ($p = 0.002$).

There was a clear preference in the population distribution mainly in the station of the Pranto River. The major factor influencing the density of individuals was the estuary salinity. Salinity was in direct opposition to precipitation. This leads to the fact that in years of higher precipitation, salinity in the estuary was lower, and the opposite was also observed. It was observed a clear separation between dry, regular and rainy years in what refers to the variation of salinity and precipitation, with these parameters being completely opposite. Individuals of the various size classes were predominantly in Pranto River, where the water temperature was higher and salinity was lower. Crabs with orange and red morphotypes were clearly associated with higher salinities, which occurred in drought years and in more downstream stations (Figure 12A).

Just as for the density, an ordination diagram for the biomass was constructed (Figure 12B). The Redundancy analysis (RDA) were performed using biomass data of the various size classes, morphotypes and both sexes at each sampling station and in different years, where the environmental variables explain 13.1% of the variation, furthermore, axis 1 and 2 were responsible for 91.5% and 7.0%, respectively, and the Monte Carlo test indicated significance of the results ($p = 0.024$).

It was possible to verify that most of the population was present in stations near the Pranto River. An area that presented a low salinity and a high temperature. Therefore, in these zones juvenile individuals were positively related with the temperature. It was possible to verify that the bigger the size class, the lower dependence with the temperature. The biomass of males was correlated with that of juveniles because, as previously verified (Figure 11), there was a greater number of male juveniles. Females were more closely related to salinity, therefore being found in stations with a greater salinity, stations located more downstream (Figure 12B).

A clear difference and opposition between the parameters of salinity and precipitation was observed in the diagram (Figure 12B). The flood years and the regular ones, presented a high precipitation, being in the bottom of the diagram. Whereas the dry years are at the upper part of the diagram, with higher values of salinity. Finally, it is also possible to observe through the diagram a typical estuarine gradient, because within a same year, it was possible to verified that next to the station of the mouth, there was a greater salinity when compared with the station of the Pranto River or north arm.

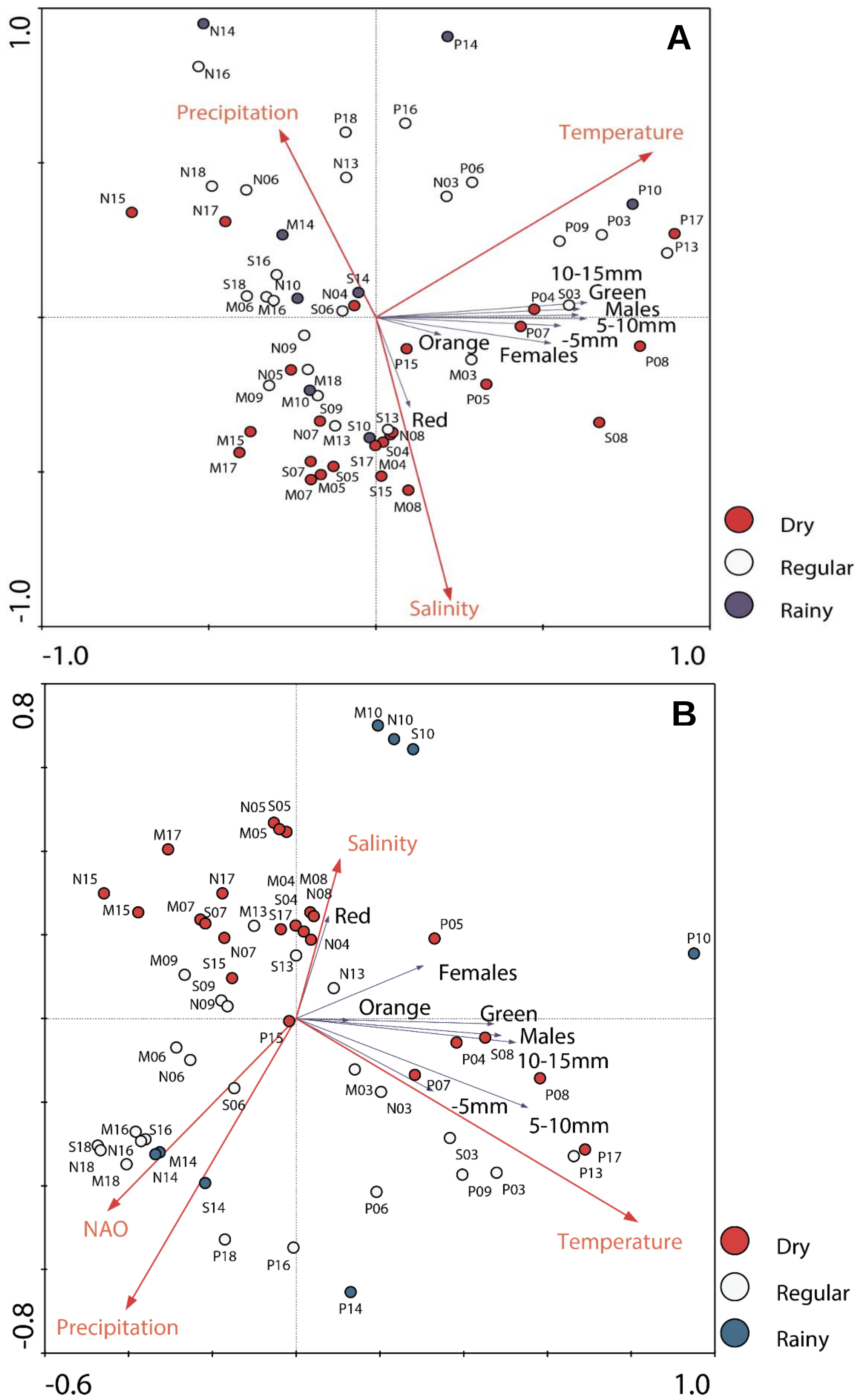

Figure 12- Ordination diagram of the redundancy analysis (RDA), using the data of the densities (A) and biomass (B) of the size classes of juveniles (< 5mm, 5 - 10 mm, 10 - 15 mm), of the three morphotypes (Green; Orange and Red) and of both sexes. Red circles correspond to dry years, white circles to regular years, and blue circles to rainy years; M- Mouth; S- South arm; P- Pranto River; N- North rm.

3.4 CUSUM analysis of *C. maenas* time-series

Considering the cumulative sums in several features of the *Carcinus maenas* population and environmental time series, different patterns emerged (Figure 13). A positive slope in the CUSUM of each time series indicates that the variable in this period was higher than the average of the whole study, and a negative slope indicates the opposite, that is, when the variable was lower than the mean.

The density of males, females and total (Figure 13 A, B, C) showed similar a trend, with an initial decline until 2005, followed by a sharp increase until 2009. After 2013 there was a decline in CUSUM density (Figure 13 A, C). The morphotypes presented different results: in case of the green morphotype (Figure 13D), there was a clear similarity to the results of the densities, with the first years of the study being below the general average but increasing afterwards. After 2013 a decline was also observable, with no values exceeding the overall mean at any date; a similar pattern was observed for the red morphotype (Figure 13F). In turn, the orange morphotype had a line decline until 2007, followed by a positive slope until 2010; after this period, once more a decrease followed until 2016, subsequently to this year and contrary to what is observed in the green and red morphotypes, a clear increase is observed (Figure 13E).

Biomass CUSUMS displayed similar patterns, with a negative slope until 2006, and, in comparison to the general average, a higher one through the years of 2007 and 2010. Once again there was a continuous decrease in biomass until 2016. After year 2016 and until the end of the study the biomass observed was higher than the average of the whole study (Figure 13 G, H, I, J, K, L).

Mean water temperature in the estuary showed a clear negative slope period up to 2007, and after this period, an upward shift was observed until 2014, when it decreased again (Figure 13M). Precipitation was highly variable throughout the time series, but with the lowest values matching the years considered dry or extremely dry: 2004, 2005, 2007, 2008, 2015, 2017 (Figure 13N). Salinity revealed an arc with a positive slope until 2010, and after 2013 all values were negative, with salinity values below the global average (Figure 13O). The NAO Index time-series showed an inverse trend with salinity (Figure 13P).

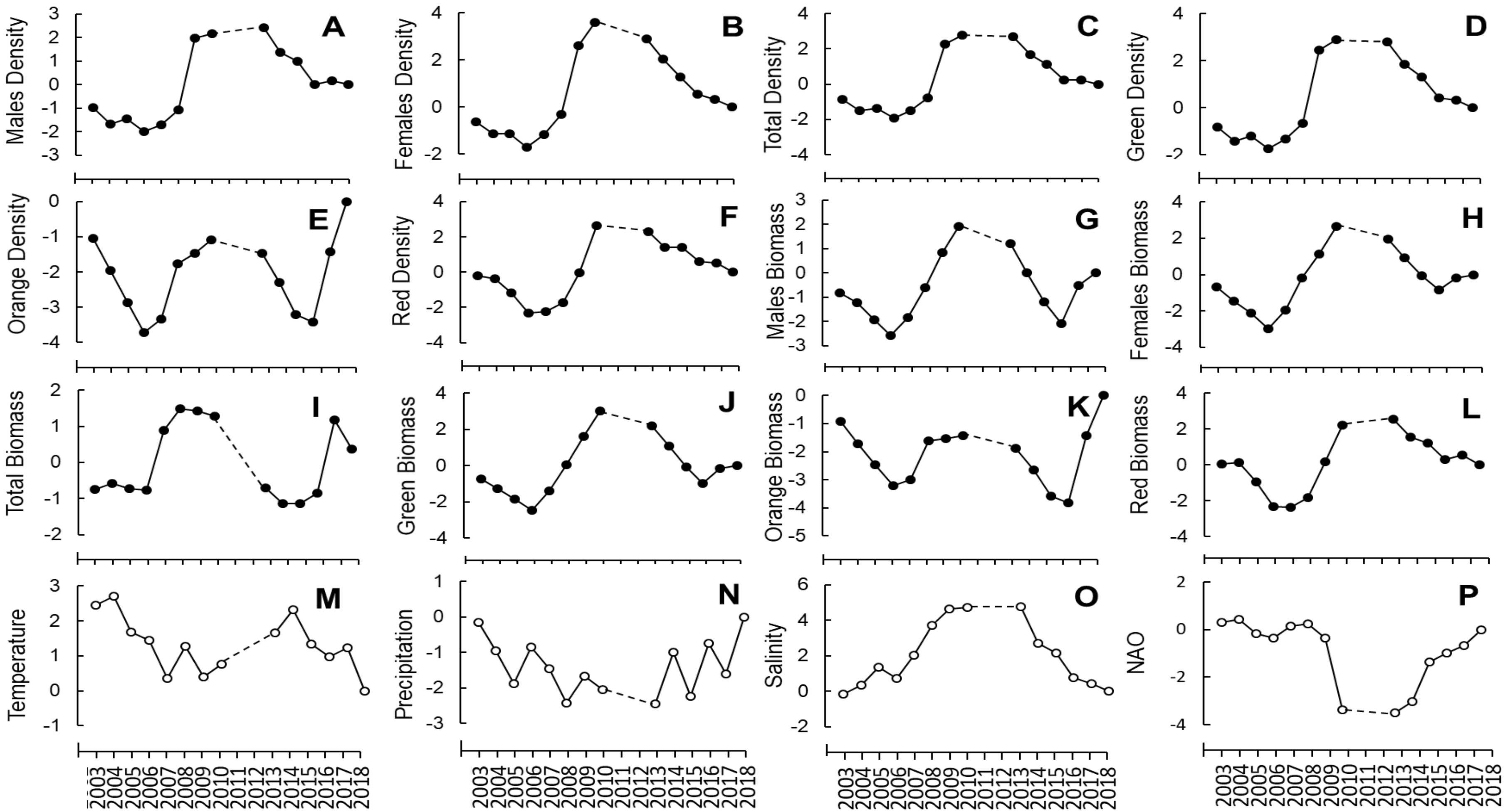

Figure 13- Cumulative sums of normal standard deviates of the *Carcinus maenas* time-series (•): (A) Males Density, (B) Females Density, (C) Total Density, (D) Green Density, (E) Orange Density, (F) Red Density, (G) Males Biomass, (H) Females Biomass, (I) Total Biomass, (J) Green Biomass,(K) Orange Biomass, and (L) Red biomass and environmental parameters (◦): (M) Water temperature, (N) Precipitation, (L) Salinity and (P) NAO Index; between 2003 and 2018, except 2011 and 2012 (dashed line).

Table 3- Pearson correlations (r) between the cumulative sums of *Carcinus maenas*, expressed as ind. 1000m^{-2}, and the environmental parameters temperature (°C), salinity, precipitation (mm) and NAO Index. Significant p-values are in bold; $^{a}0.05 > p > 0.01$; $^{b}0.01 > p > 0.001$.

	Water Temperature	**Precipitation**	**Salinity**	**NAO Index**
Male Density	-0.2087	-0.3699	**0.6874 ^{b}**	**-0.7994^{b}**
Female Density	-0.1916	-0.4188	**0.7602 ^{b}**	**-0.8216^{b}**
Total Density	-0.2022	-0.3924	**0.7216 ^{b}**	**-0.8123^{b}**
Green Density	-0.2072	-0.4068	**0.7331 ^{b}**	**-0.8168^{b}**
Orange Density	-0.1256	-0.1668	0.1088	-0.0795
Red Density	0.755	-0.2300	0.4052	**-0.8241^{b}**
Male Biomass	-0.2079	-0.2873	**0.6526 ^{a}**	**-0.6226^{a}**
Female Biomass	-0.1962	-0.3508	**0.6988 ^{b}**	**-0.7091^{a}**
Total Biomass	-0.2090	-0.3206	**0.6797 ^{b}**	**-0.6733^{a}**
Green Biomass	-0.1942	-0.4124	**0.7754^{b}**	**-0.7402^{b}**
Orange Biomass	-0.1078	0.2390	-0.202	0.1449
Red Biomass	0.1719	-0.2025	0.3786	**-0.7922^{b}**

Overall, it was observed a significant positive correlation between salinity and the majority of *Carcinus maenas* biological features, except for orange and red morphotypes, which did not correlate with salinity. In addition, a significant negative correlation between the NAO Index and the biological features of *C. maenas*, except for the orange morphotype. The remaining environmental variables did not present any clear correlation with the characteristics of *Carcinus maenas* (Table 3).

3.5 *Carcinus maenas* across the world

Due to the large distribution of *Carcinus maenas*, there are several studies on this species throughout the world. In the native populations (Table 4), it is possible to verify an increase in the maximum size of the individuals with latitude. On the other hand, in relation to the minimum size of the carapace of the females at sexual maturity, those are very similar throughout all the latitudes, varying between 28 and 36 mm. Life span tends to increase with latitude, since in Southern Europe this is 3 to 4 years and in the North, it is approximately 4 to 6 years.

Table 4- *Carcinus maenas* - Native population. Maximum size (CW, mm) and minimum size (CW, mm) reported, Female sexual maturity and the Life span in various populations of *C. maenas*. Latitude is rounded to nearest whole degree. Empty cells indicate that no data are available.[1] Van der Meerem, 1994; [2] Moksnes P.O,, 2002; [3] Moksnes et al., 2014; [4] Rasmussen E., 1973; [5] Lützen J., 1984; [6] Dries & Adelung, 1982; [7] Jungblut et al., 2017; [8] Behrens Yamada, 2010; [9] McGaw, I.J., 2011; [10] Hunter & Naylor, 1993; [11] Reid et al., 1994; [12] Broekhuysen G.J., 1936; [13] Naylor, 1962; [14] Demeusy, 1963; [15] Baeta et al., 2005; [16] Bessa et al., 2010; [17] Present study

	Location	Latitude	Maximum size (CW)		Sexual maturity (CW Female)	Life span	Reference
			Male	Female			
Native European Population	Herdla, Norway	60º N			28		[1]
	Gullmarsfjord, Swedish	58º N	100				[2] [3]
	Isefjord, Denmark	56º N	92		30		[4] [5]
	Heligoland, Germany	55º N	100				[6] [7]
	Menai Strait, UK	53º N	83.1	74.1			[8] [9]
	Ynys Faelog, Menais Strait, N. Wales	53º N	82	65			[10] [11]
	Den Helder, Netherlands	53º N	86	70	36	4 - 6 years	[12]
	Swansea, S. Wales	52º N	86	70		3 - 4 years	[13]
	Luc-Sur- Mer, France	49ºN			12	3 - 4 years	[14]
	Mondego estuary, Portugal	41ºN	71	75	29	3 - 4 years	[15] [16]
	Mondego estuary, Portugal	41ºN	78	76	27		[17]

The population of the Northwest Atlantic does not present a variation as large as the native population, since it also has a lower latitudinal distribution (Table 5). Comparing with the native population, the sexual maturity also presents superior CW values of about 35mm. The life span in the population of NW Atlantic is of 5 to 6 years.

The non-indigenous population of the Northeast of the Pacific presents fairly high values of carapace size, between 100 and 113mm. In turn the life span is identical to that of the native population, from 3 to 4 years. Finally, the populations of Argentina and South Africa present values quite similar to those recorded in the native population.

Table 5- *Carcinus maenas* – Non-native population. Maximum size (CW, mm) and minimum size (CW, mm) reported, Female sexual maturity and the life span in various populations of *C. maenas*. Latitude is rounded to nearest whole degree. Empty cells indicate that no data are available.[1]Best et al., 2017; [2]Cameron & Metaxas 2005; [3]Tremblay et al., 2006; [4]Audet et al., 2008; [5]Macdonald et al., 2018; [6]Quinn B., 2018; [7]Berrill, 1982; [8]Fulton et al., 2013; [9]Young et al., 2017; [10]Jamieson et al., 2002; [11]Kelley et al., 2015; [12]McGaw et al., 2011; [13]Gillespie et al., 2007; [14]Behrens Yamada S., 2001; [15]Hidalgo et al., 2005; [16]Vinuesa J., 2007; [17]Le Roux et al., 1990

	Location	Latitude	Maximum size (CW)		Sexual maturity (CW Female)	Life span	Reference
			Male	Female			
NW Atlantic	Placentia Bay, Newfoundland, Canada	48º N	79	72	37		[1]
	Bras d'Or Lakes, Nova Scotia, Canada	46º N	91		40		[2] [3]
	Basin Head, Prince Edward Island, Canada	46º N	89,76	76,44	36,9	5 - 6 years	[4]
	Clarke Head, Bay of Fundy, Canada	45º N	86				[5] [6]
	Boothbay Harbor, Maine, US	44º N	82	70	34	5 - 6 years	[7]
	Great Bay Estuary, New Hampshire, US	43º N	91	75			[8]
	Hampton-Seabrook Estuary, New Hampshire, US	43º N	78	88	36		[8]
	Salem Sound, Massachusetts, US	42º N	80,5	85,9			[9]
NE Pacific	Little Espinoza Inlet, British Columbia, Canada	50º N	80,3				[10]
	Pipestem Inlet, British Columbia, Canada	49º N	113				[11]
	Barkley Sound, British Columbia, Canada	49º N	106	85,4			[12]
	Vancouver Island, British Columbia, Canada	49º N	98	76			[13]
	Oregon, US	43 - 45º N	99	79		3 - 4 years	[11]
	California, US	36 - 38º N			34		[14]
Argentina	Camarones Bay, Patagonia	45º S	81,4	71,4	39,9		[15]
	San Jorge Gulf, Patagonia	45º S	73,4	64,3	45,8		[16]
South Africa	Table Bay Docks, Cape Town	34ºS	84	56			[17]

Observing the reproductive time, female ovigerous and recruitment of the native population (Table 6), there is a continuous recruitment throughout the year in Southern Europe, and a decrease in the period of reproduction, in the recruitment period and of the presence of ovigerous female with an increase in latitude.

Table 6- *Carcinus maenas* - Native population. Seasonality of reproductive events in different populations. Empty cell indicate no data are available for that location.[1]Van der Meerem, 1994; [2] Moksnes P.O., 2002; [3]Moksnes et al., 2014; [4]Dries & Adelung 1982; [5]Jungblut et al., 2017; [6]Broekhuysen G.J, 1936; [7]Naylor, 1962; [8]Amaral et al., 2009; [9]Demeusy, 1963; [10]Queiroga, H. 1994; [11]Baeta et al., 2005; [12]Bessa et al., 2010; [13]Amaral et al., 2007

	Location	Latitude	Reproduction	Female Ovigerous	Larvae Released	Reference
Native European Population	Herdla, Norway	60º N		January		[1]
	Gullmarsfjord, Swedish	58º N	August to September		July to September	[2] [3]
	Heligoland, Germany	55º N	August			[4] [5]
	Den Helder, Netherlands	53º N	July to September	November to December	February to July	[6]
	Swansea, S. Wales	52º N	August to September	February to June	June to October	[7]
	Kingbridge estuary, Salcombe, England	50º N			July to September	[8]
	Luc-Sur- Mer, France	49ºN	May to November	November to July	June – October	[9]
	Ria de Aveiro, Portugal	40º N	March to October	All year	April to October	[10]
	Mondego estuary, Portugal	40º N		All year	All year	[11] [12]
	Mira estuary, Portugal	37ºN		All year	All year	[8] [13]

In non-native populations, the same is observed: warmer waters lead to a longer period of recruitment, for example in Australia (Table 7). In the NW Atlantic population, the recruitment period occurs mainly between June and December, except for the population of Massachusetts, which shows ovigerous female from May to August.

Table 7- *Carcinus maenas* – Non-native population. Seasonality of reproductive events in different populations. Empty cell indicates that no data are available for that location. [1]Best et al., 2017; [2]Cameron & Metaxas, 2005; [3]Tremblay et al., 2006; [4]Audet et al., 2008; [5]Berrill, 1982; [6]Young et al., 2017; [7]Gillespie et al., 2007; [8]Vinuesa J., 2007; [9]Le Roux et al., 1990; [10] Garside & Bishop, 2014.

	Location	Latitude	Reproduction	Female Ovigerous	Larvae Released	Reference
NW Atlantic	Placentia Bay, Newfoundland, Canada	48º N		July to August	June to August	[1]
	Bras d'Or Lakes, Nova Scotia, Canada	46º N			June to October	[2] [3]
	Basin Head, Prince Edward Island, Canada	46º N	August to September	July	August to December	[4]
	Boothbay Harbor, Maine, US	44º N	July to October	April to August	September	[5]
	Salem Sound, Massachusetts, US	42º N		November to January; May to August		[6]
NE Pacific	Vancouver Island, British Columbia	49º N	July	April and May	May	[7]
Argentina	San Jorge Gulf, Patagonia	45º S		May to September		[8]
South Africa	Table Bay Docks, Cape Town	34ºS		July to November		[9]
Australia	New South Wales, Australia	36º S		Summer and Autumn		[10]

4. Discussion

Understanding the effects of extreme climate events on the population dynamics of *Carcinus maenas* in the Mondego estuary is extremely important due to its role as an epibenthic predator in this ecosystem. It was possible to observe that according to the type of climate event the species will present different features and dynamics, leading to differences in the number of juveniles, density and spatial distribution of the population. Although *Carcinus maenas* is a well-studied species, this work is innovative because the effect of opposite extreme climatic events (droughts and floods) has never been compared before.

4.1 Population dynamics and secondary production

In a highly dynamic system such as the Mondego estuary, the *Carcinus maenas* population presents clear seasonal and spatial distribution patterns. As in previous studies in this estuary (Baeta et al., 2005; Bessa et al. 2010), recruitment is continuous throughout the year, with breeding peaks during the winter and spring. With a higher recruitment at the Pranto River (Neves et al., 2006), which has more favourable conditions to the settlement of megalopas and development of juveniles (i.e. nursery) such as smaller subtidal area, high turbidity, algal biomass, and food abundance (Dolbeth et al., 2003; Verdelhos et al., 2005). These characteristics allow for the protection against potential predators, especially in the early stages of benthic development (Thiel & Dernedde, 1994). Recruiting variability and survival of juveniles play a crucial role in the total density of individuals in the estuary (Lee et al., 2006).

The results also showed that the population of *Carcinus maenas* is less abundant both in the mouth and in the north arm of the estuary. These sub-systems present more adverse conditions to the establishment of benthic populations such as higher water velocity and stronger tidal currents, which allow only for the occurrence of individuals with larger dimensions. The regular dredging activities in the commercial port of Figueira da Foz also contribute for a harsher environment for early life stages (Baeta et al., 2005; Veríssimo et al., 2017).

The distribution of *Carcinus maenas* along the Mondego estuary greatly depends on the environmental conditions and characteristics of each of the sub-systems (as shown by the RDA). The population is highly correlated with temperature and salinity, being present mainly in the Pranto River and in the south arm, being the juveniles present in the Pranto River, and the larger individuals in the south arm.

Carcinus maenas occur in a range of colours from green to red. They present orange and red morphotypes due to the photo-denaturing of astaxanthin pigment (turns red when denatured), in the carapace over a long inter-moult (Lee, 1977; Styrishave et al., 2004). Several studies have shown that, depending on the colour of the carapace, there is a variation in behaviour and on physiology features. Among the main differences, crabs with green morphotype are more resistant to osmotic extremes and environments with low oxygen (McGaw & Naylor, 1992; Reid et al., 1997). The obtained results indicated a high percentage of individuals with green morphotype (as expected), and a small percentage of both orange and red morphotypes in the population. These orange and red morphotypes are mostly settled in the subtidal areas of the north arm and the mouth of the estuary (as shown by the RDA). In turn, the green morphotype was found in the intertidal areas of the Pranto River, in agreement with previous studies in the Mondego estuary (Baeta et al., 2005). Due to the high estuarine dynamics, leading to several constant variations in water temperature and salinity, green crabs are more adapted to deal with these variations and, therefore, able to maintain a stable population in these habitats. Throughout the year, crabs of all colour ranges were observed, as in the British Channel (Naylor, 1962).

Evaluating the sex ratio in different classes it was possible to verify the existence of differences. For instance, the sex ratio of juveniles was extremely high (indicating a large proportion of males in the population) and as the size classes increased, sex ratio approached a 1:1 ratio. The large percentage of juvenile males may be caused by a mechanism of the species, since males present themselves as being more evasive and competitive (Styrishave et al., 2004), which will lead to a higher mortality rate in higher class sizes. In addition, females tend to hide, burrowing themselves in the sediment, which makes them less prone to being caught during the sampling surveys. The percentage of males increased again in the larger size class, since the maximum size reached by the females is smaller than the males, being the maximum size of females approximately 75 mm.

Estimated annual production varied significantly throughout the study period, which most probably resulted of variation of population density and frequency of size of the individuals, considering this large variation, values of the $P/\overline{B}$ ratio were distinct in all years, presenting higher values in years where droughts occurred. Although the data used during 2003 to 2007 are the same as in previous studies (Baeta et al., 2005; Bessa et al., 2010), the annual value of $P/\overline{B}$ in the Mondego estuary was different, since in the present study 4 sampling stations were analysed and in the previous studies only 3 stations of them were, the north arm was not analysed.

Studying and analysing the secondary production was important, because in this way it is possible to measure the fitness of the population, since it integrates individual growth and population mortality, and it is also possible to perceive and identify functional responses of the population to environmental stress. Having this, combining secondary production with the long-term data-sets will upgrade the level of understanding of ecosystem functioning (Dolbeth et al., 2012).

4.2 Extreme climate events and its impacts on the *Carcinus maenas* population

In the last decades, global climate has undergone many changes, showing a tendency to increase the global air and water temperature as well as the frequency and intensity of extreme climate events. Portugal is no exception, with several changes in the climate documented and a great number of extreme climate events in the last decades, being these mostly droughts (Cardoso et al., 2008; Neto et al., 2010). These types of extreme climate events, associated to anthropogenic impacts observed in recent years in the Mondego estuary (Neto et al., 2010; Baptista et al., 2015), led to major disturbances (Dolbeth et al., 2003; Pardal et al., 2004; Cardoso et al., 2008).

The strongest extreme climate event that occurred in Portugal in recent years was the extreme drought of 2004/2005. An extreme drought was also observed in the years of 2007 and 2008, critically affecting the country since it was still recovering from the drought of 2004/2005. There were also flood periods in 2010 and 2014. The year of 2010 was considered a rainy year in which monthly precipitation registered was always higher than the normal climatological. Recently, 2015 and 2017, presented precipitation values much lower than those of the climatological normal, leading to an extreme drought of the whole country during these years.

Due to the occurrence of extreme drought periods (2004, 2005, 2007 and 2008, 2015 and 2017), several changes occurred in the Mondego river basin (Martinho et al., 2007; Marques et al., 2007). An increase in water salinity was observed during drought events, explained by extremely low river runoff during this period that led to an increase in the incursion of oceanic water in the estuary (Marques et al., 2007). In the event of floods (2010 and 2014), an increase of precipitation led to a decrease in the salinity of the estuarine water, due to an increase of the river flow mainly in the north arm (Teixeira et al., 2008). Changes of the salinity gradient and the flow in the estuary, due to extreme climate events, led to drastic changes in the fish and benthic communities present in the estuary (Cardoso et al., 2008; Grilo et al., 2011).

In our study, during the drought events there was an increase in the salinity of the estuarine water and an increase in the recruitment of juveniles (Figure 8). Salinity and its potential consequences are among the main factors influencing reproduction, recruitment and dispersal of marine and estuarine organisms (Anger, 2003). *Carcinus maenas* is considered a euryhaline species, tolerating a wide salinity range between 4 and 54 ‰ (Broekhuysen, 1936; Crothers, 1967), and the larval development of this species require high salt concentration (Nagaraj, 1993), these results are observable in the Redundancy Analysis (RDA) diagrams.

The CUSUM analysis allowed the detection of critical points during the study period, being therefore a very interesting way of evaluating long term data-sets, because in this way it is possible to verify the differences throughout the study period. It was possible to verify that most of the biological parameters have the same pattern, only the CUSUM of the orange and red morphotypes present different patterns. The abiotic parameters present many variations due to the existence of several extreme climatic events that led to the existence of critical points throughout the analysis. These are easily observed in the CUSUM of precipitation (Figure 12N) and salinity (Figure 12O). The salinity results are positively correlated with the biological parameters, because *Carcinus maenas* is quite dependent on the salinity and present a better recruitment with higher levels of salinity. In addition to a positive correlation between the biological parameters and the salinity, it is also possible to verify a negative correlation with the North Atlantic oscillation index (NAO Index). The negative correlation between the NAO index and the characteristics of *Carcinus maenas* was since NAO is a phenomenon that occurs mainly in winter (Ottersen et al., 2001), it also happens during the winter when *C. maenas* reproductive period occurs.

Previously studies on the effects of extreme climatic events on other species showed different effects depending on the species under study. However, in the majority of cases, extreme droughts have led to an increase in species density (Martinho et al., 2007; Rito, 2009) and a higher recruitment (Rito, 2009; Bessa et al., 2010). Only in *Pomatoschistus microps* and *Dicentrarchus labrax* a population decrease was observed during periods of drought (Martinho et al., 2007; Bento et al., 2016), mainly due to the increase in the salinity of the estuarine water and the reduction of river flow. The opposite occurs in floods, where there was a decrease in the recruitment of *Scrobicularia plana* (Rito, 2009) and a decrease in the density of *Hydrobia ulvae* and *Scrobicularia plana* (Cardoso et al., 2008). A decreased recruitment and density were observed in *Carcinus maenas*, caused by increased of the river flow and lower salinity values. An increase in the river flow leads to a fewer number of megalopae being able to return to the estuary, furthermore, larval development of this species require high salt concentration (Nagaraj, 1993).

Understanding the effects of extreme climate events is of great importance as these events can cause small changes in populations, but when coupled with anthropogenic stress, can lead to drastic and irreversible changes. The estuarine and marine environments are subjected to a high anthropogenic stress. Due to these impacts, several processes and mechanisms were lost and destroyed in the Mondego estuary, an example of which is the high decrease of *Zostera noltii* (Pardal et al., 2004; Verdelhos et al., 2005). This drastic reduction of *Zostera noltii* can lead to severe alterations in the estuarine benthic community, and in the long term originate a possible new trophic network (Marques et al., 2003).

4.3 Features of *Carcinus maenas* across different latitudes

Carcinus maenas is listed among the 100 most invasive species due to their ease of dispersion, a high phenotypic plasticity and a high tolerance to a high range of salinity and temperature, in this sense, it is important to know the specific characteristics of both native and non-native populations. In recent years, the green crab has increased its invasive area, which led to a drastic reduction native species in northern New England and southeast Canada, such as the bivalve *Mya arenaria* (Cohen et al., 1995).

Along its main geographical distribution range, the green crab presents different biological characteristics. The main observable differences between the population of the Mondego estuary and the remaining populations were the recruitment period and the maximum size of the individuals. Although the recruitment of *Carcinus maenas* in South Europe is observed throughout the year (Amaral et al., 2007; Baeta et al., 2005), with breeding peaks in winter and spring, this is not observable in the rest of the world population. The recruitment period decreased with increasing latitude. For example, in Mira estuary, Portugal (37° N) the recruitment period occurs during all year (Amaral et al., 2007) while in Gullmarsfjord, Sweden (58° N) recruitment of larvae occurs from July to September (Moksnes et al., 2014). Similar patterns were also found in copulation periods and the presence of ovigerous female, which are likely to occur due to the lower temperatures in areas with higher latitudes combined with a reduced temporal window of favourable conditions.

In addition to distinct reproductive characteristics, it was possible to observe morphological differences between populations. The maximum size of the carapace (CW) varies a lot, being the maximum size registered in Portugal (41ºN) of 78 mm. With the latitude increase, the maximum CW increases, in Northern Europe, in Sweden (58º N) the maximum size recorded was 100mm. This characteristic possibly occurs due to an evolution of the species, owing to the fact that in colder areas these have larger dimensions, this is explained by Bergmann's rule, which says that in cold places there will be populations of larger size and the opposite will be observed in warmer areas (Papacostas & Freestone, 2016). In previous studies, it was possible to verify a thermogeographic variation in body size in the non-indigenous population of the west coast of North America (Kelley et al., 2015).

The life span of *Carcinus maenas* also differed according to latitude. The life span in Portugal (41º N), France (49º N) and Wales (52º N) is approximately 3 - 4 years, in turn, in the Netherlands (53º N) the life span is a little bigger, being found individuals between 4 - 6 years. In the non-native population of the North-western Atlantic (USA and Canada), the life span has been reported to achieve also 5 - 6 years, which may also be a consequence of colder waters recorded in countries with a greater latitude.

Although the green crab presents a high phenotypic plasticity and a high tolerance to a high range of salinity and temperature (Marculis & Lui, 2015; Macdonald et al., 2018), *Carcinus maenas* will present different behaviours and features according to different environmental conditions, leading to a greater number of juveniles in lower salinities and consequently a higher population density. In addition to salinity, the temperature variation also leads to changes, and the water with higher temperatures show a longer recruitment period and in low water temperatures there is a larger size of the carapace of the individuals (Young et al., 2017).

According to forecasts by the Intergovernmental Panel on Climate Change (IPCC), the occurrence of extreme climate events will be increasing in its frequency, in case of Portugal this will be essentially droughts (IPCC, 2014). Due to increased droughts in Portugal it is possible to predict through the results of this study, that there will be an increase of the *Carcinus maenas* population in the Portuguese estuaries.

4.4 Final considerations

This study elucidated the importance of the analysis of the effects of extreme climatic events on estuarine ecosystems and their populations. The use and creation of long-term data sets (LTDs) is of the utmost importance for these effects to be understood. Due to the increase in the frequency of extreme climatic events, it is necessary to continue to carry out studies of how species, especially key species, are affected by this type of events. In this study and with the use of LTDs it was possible to verify that according to the existence of droughts and floods, the population of *Carcinus maenas* will present different characteristics and dynamics. It was also concluded that salinity and water temperature play a crucial role in population dynamics of *Carcinus maenas*, and that the river flow will lead to different levels of recruitment success.

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