

Effects of Climate Change on Limpets (*Patella* spp.): Biology and Distribution

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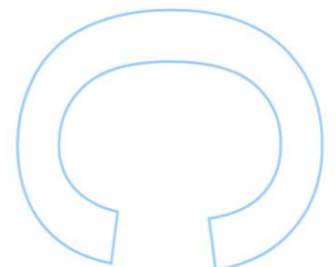
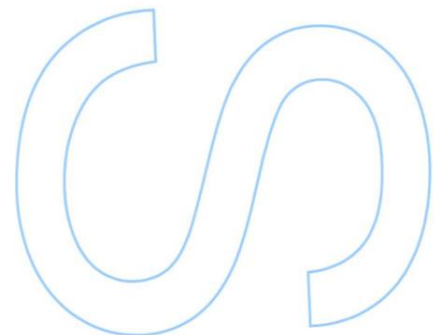
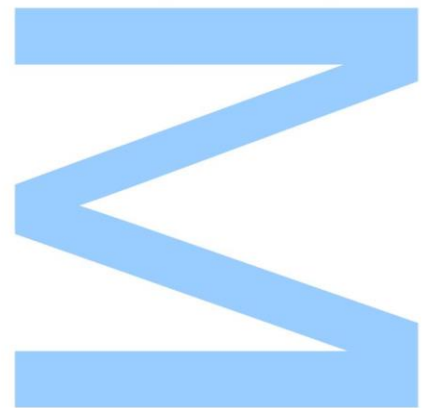
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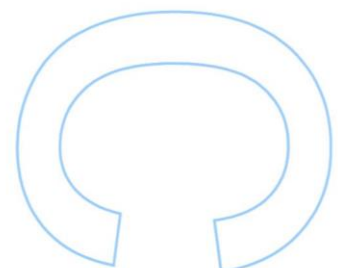
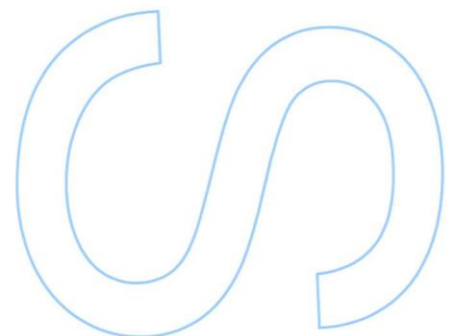
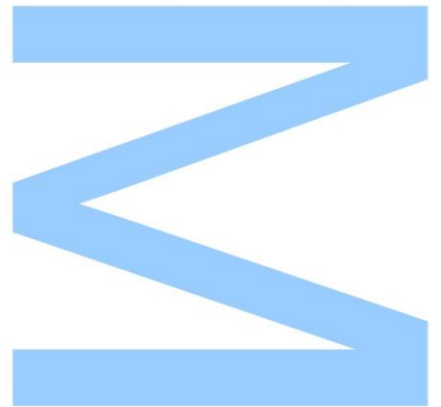
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Resumo

A temperatura é um dos fatores de maior importância que afeta a fisiologia, comportamento e distribuição de espécies marinhas, sobretudo aquelas que vivem na zona intertidal. As lapas (*Patella* spp.) são gastrópodes marinhos herbívoros que habitam as costas rochosas da Europa, do Mediterrâneo, da Macaronésia e do Noroeste de África. Sendo consideradas espécies-chave, as lapas desempenham um papel importante na regulação de macroalgas em comunidades costeiras. Este trabalho teve como objetivo investigar a influência da temperatura na taxa metabólica (através do consumo de oxigénio) e na sobrevivência de quatro espécies da costa portuguesa - *Patella ulyssiponensis*, *Patella vulgata*, *Patella depressa* e *Patella rustica*. Adicionalmente, avaliou-se a distribuição atual destas espécies e previu-se a sua distribuição futura sob o pior cenário de alterações climáticas, ao longo do Atlântico Norte. Os indivíduos foram recolhidos em praias rochosas da costa portuguesa. No laboratório, foram expostos a dois períodos de aclimação. Para medir o consumo de oxigénio, os testes foram executados num sistema com três câmaras independentes e em simultâneo. Dentro de cada câmara foi colocada uma lapa e o consumo de oxigénio foi registado com o auxílio do software PreSens Measurement Studio 2. O intervalo de temperaturas testado foi entre os 6°C e os 28°C. Nos testes de sobrevivência, as lapas foram deixadas em tanques a diferentes temperaturas durante quinze dias. A proporção lapas vivas/mortas foi calculada posteriormente. Modelos de distribuição de espécies foram construídos para cada espécie usando três algoritmos diferentes: modelos lineares generalizados, modelos aditivos generalizados e o Maxent. Dados de ocorrência foram recolhidos das bases de dados online: OBIS e GBIF. Os resultados mostraram que aumentos da temperatura levam a aumentos do consumo de oxigénio em *Patella ulyssiponensis*. Comparativamente às restantes espécies estudadas, esta espécie exibiu uma taxa metabólica mais sensível à temperatura. Os limites termais mínimo e máximo para todas as espécies variaram entre 8.4°C e 10.7°C e entre 24.3°C e 25.3°C, respetivamente. A temperatura da superfície da água do mar demonstrou ser a variável mais importante para a distribuição das quatro espécies de lapas. No futuro, prevê-se que todas as espécies movam os seus limites para o Norte. A temperatura mostrou ser um fator que influencia a biologia e distribuição das lapas. Dados o cenário futuro de alterações climáticas, particularmente com o aumento das temperaturas previsto, é crucial implementar medidas de conservação para espécies intertidais.

Palavras-chave: Lapas; Testes de consumo de oxigénio; Metabolismo; Energia de ativação; Limites de distribuição

Abstract

Temperature is one of the most important factors affecting the physiology, behaviour, and distribution of marine species, especially those living in the intertidal zone. Limpets (*Patella* spp.) are marine herbivorous gastropods that inhabit rocky shores along the coast of Europe, the Mediterranean, the Macaronesia, and the Northwest coast of Africa. Considered key species, limpets have an important role regulating seaweed assemblages in coastal communities. This work aimed to investigate the influence of temperature on the metabolic rate (oxygen consumption) and survival of four species - *Patella ulyssiponensis*, *Patella vulgata*, *Patella depressa* and *Patella rustica* - in the Portuguese coast. Additionally, it intended to assess the current distribution of these species and predict their future distribution under the worst climate change scenario, along the Northern Atlantic Ocean. Individuals were collected from rocky shores in the Portuguese coast. In the laboratory, they were exposed to two acclimation periods. For oxygen consumption, the trials were run in a system with three simultaneous independent chambers. One limpet was placed inside each chamber and oxygen consumption was recorded with the aid of software PreSens Measurement Studio 2. The tested temperatures ranged from 6°C to 28°C. For the survival trials, limpets were left in tanks at different temperatures for fifteen days. The proportion of alive/dead was then calculated. Species distribution models were built for each species using three different algorithms: generalized linear models, generalized additive models and Maxent. Occurrence data was retrieved from online databases: Ocean Biogeographic Information System (OBIS) and Global Biodiversity Information Facility (GBIF). The results showed that increasing temperatures lead to an increase in the oxygen consumption of *Patella ulyssiponensis*. Comparing with the remaining tested species, this species presented higher sensitivity of the metabolic rate to temperature. The minimum and maximum thermal limits of all species ranged from 8.4°C to 10.7°C and from 24.3°C to 25.3°C, respectively. Sea surface temperature was the most important variable for the distribution of the four limpet species. In the future, all species were predicted to shift their range towards the north. The temperature confirmed to be an important driver in the biology and distribution of limpets. Given climate change future scenarios, particularly with the predicted increase in temperature, it is crucial to implement conservation measures for intertidal species.

Keywords: Limpets; Oxygen consumption tests; Metabolism; Activation energy, Range distribution

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List of abbreviations

CCR	Correct Classification Rate
Ea	Activation Energy
EGV	Environmental Factors or Ecogeographical Variable
GAM	Generalized Additive Model
GBIF	Global Biodiversity Information Facility
GLM	Generalized Linear Model
HTT ₅₀	High Thermal Threshold for 50 % of the population
IPCC	Intergovernmental Panel for Climate Change
LTT ₅₀	Low Thermal Threshold for 50 % of the population
MPAs	Marine Protected Areas
MTE	Metabolic Theory of Ecology
NNI	Nearest Neighbour Index
OBIS	Ocean Biodiversity Information System
PNSACV	Parque Natural do Sudoeste Alentejano e Costa Vicentina
RCP	Representative Concentration Pathway
SDMs	Species Distribution Models
TSS	True Skill Statistic

1. Introduction

Marine ecosystems are the largest, most productive, and diverse ecosystems on Earth (UNESCO, 2017). They are a fundamental source of support services, serving as suppliers of water, energy and habitats to an immeasurable number of organisms (Costanza, 1999). Oceans are particularly important as they control changes in atmospheric temperature, humidity, and stability (Costanza, 1999; Borja, 2014). Additionally, they also play an important role for supporting numerous ecological functions of the planet.

The intertidal zone is a biotope of high biological interest that establishes the boundary between land and marine environments (Chappuis *et al.*, 2014). It is subject to considerable natural environmental changes (Tait & Dipper, 1998). Intertidal rocky shores are heterogeneous ecosystems that support a wide variety of living forms and occur throughout the world's coastlines (Thompson *et al.*, 2002). They are characterised by the presence of a large and stable substrate that allows organisms to settle and develop (Underwood & Jernakoff, 1981). These ecosystems have multiple typical inhabitants, such as sea urchins, anemones, crabs, mussels, barnacles, limpets and seaweed (Littler & Murray, 1975; Boaventura *et al.*, 2002b; Araújo *et al.*, 2005). High biodiversity levels are due to the existence of numerous microhabitats (e.g. sheltered protrusions and deep or shallow puddles) that provide refuge and nursery areas for many species (Tait & Dipper, 1998; Thompson *et al.*, 2002). All intertidal organisms, including sessile species, compete for food and space, the most important resources to survive in the intertidal zone. Along the rocky substrate, species are distributed according to their ability to tolerate physical changes (e.g. gradient of emersion/immersion, exposure to waves or salinity fluctuation) (Raffaelli & Hawkins, 1996). The distribution patterns of organisms in the rocky shores have been studied by several authors (Raffaelli & Hawkins, 1996; Boaventura *et al.*, 2002b; Araújo *et al.*, 2005). The distribution of the species follows a vertical line on a shore and it is known as littoral zonation (Raffaelli & Hawkins, 1996). This phenomenon occurs at specific levels - from the lower to the upper shore - and can be defined as the distribution of species and communities along environmental gradients (Stephenson & Stephenson, 1949; Thompson *et al.*, 2002; Chappuis *et al.*, 2014). In general, this gradient considers three main zones on the shore, each containing distinct organisms: the upper-shore, the mid-shore, and the low-shore. The organisms that inhabit rocky shores are adapted to a turbulent environment with extremely unstable conditions (Thompson *et al.*, 2002), which affect their physiology and

behaviour, having implications in their metabolism patterns, respiration, growth, reproduction and distribution (Newell, 1973).

1.1 Ecological role of limpets

Limpets (*Patella* spp.) are mainly herbivore marine gastropods that inhabit exposed and sheltered rocky shores along the western coast of Europe, the Mediterranean coast, the Northwest of Africa and the Macaronesian islands (Guerra & Gaudencio, 1986; Borges *et al.*, 2015) (Figure 1). They are considered key species that play an important ecological role in marine communities, exerting strong competitive intraspecific and interspecific pressures (Underwood, 1979; Underwood & Jernakoff, 1981; Boaventura *et al.*, 2002a). As grazers, limpets feed on large amounts of seaweed propagules, controlling their growth and regulating the ecological succession of biological communities established in the intertidal areas (Boaventura *et al.*, 2002b). By studying the effects of limpets' grazing on red seaweed turf at moderate exposed shores in Portugal and Britain, Boaventura *et al.* (2002) showed that grazers play a major role in directly setting the upper-limits of low-shores' turfs in intertidal in rocky shores. Limpet removal has resulted in a significant increase in seaweed turf in both locations, allowing natural variation in algal colonization (Boaventura *et al.*, 2002b). Several other studies were undertaken to understand the relationship between grazers and seaweed communities (Jenkins *et al.*, 2001; Boaventura *et al.*, 2002b; Arrontes *et al.*, 2004; Jenkins *et al.*, 2005). Arrontes *et al.* (2004) observed that the absence of limpets would result in abnormal development of seaweed diversity or the occupation of limpets' ecological niche by competing organisms such as barnacles or sea urchins on shores in Northern Spain. Also, Jenkins *et al.* (2005) concluded that a small difference in the relative abundance of grazers leads to a significant change in the balance between grazers and seaweed in coastal communities of the British Isles.



Figure 1: *Patella* spp. aggregation in a rocky shore.

The ability of limpets to control seaweed growth and to influence the abundances of other species is well known. However, the dynamic of a population is also controlled by their proximal environment and interactions with biotic and abiotic factors (Underwood, 1979). These are responsible for the variations in limpet populations, regulating recruitment, settlement, growth, reproduction, larvae development and metabolic activity (Parry, 1978).

The Metabolic Theory of Ecology (MTE) offers a predictive framework for assessing and understanding changes in the abundance, distribution and diversity of organisms and the fluxes of energy and materials in ecological systems (Brown *et al.*, 2004). According to the MTE, organisms that are more metabolically active will also have great energetic demands and, therefore, a need to increase their feeding or photosynthetic rates (Brown *et al.*, 2004). Thus, the effect of temperature in heterotrophic respiration and autotrophic productivity is scaled differently (Gillooly *et al.*, 2001; Allen *et al.*, 2005). The interactions between herbivores and primary producers are significantly affected by small temperature increases (Yvon-Durocher *et al.*, 2010). The MTE suggests that producers will show a smaller temperature response than their consumers. The increasing temperature will affect the performance of an organism by increasing its metabolic rate and consequently its grazing activity until a threshold is reached (Connor, 2009; Connor *et al.*, 2011). In other words, at higher temperatures grazers will be more sensitive to temperature increases than to food sources, and the balance between grazers and feeders might be altered (Hawkins *et al.*, 2009; Connor *et al.*, 2011). The grazing activity will occur until a lethal temperature level is reached, after which limpets' herbivory pressure decreases (Mertens *et al.*, 2015). The effect of reducing or removing grazers on the community is known to result in important changes in community structure, such as the development of new seaweed assemblages with an associated increase in diversity and community complexity (Coleman *et al.*, 2006).

1.2 Limpet harvesting

Rocky shores are typically open systems and their easy accessibility makes them vulnerable to a variety of anthropogenic impacts (Thompson *et al.*, 2002). Many locations with long-established human populations have traditions of local exploitation of marine resources (Almeida *et al.*, 2015). Mobile grazing herbivores are targeted species for human exploration. Among them, limpets have been subject to negative anthropogenic influences for many years, leading to overexploitation of several populations (Hawkins *et al.*, 2000). The effects of human activity on rocky intertidal communities have been the focus of many studies, particularly in South Africa (Branch, 1975; Branch & Odendaal, 2003; Nakin & Mcquaid, 2014), Chile (Moreno *et al.*, 1986; Durán & Castilla, 1989; Espoz *et al.*, 2004) and Hawaii (Mccoy, 2008), where, in the past, limpets played an important role in the diet of native people.

Portugal is the country with the highest seafood consumption in Europe and one of the major consumers in the world (Almeida *et al.*, 2015). For this reason, marine living resources, particularly limpets, have been intensely exploited by humans. The observed decrease in the abundance of several limpet species has been the subject of many studies in the Portuguese mainland (Southwest coast of Alentejo) and archipelagos (Azores and Madeira) (Côrte-Real *et al.*, 1996; Hawkins *et al.*, 2000; Weber & Hawkins, 2002; Martins *et al.*, 2008). In the Azores archipelago, limpets has been exploited since the human colonisation of the islands, in the 15th century (Ferraz *et al.*, 2001). Limpets have become popularly used as seafood and important protein source, therefore increasing their commercial interest (Martins *et al.*, 2008). Currently, they are part of the cultural identity of the Azores. In this archipelago, two species - *Patella candei* d'Orbigny, 1840 and *Patella aspera* Röding, 1798 - were explored and overharvested during the 80's, leading to drastic reductions of their populations (Martins *et al.*, 2008). *P. candei* has been mainly exploited on a subsistence or recreation basis and *P. aspera* has been exploited by both unlicensed and licensed divers (Martins *et al.*, 2008). In São Miguel, *P. aspera* was the most important commercially explored species, which has contributed to its drastic decline in the archipelago (Martins *et al.*, 2011). Despite the approved legislation to protect limpet populations, dating from 1993 (Decreto Regulamentar Regional nº 14/93/A de 23 Abril de 1993 da Região Autónoma dos Açores), limpet populations have not recovered from overexploitation and scarcity of this species on the island's coast is visible (Martins *et al.*, 2011). Limpet harvesting can result in catastrophic effects on coastal communities leading to a cascade of changes (Moreno *et al.*, 1984). Their recovery will therefore depend on the ecosystem's resilience (Castilla *et al.*, 1994). Overharvesting of limpets allows the development of well-established assemblages of

seaweed turfs and can raise their upper vertical limit (Underwood, 1979, Boaventura *et al.*, 2002b, Arrontes *et al.*, 2004; Jenkins *et al.*, 2005). Furthermore, limpets are an important component in the diet of several marine predators (e.g. birds and crabs). Hence, decreasing abundances of limpets may also affect the structure of intertidal systems at higher levels (Martins *et al.*, 2010).

The same situation has been observed in Madeira with these two limpet species (Hawkins *et al.*, 2000). *P. candei* and *P. aspera* are used in the most profitable commercial activities at small scale fisheries (Henriques *et al.*, 2012). Due to their high economic value, concerns on limpet conservation have been increasing, being the target of several studies. Since 2006, limpet harvesting has been regulated according to the guidelines obtained from the first stock assessment performance on the stocks for these two species (Regional Legislative Decree N° 11/2006/M, 18 April 2006). Also, studies about long-term population status have been developed to understand how the limpet species respond to the harvesting pressure (Sousa *et al.*, 2019). Considering the unremitting and intense pressure acting on these resources, continuous monitoring of population status is required to assess stock vulnerability and evolution to assure its sustainable management (Henriques *et al.*, 2012; Sousa *et al.*, 2019).

In Portuguese mainland, limpet harvesting is practiced in the Southwest coast of Alentejo (Castro & Cruz, 2009). In 1995, a marine zone with 2 km was designated in natural park Parque Natural do Sudoeste Alentejano e Costa Vicentina (PNSACV), located in the Southwest coast of Portugal (Decreto nº 26/95 de 21 de setembro do Ministério do Ambiente e Recursos Naturais, 1995). This marine zone was created to allow specific sustainable exploration of certain species and to mitigate the effects of catches in this area.

Harvesting of intertidal molluscs, when excessively done, can lead to a cascade of changes on coastal communities (Moreno *et al.*, 1984). This situation has occurred in the past and measures to prevent catastrophic results had to be taken (Martins *et al.*, 2011; Henriques *et al.*, 2012). Past situations such as these should serve as an example for the present and the future. Limpet harvesting is still a common activity in certain areas of Portugal (Castro & Cruz, 2009). Together with the uncertainties of climate change, it can have more destructive impacts than in the past. Therefore, the urgency for prevention measures has never been higher.

1.3 Climate Change

Climate change refers to the long-term shifts in weather patterns, most likely caused by a combination of natural processes and external anthropogenic activities (IPCC 2018). The marine environment has been changing throughout the years, with climate change causing profound and diverse consequences in these ecosystems (Hoegh-Guldberg & Bruno, 2010). These consequences are already observed at regional, continental, and global scales, due to the increasing concentration of greenhouse gases (Borja, 2014). Globally, it has resulted in seawater level rise, increase of atmospheric and seawater temperatures, oceanic pH and changes in precipitation patterns (Doney *et al.*, 2012). The seawater level rise is the result of the glacier melting, while seawater acidity increases due to increasing CO₂ concentrations (Doney *et al.*, 2012; Borja, 2014). Responses to climate change are particularly rapid and strong in marine ecosystems (Hoegh-Guldberg & Bruno, 2010), especially in the intertidal zone where species often live at their upper temperature limits (Somero, 2002).

The intertidal zone, as the interface between the marine and terrestrial realms, is prone to both land and ocean impacts of climate change (Helmuth *et al.*, 2006). The rocky intertidal zone in particular has long been viewed as a “natural laboratory” for studies of species responses to extreme environmental conditions, largely due to the severity of the physical environment and the rapid turnover of individuals in the community (Somero, 2002; Helmuth *et al.*, 2006). As such, they provide a model system for examining the effects of climate change on species (Helmuth *et al.*, 2006). In rocky intertidal shores, fluctuations of abiotic factors such as increases in temperature, acidity, salinity, current velocity and seawater level, affect the physiology, behaviour and distribution ranges of intertidal organisms (Borja, 2014). Several studies have documented how the impacts of climate change may affect the intertidal organisms and consequently translate into community changes (Southward *et al.*, 1995; Harley *et al.*, 2004; Hawkins *et al.*, 2009; Wethey *et al.*, 2011; Jueterbock *et al.*, 2013; Ng *et al.*, 2017). For example, some organisms might be tolerant to or even adapt to these new conditions by increasing their abundance, reproduction and survival rate (Hawkins *et al.*, 2009; Doney *et al.*, 2012). Other organisms might yet be intolerant to such changes, resulting in migration, death, or even local extinctions (Hawkins, *et al.*, 2009; Doney *et al.*, 2012).

Climate change directly affects organism body temperatures, having significant impacts on biological processes (Harley, 2011). Temperature variations are direct drivers of change for intertidal species, as they have strong control over the organisms development rate at all life stages, metabolic and physiological processes (e.g. growth, reproduction and survival) and responses at biogeographic boundaries (Helmuth *et al.*,

2006; Firth *et al.*, 2010; Moore *et al.*, 2011). Changes in seawater temperature have a considerable influence in both cold-water and warm-water species distributions (Southward *et al.*, 1995; Helmuth *et al.*, 2006; Hawkins *et al.*, 2009). In general, cold-water species are decreasing in abundance and shifting poleward, while warm-water species are increasing in abundance and moving northwards (Helmuth *et al.*, 2006). Changes in species distribution have resulted in changes in communities composition, not only by the loss but also by the gain of new species, especially in intertidal zones, where Northern species are often more competitive than Southern species (Hawkins *et al.*, 2009).

Limpets tolerate many environmental challenges of the intertidal zone, which makes them relevant study objects (Branch, 1975). Variations in environmental conditions, as a result of climate change, influence the physiological and biochemical processes of limpets (Hawkins *et al.*, 2009). This influence ranges from impacts on physiology (Prusina *et al.*, 2014) and morphology (Harley *et al.*, 2009) - affecting behaviour and biotic interactions (Firth *et al.*, 2010) - to impacts on vertical (Somero, 2002) and geographic distributions (Sousa *et al.*, 2012). Understanding limpets' behaviour, physiological capacities and distribution patterns under climate change can contribute positively to the efforts for their conservation.

1.4 Species distribution models

Species Distribution Models (SDMs) mathematically relate species distribution data (occurrence or abundance at known locations) with information on the environmental and spatial features of those locations (Guisan & Thuiller, 2005 ; Elith *et al.*, 2009). They are important tools to address various issues in ecology, biogeography, evolution, conservation biology, and climate change research (Guisan & Zimmermann, 2000). SDMs are advantageous because they allow for estimating species ranges, identifying suitable habitats, and identifying predictors affecting species distribution (Guisan & Thuiller, 2005).

SDMs can be divided into two major groups: mechanistic and correlative (Guisan & Zimmermann, 2000). Mechanistic models are based on direct experimental quantifications of variable effect on species while correlative models are based on statistical correlations between species' occurrence records and environmental variables, such as salinity and wave exposure (Guisan & Zimmermann, 2000; Guisan & Thuiller, 2005; Kearney & Porter, 2009). Correlative models are more often used than mechanistic models due to the data availability. Within correlative models, there are several types of algorithms depending on the type of input data applied (Guisan & Zimmermann 2000). Species occurrence data can be recorded as presence/absence, abundance or presence-only (Guisan & Zimmermann, 2000).

Different modelling techniques are commonly applied to predict current species distribution and to project future distributions under global change scenarios (Thuiller, 2003). Generalized Linear Models (GLMs) are regression-based models and considered pioneer method in the SDMs field. They assume a relationship between the mean of the response variables and the linear combination of explanatory variables (Guisan *et al.*, 2002). Generalized Additive Models (GAMs) are non-parametric extensions of GLMs (Guisan *et al.*, 2002). They are able to deal with non-linear relationships between the mean of the response variables and the explanatory variables and allow a wide range of response curves (Guisan *et al.*, 2002). GLMs and GAMs model the realised niche, i.e. where the species actually exist, rather than the possible distribution expressed by the fundamental niche (Guisan *et al.*, 2002). These two methods use presence and absence data (Elith *et al.*, 2009). The maximum entropy model (implemented in the software Maxent) is a general approach of species distribution that uses presence-only and background data (Phillips *et al.*, 2006). This method estimates a target probability distribution by finding the probability distribution of maximum entropy (Phillips *et al.*, 2006). Maxent generally performs better than other algorithms, even with very low sample sizes (Phillips & Dudík, 2008; Elith *et al.*, 2011).

1.5 Objectives

The goal of this study was to evaluate the influence of temperature on the metabolic rate of four species of the genus *Patella*. The tested hypothesis was that increases of seawater temperature will result in increases of the metabolic rate across the four species of *Patella* in line with predictions from the Metabolic Theory of Ecology. For this purpose, trials were performed for assessing oxygen consumption rates in adult limpets under different temperatures.

This work also intended to study the influence of temperature on the limpet probability of survival for three species of the genus *Patella* and to obtain their maximum and minimum temperature limits of survival.

Additionally, this study aimed to assess the distribution of these four species and to predict their future distribution under climate change scenarios. This approach is relevant for assessing the present distribution of limpets on rocky shores in the Atlantic coast and foresee the distributional tendency under future climate change scenarios. The identification of geographical areas of expansion or retreat in *Patella* spp. distribution, following the Metabolic Theory of Ecology will signalise possible future ecological impacts that might be mitigated with appropriated conservation measures.

2. Material and methods

2.1 Study organisms and spatial distribution

The geographical distribution of *Patella* spp. is restricted to the North-eastern Atlantic ocean and Mediterranean Sea (Jenkins *et al.*, 2001; Lima *et al.*, 2006; Henrique *et al.*, 2012). Four species of genus *Patella* were studied: *Patella ulyssiponensis* Gmelin, 1961; *Patella vulgata* Linnaeus, 1758; *Patella depressa* Pennant, 1777 and *Patella rustica* Linnaeus, 1758.

P. ulyssiponensis are usually oval and larger in size, with red seaweed associated on the top of their shells (Figure 2a). These species appear in the British Isles, Portugal and North Africa (McCarthy *et al.*, 2008). The shell of *P. vulgata* is generally pointed, and round, with transparent tentacles at the edge of the mantle (Figure 2b). These species can be found from Northern Norway, around the British Isles to the North of Portugal, in sheltered shores (Guerra & Gaudencio, 1986; Borges *et al.*, 2015). *P. depressa* has a pointed shell with a visible triangular pattern and the mantle tentacles are bright and visible to the naked eye (Figure 2c). *P. depressa* distribution ranges from Southern British islands and Wales to Portugal and Northern Africa (Guerra & Gaudencio, 1986; Borges *et al.*, 2015). *P. rustica* is identified by the characteristic black spots on the shell (Figure 2d). Generally, this species can be found from the Mediterranean to the Atlantic coast of Iberian Peninsula and North Africa (Lima *et al.*, 2006). In the Atlantic ocean, the Northern limit is located at the French Basque Country and the Southern limit is speculated to occur further south than Mauritania (Lima *et al.*, 2006).

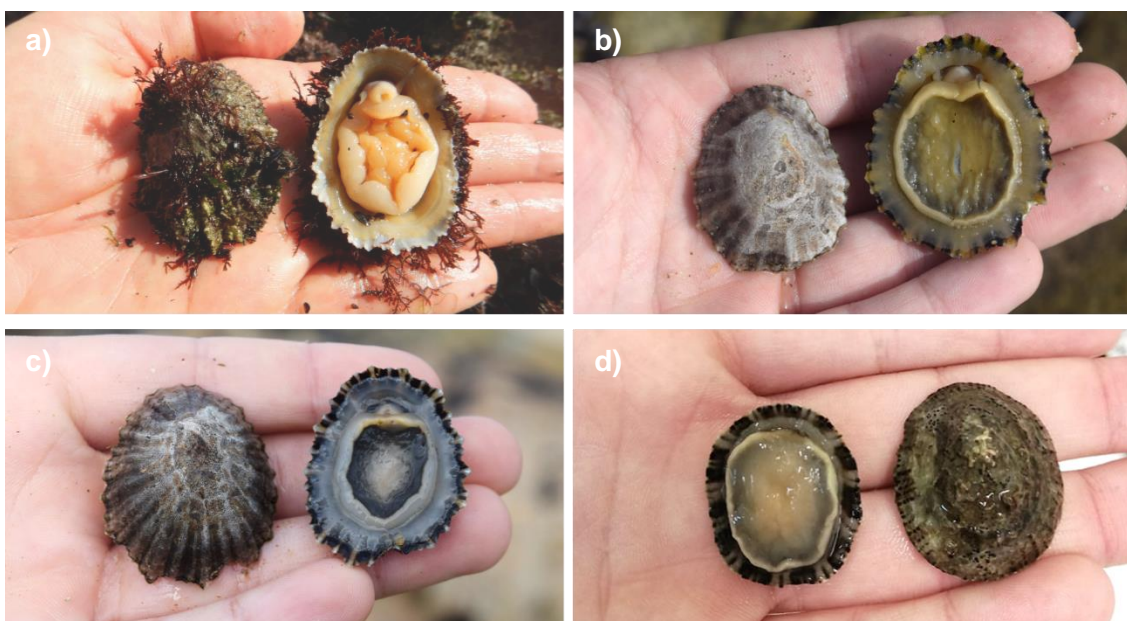


Figure 2: Dorsal and ventral view of *Patella* spp. a) *Patella ulyssiponensis* b) *Patella vulgata* c) *Patella depressa* and d) *Patella rustica*.

In Portugal, *Patella* spp. predominate the intertidal zone on exposed and sheltered rocky shores, occurring at all tide levels (Guerra & Gaudencio, 1986). In the Northwest coast of the country, the most abundant species are *P. ulyssiponensis*, *P. vulgata* and *P. depressa* (Casal *et al.*, 2018). *P. ulyssiponensis* and *P. vulgata* are reported as the dominant species along the Portuguese coast in sheltered areas, and in exposed areas *P. depressa* is dominant (Casal *et al.*, 2018). These three species coexist in the intertidal zone but at different tide levels. Usually, *P. ulyssiponensis* occurs on the low-shore and can also be found in tide pools on the mid-shore (Boaventura *et al.*, 2002a). *P. vulgata* occupies the region between the mid-shore and the upper-shore (Blackmore, 1969; Boaventura *et al.*, 2002a). *P. depressa* is present from the mid-shore to the low-shore, coexisting with *P. vulgata* (Boaventura *et al.*, 2002a; Silva *et al.*, 2003). In the Southern coast of Portugal, *P. rustica* is the most abundant species. This species occupies the upper-shore (Lima *et al.*, 2006). Until the late 1990s, *P. rustica* had a distribution gap in Northern Portugal, placed between La Coruña and Nazaré (Lima *et al.*, 2006; Sousa *et al.*, 2012). Despite this distribution gap, as proposed by Lima *et al.* (2006), since 2003 this species has dispersed and the number of individuals along the sites of distribution has increased.

2.2 Experimental design

2.2.1 Sampling design

The organisms were collected in the intertidal zone during low tide at three rocky shores in the North of Portugal: Praia Norte (Viana do Castelo, 41.696944 N 8.853056 W); Praia do Molhe (Porto, 41.157583 N 8.683500 W); Praia da Aguda (Vila Nova de Gaia, 41.045333 N 8.653139 W); and one in the South of Portugal: Praia dos Barcos (Peniche, 39.376556 N 9.339947 W) (Figure 3). The limpets were randomly collected and removed from the rock with a pocket knife and were immediately transported to CIIMAR (Matosinhos) in net bags inside small plastic boxes filled with seawater. In addition, some stones with biofilm were also collected for food provision during the acclimation period.



Figure 3: Location of the sampling sites along the coast of Portugal.

2.2.2 Acclimation period and routine procedures

In the laboratory, limpets were exposed to two acclimation periods: during the first period, limpets were placed on rocks for one week, inside tanks with aeration and filtered seawater at the same temperature of the collection site (Figure 4). After that period, the animals were moved to a new system. This system comprehended fourteen tanks, grouped in pairs used as water baths under different temperatures (6°C, 8°C, 12°C, 16°C, 20°C, 24°C, and 28°C). Each tank had two cylinders with two liters capacity, and inside each cylinder was placed one rock with two limpets covered by a mesh to prevent the escape (Figure 5). The tanks were aerated, and the seawater flow monitored (every 20 minutes, new seawater entered the cylinder for 1 minute). Overall, for each tested temperature there were a total of eight limpet replicates.



Figure 4: Example of the first acclimation period: limpets were placed on rocks, inside tanks with aeration and filtered seawater at the same temperature of the collection site.

The water temperature in each tank was increased or decreased one degree per day from the initial temperature of collection up to the established temperature to be tested. When the target temperature was achieved, limpets were left under these settings for two days for adaptation to the new conditions.

Every day, during the both acclimation periods, the mortality and temperature in each tank were recorded. The limpets that died were removed from the system and body weight, volume, width and height were recorded.

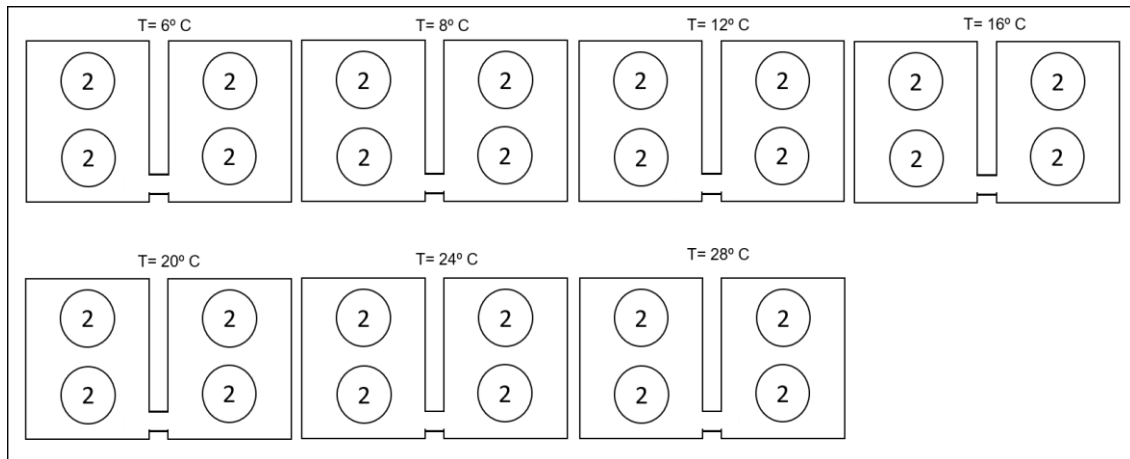


Figure 5: Scheme of the second acclimation period: system with fourteen tanks, grouped in pairs used as water baths under different temperatures.

2.2.3 Metabolic rate

The metabolic rate estimated was the oxygen consumption ($\mu\text{mol O}_2 \text{ g}^{-1} \text{ h}^{-1}$) (respiration rate). Prior to measuring oxygen consumption under different temperatures, the shells were cleaned to remove the attached organisms.

The system for the metabolic trials allowed three simultaneous and independent chambers with one limpet placed inside each chamber, on top of a rock, with a known volume of filtered seawater (Figure 6). To maintain the established temperature of the water in each chamber, a peristaltic pump transferred the bath water over the chambers. The duration of each incubation must be long enough to allow the organisms to adapt to the new conditions in the chamber. The incubation period lasted for one hour and twenty minutes, the oxygen concentrations were measured every twenty seconds with optical O_2 sensors (PreSens Oxy-4) and recorded with the aid of software PreSens Measurement Studio 2.

For each temperature, oxygen consumption per individual was calculated from oxygen concentration changes in each chamber during the incubation and correcting by the volume of water. During the trials, after the stabilization period, the oxygen consumption varied negatively with time. The slope of the initial linear trend represents the oxygen consumption under the tested temperature. This slope was extracted from all replicates, the blank controls were subtracted, and the mean of slopes were calculated per temperature. The mean values were plotted to assess the relationship between oxygen consumption and temperature.



Figure 6: System to measure the oxygen consumption ($\mu\text{mol O}_2 \text{ g}^{-1} \text{ h}^{-1}$) with three chambers.

After each incubation, the individual's volume was measured to be used for later calculations. Afterwards, the shells were removed, and the limpet body mass was left for 48 hours at 60°C to estimate the dry weight. The respiration rate was expressed as $\text{O}_2 \text{ g}^{-1} \text{ DW h}^{-1}$.

2.2.4 Activation energy

The metabolism is the process by which energy and materials are transformed within an organism and exchanged between itself and the environment (Gillooly *et al.*, 2001). The MTE is based on the principle that metabolic rate varies according to the organism's body mass and the environmental temperature, as described by equation 1 (Brown *et al.*, 2004):

$$I = I_0 M^{3/4} e^{-E_a/kT} \quad (\text{equation 1})$$

where I is the metabolic rate, I_0 is a normalization constant, independent of the body size and temperature, M is the body mass raised to $3/4$ power (g), E_a is the activation energy expressed in electron volts (eV), K is Boltzmann's constant ($8.61733 \times 10^{-5} \text{ eV K}$) and T is the absolute temperature (kelvin).

The terms of equation 1 can be rearranged to yield equation 2. This equation considers “mass-corrected” metabolic rate, I , by incorporating the logarithm of mass raised to the $3/4$ power.

$$\ln (IM^{-3/4}) = -E_a (1/kT) + \ln (I_0) \quad (\text{equation 2})$$

This method facilitates quantitative evaluation of the mass and temperature dependence predicted by equation 1, by incorporating the predicted scaling into the analysis and into the y-axis of bivariate plots. The slope of this relationship gives the activation energy of metabolism. The activation energy (E_a) reflects the sensitivity of the metabolic rate to temperature (Watson *et al.*, 2014). According to Gillooly *et al.* (2001), the activation energy values expected for plants, invertebrates, fishes, amphibians and reptiles range between 0.2 eV and 1.2 eV with an average of $E_a = 0.65$ eV. Brown *et al.* (2004) referred E_a values between 0.60 eV and 0.70 eV. This energy was calculated for the *P. ulyssiponensis*, *P. vulgata*, *P. depressa* and *P. rustica*.

2.2.5 Mortality trials

In parallel with the study of the influence of the temperature on the oxygen consumption, the influence of temperature on the limpet probability of survival was investigated for *P. ulyssiponensis*, *P. vulgata* and *P. depressa*. In these trials, during the second acclimation period, the water temperature was increased or decreased one degree every thirty minutes, until the final established temperature was achieved (6°C, 8°C, 12°C, 16°C, 20°C, 24°C and 28°C). For each temperature, there are two cylinders, each with three limpets placed on a rock, making up a total of twelve replicates. The limpets were then left in the tanks at the final temperature and the ratio of alive/dead individuals was estimated every day for fifteen days. Mortality was assessed by verifying the number of limpets without movement and detached from the rock. The mortality was equal to the sum of all dead individuals after fifteen days of exposure to each temperature. To ensure starvation was not influencing the probability of survival records, the rocks in each tank were replaced every five days.

The Low Lethal Temperature for 50% of the population (LTT₅₀) and the High Lethal Temperature for 50% of the population (HTT₅₀) were calculated based on the probability of survival plots for lower (6°C to 12°C) and higher (16°C to 28°C) temperatures, respectively.

2.3 Species distribution models

2.3.1 Species data

Species occurrence data was retrieved from Ocean Biogeographic Information System (OBIS) (<https://obis.org/>) and Global Biodiversity Information Facility (GBIF) (<https://www.gbif.org/>). A total of 2 924 georeferenced observations were retrieved from OBIS: 280 were *P. ulyssiponensis*, 2 000 of *P. vulgata*, 153 of *P. depressa* and 491 of *P. rustica*. From GBIF, a total of 3 436 georeferenced observations were found for *P. ulyssiponensis* (2 287), *P. vulgata* (10 000), *P. depressa* (882) and *P. rustica* (257). GBIF and OBIS datasets were merged to create a unique dataset for each species. Duplicate records are points that have the same coordinates or that are repeated within the considered pixel (5 arcmin) and they are removed from the dataset. Records that fall in land were also checked and removed from the dataset. Clustering of observations was decreased by randomly removing records that were clustered according to the Nearest Neighbour Index (NNI). The NNI is expressed by the ratio of the observed mean distance to the expected mean distance between neighbours in a hypothetical random distribution (Clark & Evans, 1954). The expected distance is the average between neighbours in a hypothetical random distribution (Clark & Evans, 1954). Analysis were performed using the package “spatialEco” using RStudio (RStudio Team, 2018). The final dataset included 89 observations of *P. ulyssiponensis*, 126 of *P. vulgata*, 98 of *P. depressa* and 45 of *P. rustica* (Appendix II, Table 4).

2.3.2 Environmental data

Environmental factors or ecogeographical variables (EGVs) were downloaded from Global Marine Database (Bio-oracle, Assis *et al.*, 2017). A total of fourteen EGVs were downloaded with a resolution of 5 arcmins (~ 9.2 km at the equator) for the present (2000 - 2014) and for two different years in the future (2050 and 2100), for the worst case scenario, the Representative Concentration Pathways (RCP8.5). The RCP8.5 scenario is characterized by increasing greenhouse gases concentration levels and air pollutants, considering the high emission scenario (Vuuren *et al.*, 2011). EGVs included the maximum, minimum, mean and range of salinity, current velocity and temperature (Table 1). Correlation among variables were tested using the Pearson's correlation in RStudio (RStudio Team, 2018). A total of nine variables were selected based on the lowest correlation ($r < 0.7$) and the highest relevance for the species ecology (Table 1).

Table 1: Environmental variables (EGVs) used for modelling the distribution of four target species. Description, code, range, and units.

Description	Code	Range	Units
Maximum current velocity	maxV	[0.002 - 2.697]	m ⁻¹
Minimum current velocity	minV	[0.000 - 1.826]	m ⁻¹
Range current velocity	rV	[0.000 - 1.650]	m ⁻¹
Maximum salinity	maxSal	[5.473 - 41.126]	PSS
Minimum salinity	MinSal	[1.714 - 39.669]	PSS
Range salinity	rSal	[0.149 - 26.380]	PSS
Maximum sea surface temperature	maxSST	[-1.733 - 34.695]	°C
Minimum sea surface temperature	minSST	[-1.940 - 29.276]	°C
Range sea surface temperature	rSST	[0.090 - 27.834]	°C

2.3.3 Modelling

Species Distribution Models (SDMs) were built for each species in the Northern Atlantic Ocean Area. This area was selected for training the models as it comprises the entire known distribution of the target species (Guerra & Gaudencio, 1986; Lima *et al.*, 2006; Borges *et al.*, 2015). Models should include the complete species' environmental range or at least data from a complete biogeographical area (Pearson *et al.*, 2002; Thuiller *et al.*, 2004; Barbet-Massin *et al.*, 2012; Vale *et al.*, 2014).

SDMs were built using three selected algorithms: Generalized Linear Model (GLM), Generalized Additive Models (GAM) and Maximum Entropy Modelling (Maxent) implemented in the R package "Biomod2" (Thuiller *et al.*, 2016). They require distinct observational data: GLM is a regression like method that relates presence records and absence, GAM used presence and absence, and Maxent aims to maximize the entropy of the species probability distribution using presences and background (Phillips *et al.*, 2006). All models were built using the R package "Biomod2" (Thuiller *et al.*, 2016). As there are no true absences, two datasets (10 000) of pseudo-absences were randomly created for each species (Barbet-Massin *et al.*, 2012). The number of pseudo-absences was chosen to have the same weight as presence data in the calibration process (prevalence = 0.5). 75 % of data was used to build the models while the remaining 25 % was used for testing the models. Individuals models were evaluated using True Skill Statistic (TSS), which has been demonstrated as highly effective for assessing model performance (Allouche *et al.*, 2006). TSS is a measure of models accuracy based on the confusion matrix (Allouche *et al.*, 2006). Predictions are compared to a test dataset to derive the model's sensitivity (i.e. proportion of presences accurately predicted) and

specificity (i.e. proportion of absences accurately predicted; Allouche *et al.*, 2006). It is defined as sensitivity + specificity – 1, and ranges from –1 to +1, where +1 indicates perfect agreement and zero or less indicate a performance no better than random (Allouche *et al.*, 2006). Only models with TSS > 0.70 were kept for further analysis. The TSS threshold was also used to calculate binary models for each algorithm. Then, they were combined to assess the area of agreement among them. In order to visualize modelling results in coastal areas, final maps were cropped by a polygon defined by the 200 meters bathymetric contour (<https://www.gebco.net/>) in QGIS Desktop 3.4.14.

To evaluate model performance, a validation dataset was created with the occurrences data that were not used to build the SDMs. The clustering of observations was decreased by randomly removing localities that were clustered according to the NNI. To calculate the Correct Classification Rate (CCR) of data, the validation datasets were intersected with SDMs for the three algorithms in QGIS Desktop 3.4.14. The CCRs equation is described by:

$$\text{CCR} = [(N_{\text{validation}}) / (Nt_{\text{validation}})] * 100 \quad (\text{equation 3})$$

where N is the number of validation data correctly classified and Nt is the total number of validation data.

2.4 Statistical analysis

The statistical analyses were performed with RStudio version 3.6.0 (RStudio Team, 2018). The alpha level considered for all analysis was 0.05.

A linear regression model was used to assess the relationship between the temperature (°C) and the oxygen consumption ($\mu\text{mol O}_2 \text{ g}^{-1} \text{ h}^{-1}$). Also, a linear regression model was used to assess the relationship between mass-corrected metabolic rate ($\text{Ln}(\text{IM}^{-3/4})$) and temperature ($1/\text{kT}$) for estimating the activation energy.

A logistic regression model was used to assess the relationship between temperature and the probability of survival, using the penalized likelihood method. This regression was performed using the package “logistf” (Heinze & Ploner, 2018).

3. Results

3.1 Metabolic rate

The oxygen consumption ($\mu\text{mol O}_2 \text{ g}^{-1} \text{ h}^{-1}$) rates variation with temperature level ($^{\circ}\text{C}$), for the four species is represented in Figure 7. *P. ulyssiponensis* was the only species where the linear relation between temperature and oxygen consumption was statistically significant ($p < 0.05$) (Figure 7a). For the remaining species, there were no statistically significant linear relation ($p > 0.05$) even though they all exhibit the same tendency - an increase of oxygen consumption with an increase of temperature, demanding however further studies. Within the four species, *P. ulyssiponensis* reveals the highest correlation coefficient value (0.77), followed by *P. vulgata* (0.52), *P. depressa* (0.48), and finally *P. rustica* with the lowest correlation coefficient (0.39).

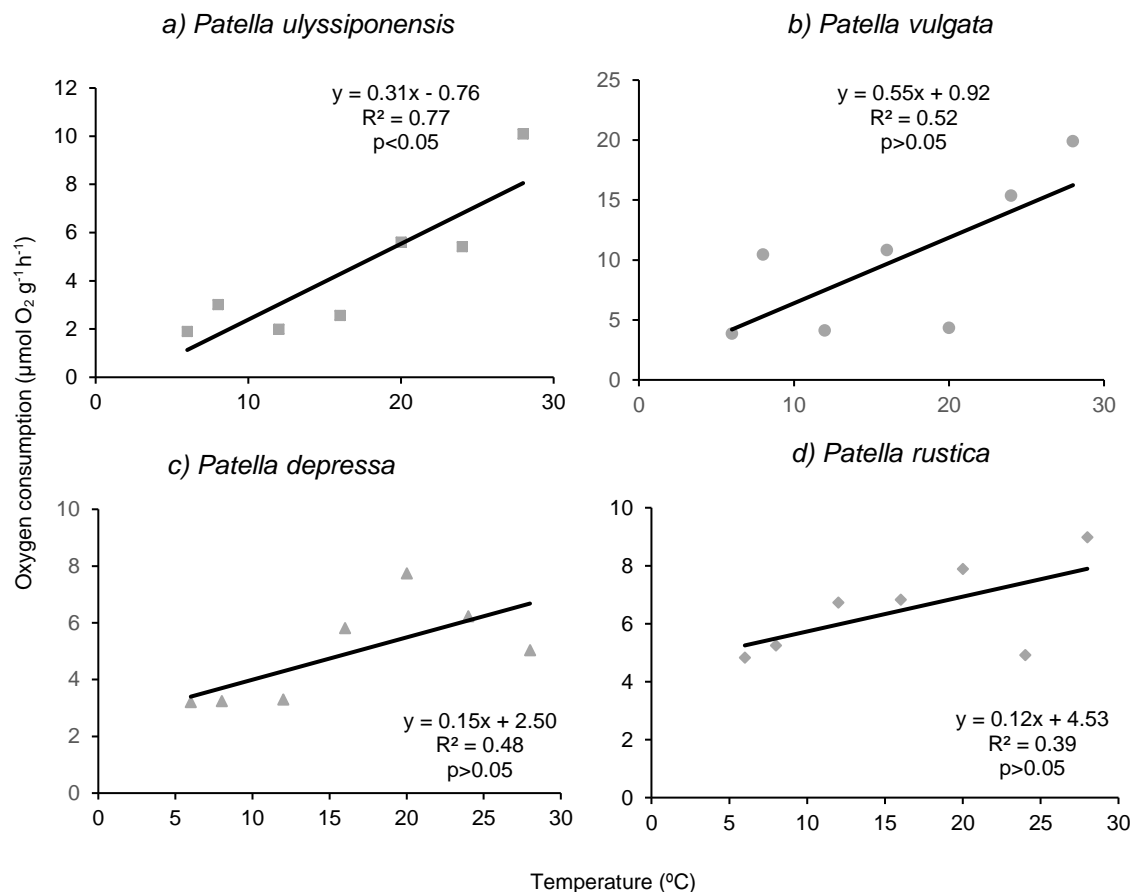


Figure 7: Mean oxygen consumption ($\mu\text{mol O}_2 \text{ g}^{-1} \text{ h}^{-1}$) (n=6) variation with temperature ($^{\circ}\text{C}$) for a) *P. ulyssiponensis*, b) *P. vulgata*, c) *P. depressa* and d) *P. rustica*.

3.2 Activation energy

The activation energy values obtained for the four species ranged between 0.33 eV to 0.76 eV (Figure 8 and Figure 9). *P. ulysiponensis* was the species with the highest activation value (0.76 eV) (Figure 8). For the remaining three species, the activation energy values were quite similar (Figure 8 and Figure 9), *P. rustica* having the lowest value (0.33 eV). Despite the low r-squared, the p-values still indicate a real relationship between the mass-corrected metabolic rate ($\text{Ln}(IM^{-3/4})$) and temperature ($1/kT$) ($p < 0.05$).

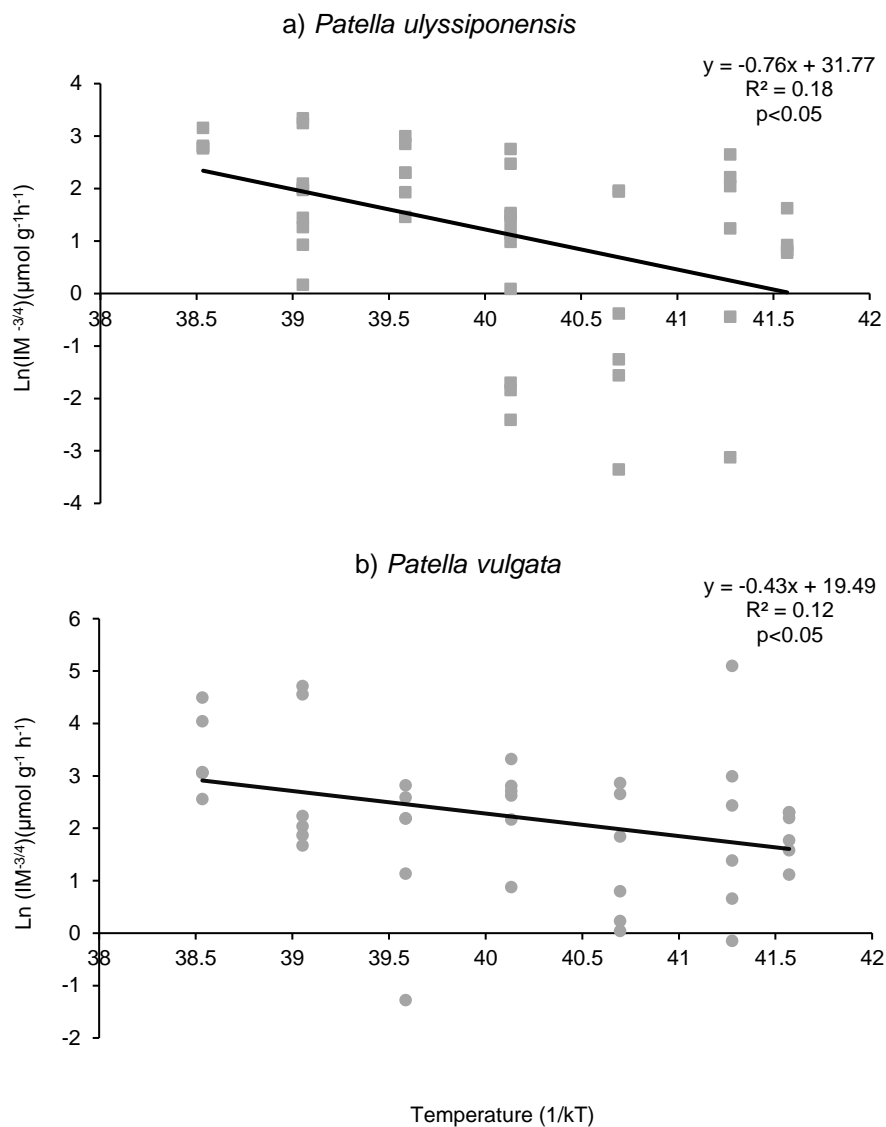


Figure 8: Relationship between mass-corrected metabolic rate ($\text{Ln}(IM^{-3/4})$) and temperature ($1/kT$) for a) *P. ulysiponensis*, b) *P. vulgata*.

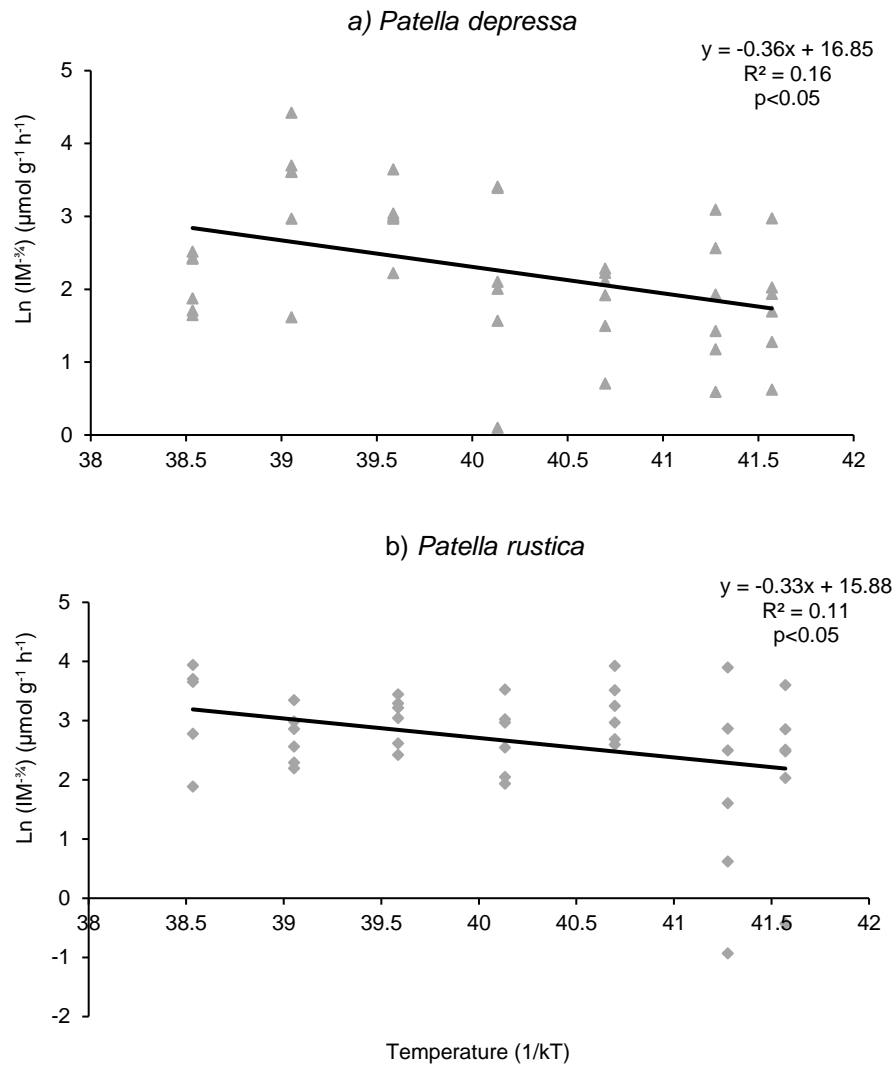


Figure 9: Relationship between mass-corrected metabolic rate ($\text{Ln } (IM^{-3/4})$) and temperature (1/kT) for a) *P. depressa*, b) *P. rustica*.

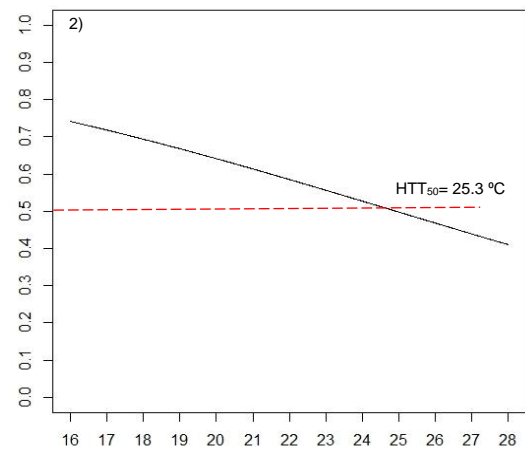
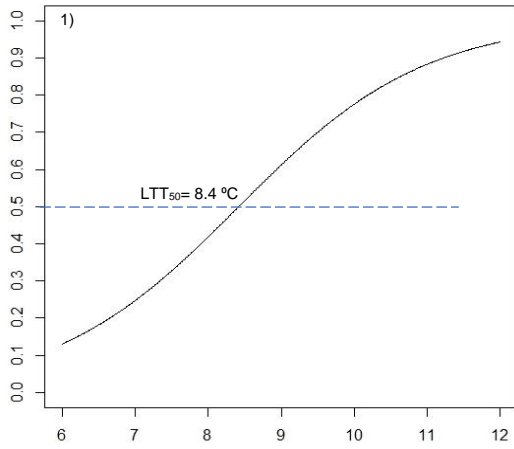
3.3 Mortality trials

For all the species the logistic regressions of the probability of survival (%) under lower temperatures (between 6°C and 12°C) and higher temperatures (between 16°C and 28°C) were statistically significant ($p < 0.05$) (Figure 10a and Figure 10b). The LTT_{50} and HTT_{50} values were very similar for both *P. vulgata* (10.3°C and 24.3°C respectively) and *P. depressa* (10.7°C and 24.8°C respectively). *P. ulysiponensis* had the lower LTT_{50} value (8.4°C) and a higher HTT_{50} value (25.3°C) compared to the other species.

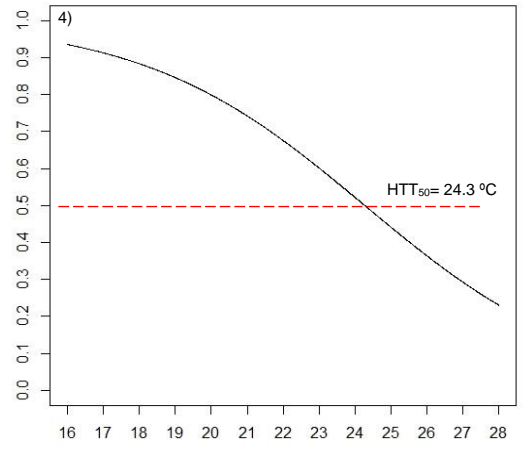
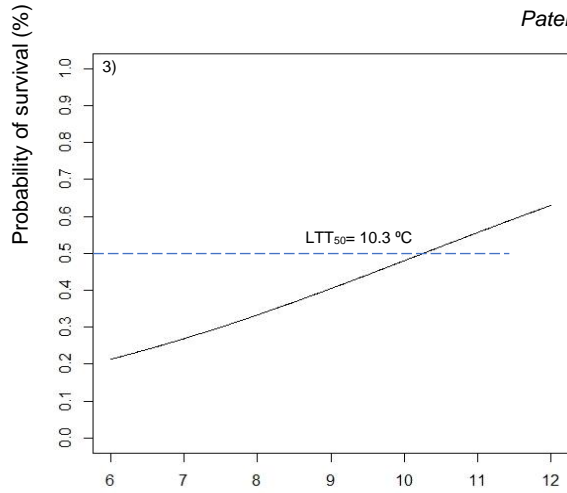
a) Low thermal threshold

b) High thermal threshold

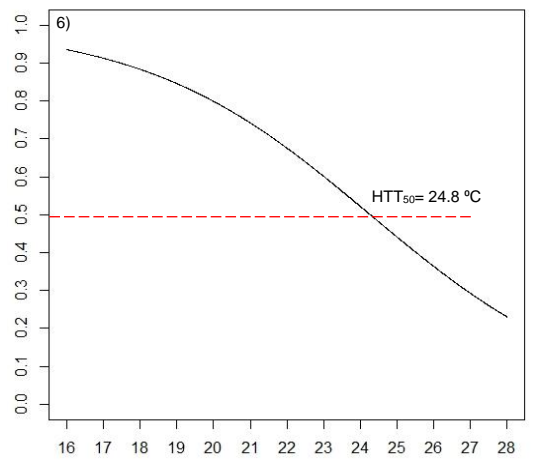
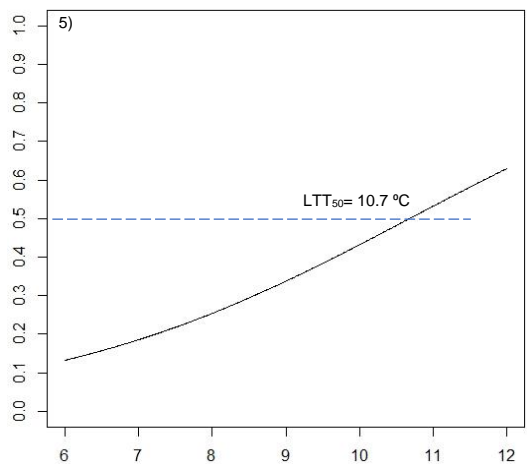
Patella ulyssiponensis



Patella vulgata



Patella depressa



Temperature (°C)

Figure 10: a) Probability of survival of three species at the end of the experimental period for lower temperatures: 1) *P. ulyssiponensis* ($y = \frac{e^{-6-6+0.784x}}{1 + e^{-6-6+0.784x}}$, $p < 0.05$); 3) *P. vulgata* ($y = \frac{e^{-3.14+0.306x}}{1 + e^{-3.14+0.306x}}$, $p < 0.05$); 5) *P. depressa* ($y = \frac{e^{-4.29+0.402x}}{1 + e^{-4.29+0.402x}}$, $p < 0.05$). b) Probability of survival of three species at the end of the experimental period for high temperatures: 2) *P. ulyssiponensis* ($y = \frac{e^{3.97+0.172x}}{1 + e^{3.97+0.172x}}$, $p < 0.05$); 4) *P. vulgata* ($y = \frac{e^{7.85+0.323x}}{1 + e^{7.85+0.323x}}$, $p < 0.05$); 6) *P. depressa* ($y = \frac{e^{15.9-0.664x}}{1 + e^{15.9-0.664x}}$, $p < 0.05$).

3.4 Species distribution models

There is confidence in model's prediction for all species. TSS values ranged from 0.54 (*P. rustica*; GLM models) to 0.85 (*P. vulgata*; Maxent models) and their mean was 0.74 (Table 2b). Comparing the TSS values of the four species, Maxent models had the highest values. Binary maps identified suitable cells for each species. Agreement among algorithms predictions ranged from 12 % to 30 % of the total area predicted for each species. The percentage of CCR ranged from 56 % to CCR 99 % (Appendix I, Table 3).

The three algorithms used for predicting the distribution of species have identified different EGVs related to species distribution (Table 2a). GLM models identified rSST as the most important variable for the distribution of *P. ulyssiponensis* and *P. depressa* and minimum (minSal) and maximum (maxSal) salinity for *P. vulgata* and *P. rustica* distributions, respectively. GAM models identified rSST as the most important variable for the distribution of *P. ulyssiponensis* and *P. vulgata* and minimum and maximum SST for *P. depressa* and *P. rustica*, respectively. The variable minSST was the driver of *P. ulyssiponensis*, *P. depressa* and *P. rustica* distributions when Maxent was used (Table 2a).

Table 2: a) Importance of environmental variables for the distribution each: *P. ulyssiponensis* (Pu), *P. vulgata* (Pv), *P. depressa* (Pd) and *P. rustica* (Pr). Code of variables and description in Table 1. (b) Values of TSS (True Kill Statistic) for each species and modelling approach.

	GLM				GAM				Maxent			
	Pu	Pv	Pd	Pr	Pu	Pv	Pd	Pr	Pu	Pv	Pd	Pr
a) Code	Variable importance											
maxV	0.185	0.341	0.142	0.085	0.351	0.339	0.250	0.282	0.263	0.252	0.178	0.238
minV	0.141	0.081	0.121	0.042	0.250	0.211	0.285	0.274	0.104	0.067	0.132	0.056
rV	0.039	0.147	0.065	0.048	0.149	0.184	0.203	0.237	0.049	0.058	0.041	0.091
maxSal	0.418	0.909	0.583	0.687	0.956	0.984	0.959	0.890	0.004	0.030	0.211	0.141
minSal	0.454	0.954	0.631	0.269	0.967	0.986	0.991	0.949	0.031	0.018	0.024	0.016
rSal	0.426	0.898	0.533	0.197	0.915	0.927	0.930	0.961	0.140	0.341	0.326	0.102
maxSST	0.611	0.929	0.671	0.129	1.000	1.000	0.977	0.992	0.377	0.592	0.531	0.056
minSST	0.559	0.891	0.656	0.041	0.967	0.928	0.994	0.930	0.679	0.499	0.599	0.565
rSST	0.869	0.802	0.955	0.072	1.000	1.000	0.009	0.939	0.148	0.128	0.147	0.060
b) Evaluation test												
TSS	0.63	0.84	0.73	0.54	0.75	0.83	0.81	0.56	0.81	0.85	0.84	0.71

For *P. ulyssiponensis*, the predicted current distribution ranged from North Norway to Northern Africa, including the British Islands and Portugal (Figure 11a, Appendix III, IV, V, VI). Models have also predicted isolated populations in North America and the Mediterranean Sea (Figure 11a). Projections for the future conditions showed a northward expansion in 2050 and 2100 (Figure 11a). An increase of *P. ulyssiponensis* distribution area in Iceland was projected to 2100 (Figure 11a). The predicted current distribution of *P. vulgata* ranged from North Norway to Portugal, with its Southern limit in the centre of Portugal (Figure 11b). Current models have also predicted isolated populations in the Mediterranean Sea and North America (Figure 11b, Appendix III, IV, V, VI). In 2050, *P. vulgata* will expand northward and the isolated populations in Mediterranean Sea will disappear. In 2100, the species distribution will shift northward and its Southern limit will be set in the South coast of France. The predicted current distribution models of *P. depressa* ranged from British islands to North Africa, including Portugal and the Mediterranean Sea (Figure 11c, Appendix III, IV, V, VI). The models have also predicted an isolated population in North America (Figure 11c). A northward expansion to the south of Norway was predicted for 2050. In 2100, the models have projected an expansion to the Northern Sea. The predicted current models of *P. rustica* ranged from the Mediterranean Sea to North Africa (Figure 11d, Appendix III, IV, V, VI). Isolated populations were also predicted in the Southern part of North America (Figure 11d). Projected models for 2050 have shown that this species will continue to appear in the Mediterranean Sea and will expand towards Southern Africa. This expansion will continue in 2100. Also, the projections models for 2050 and 2100 have predicted an increase of isolated populations in Red Sea.

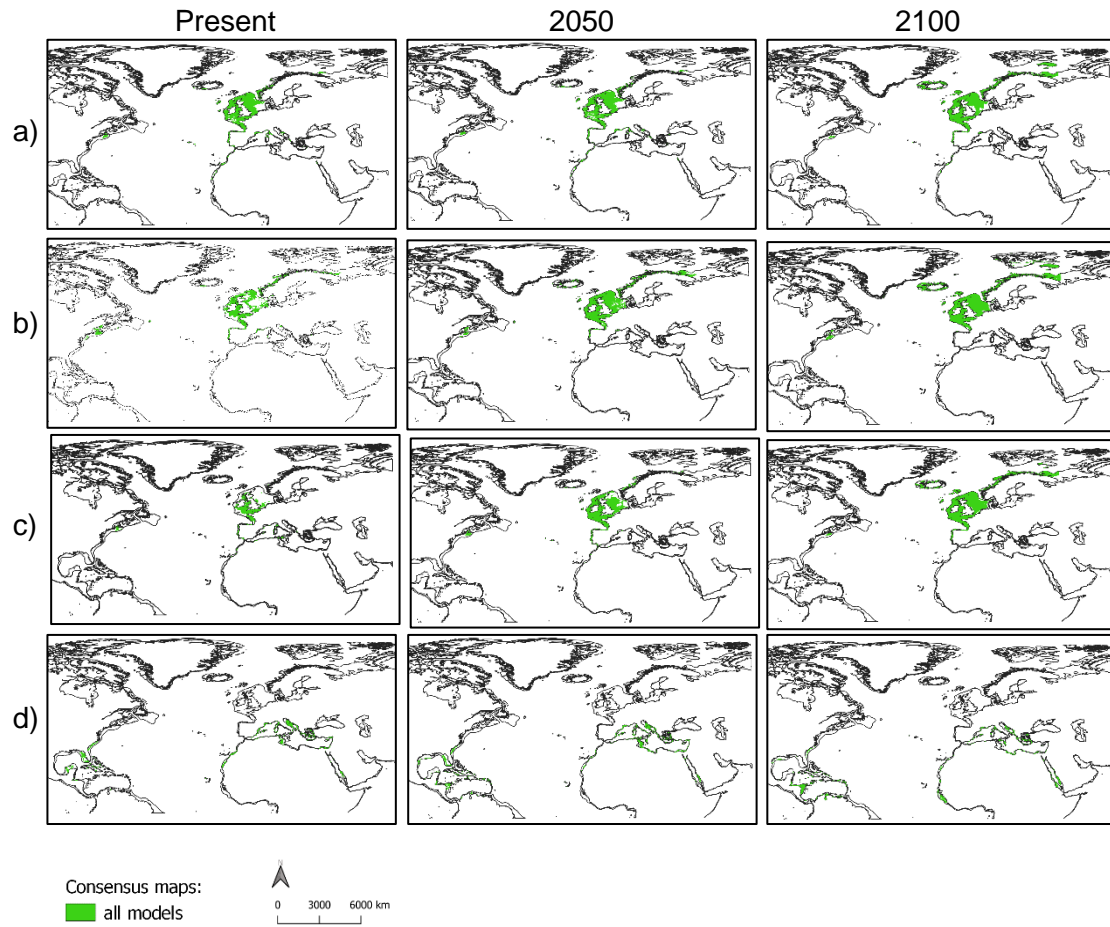


Figure 11: Predicted suitable areas of the target species in current conditions and projections for 2050 and 2100 under the RCP8.5 scenario: a) *Patella ulysiponensis*, b) *Patella vulgata*, c) *Patella depressa* and d) *Patella rustica*.

4. Discussion

4.1 Metabolic rate

Among intertidal organisms, the metabolism is regulated by environmental conditions, as well as physiological factors (e.g. body size, activity level, growth and reproduction) and have been the target of many studies (Davies, 1966; 1967; Newell, 1973; Branch & Newell, 1978; Newell & Branch, 1980; Branch *et al.*, 1988). For example, Newell *et al* (1973) suggested that the capacity of an organism to increase its activity and metabolic rate when suitable environmental conditions prevail is a crucial adaptation and allows the reduction of the use of metabolic reserves during the stress periods. Environmental factors, normally associated with the presence of food, may induce high levels of activity in intertidal organisms and it is associated with an increase in the metabolic rate (Newell & Roy, 1973). In contrast, situations of environmental stress such as extreme temperatures or starvation may reduce the slope of activity and consequently decrease the metabolic rate (Newell, 1973). Branch *et al* (1988) demonstrated the influence of temperature and food availability in oxygen consumption of intertidal organisms. A comparison between the species allowed them to conclude that temperature should not be the only factor considered when studying oxygen consumption variations, since it is influenced by other activities such as growth and reproduction (Branch *et al.*, 1988). Additionally, Parry (1978) indicated that seasonal modifications in oxygen consumption of the limpet *Cellana tramoserica* can be predicted by an increased growth rate.

Davies (1996; 1997) studied the effect of body size, temperature, and environmental acclimation on the metabolic rate in *P. vulgata* and *P. aspera* (now called *P. ulyssiponensis*). The results suggested that the low respiration rate of high-level limpets could result from either acclimation to the higher temperatures or lower nutritional conditions of the habitat. The maximum metabolism of *P. vulgata* coincides with the period in which food is most abundant (Davies, 1967). That indicates that seasonal changes in the growth of *P. vulgata* are related to food availability. The higher nutritional level of *P. vulgata* during the summer causes a more rapid growth, which, in turn, results in a higher metabolic rate (Davies, 1967).

Although the temperature is not the only environmental parameter considered when studying the metabolic rate (e.g. oxygen consumption) it is one of the most influencing factors in terms of its effect on an organisms performance (Somero, 2002). Understanding how various species will respond to higher temperatures will be crucial to predict the effect of changing conditions on natural populations and community structures (Helmuth *et al.*, 2006). The present study aimed to evaluate the influence of

temperature on the oxygen consumption of four species of the genus *Patella*. The oxygen consumption of *Patella* spp. was investigated for the first time for populations from the Portuguese coast.

The oxygen consumption for *P. ulyssiponensis* increased linearly with temperature within the range of tested temperatures (6°C to 28°C) (Figure 7). This outcome is in agreement with the MTE, which predicts that biological rates (e.g. respiration rate) show a similar temperature dependence (Brown *et al.*, 2004). Several authors confirmed the effect of temperature in other marine species such as various sea urchins indicate that the rate of oxygen consumption for these organisms increases significantly with the acclimation temperatures (Ulbricht & Pritchard, 1972; Díaz *et al.*, 2017). Noisette *et al.* (2015) demonstrated the same temperature dependence for the mollusc *Crepidula forficata*. Furthermore, the literature indicates a linear increase of the oxygen consumption with increasing temperatures for *P. vulgata* and *P. aspera* (*P. ulyssiponensis*) species (Davies, 1996; 1997; Tagliarolo *et al.*, 2013).

For the remaining species, *P. vulgata*, *P. depressa* and *P. rustica*, the results showed no statistically significant linear relation between the variables. Despite non-significant, the results suggest an increase of the oxygen consumption with the temperature (Figure 7), similar to the tendency observed for *P. ulyssiponensis*. However, to confirm this outcome further studies are required, such as the use of large replicated studies, which will help to find the real relationship between the temperature and oxygen consumption.

4.2 Activation Energy

The activation energy determines the sensitivity of the metabolic rate to temperature (Watson *et al.*, 2014). In this study, the activation energy was determined using oxygen consumption ($\mu\text{mol O}_2 \text{ g}^{-1} \text{ h}^{-1}$) under different temperatures. Gillooly *et al.* (2001) and Brown *et al.* (2004) studied the activation energy of both marine and freshwater species, achieving a general interspecific mean activation energy of 0.65 eV. However, variations from this value are often found ranging from 0.2 eV to 1.2 eV (Gillooly *et al.*, 2001). The values of activation energy for *Patella* spp. ranged from 0.33 eV to a maximum of 0.76 eV, with an average of 0.47 eV (Figure 8 and Figure 9), being within the predicted range by the MTE.

Angilletta *et al.* (2010) explain that interspecific differences in thermal sensitivity are generally correlated to habitat characteristics. In addition, Watson *et al.* (2014) added that daily temperature fluctuation has been shown to produce different effects on aquatic animals. Thermal sensitivity in marine invertebrates varies considerably depending on

the taxa (Watson *et al.*, 2014). The thermal sensitivity, growth and performances of several organisms are low under highly variable environments, with frequent extreme temperature events, such as those experienced on intertidal habitats (Folguera *et al.*, 2011). The thermal metabolic insensitivity recorded at high temperature in intertidal habitats has been shown to be an energy saving adaptation during low tide periods (Sokolova & Pörtner, 2003).

The activation energy obtained for *P. ulyssiponensis* (0.76 eV) shows that this species is more sensitive to temperature variations. This could be related to its rocky shore usual location, since this species can be normally found in the low-shore or tide pools. Due to its location in the shore, during the low tide, *P. ulyssiponensis* is exposed to short periods of emersion, being protected from extreme temperature variations along the day. For the remaining species - *P. vulgata* (0.43 eV), *P. depressa* (0.36 eV), and *P. rustica* (0.33 eV) - the activation energy values obtained demonstrated the lower sensitivity of these species to temperature changes. These limpets are usually found in the mid and upper-shore (Boaventura *et al.*, 2002a), revealing a higher capacity to tolerate higher temperatures than limpets located in the low-shore. Despite the exposure to environmental stressors during the emersion (e.g. air temperature, desiccation and solar radiation) these species are well adapted and survive these extreme temperature variations.

The relationship between the thermal sensitivity of the oxygen consumption and the location of the organisms in the shore could be further investigated by studying intraspecific and interspecific variations at different tide levels. For example, individuals from the same or different species would be collected from the low and high shore and its activation energy for the oxygen consumption investigated at both shore levels. Initially this study could be performed at one shore and then generalised to other shores to investigate for general patterns.

4.3 Mortality trials

In the intertidal zone, the survival of the organisms living in the interface of the marine and terrestrial realms requires withstanding of a broad array of abiotic factors. Temperature gradients depend not only on the climate and seasons, but also fluctuate regularly during emersion and immersion through each tidal cycle (Harley *et al.*, 2009). Thermal stress in the intertidal zone differs at a variety of spatial and latitudinal scales, which may exceed optimum or even critical temperature limits of animals for short periods (Davenport & Davenport, 2005). Understanding the organism's thermal limits will

be useful to investigate how the climate warming can influence the behaviour and distributions ranges.

Patella spp. are susceptible to fluctuations in aerial conditions and sea surface temperature and therefore, considered indicators of climatic variability (Lima *et al.*, 2006). This section of the work aimed to evaluate the temperature effects in the limpet's probability of survival. For temperatures between 6°C and 12°C, the LTT₅₀ of survival was 8.4°C for *P. ulyssiponensis*, 10.3°C for *P. vulgata* and 10.7°C for *P. depressa* (Figure 10a). These values are the lower temperature limits for each species studied, indicating that *P. ulyssiponensis* tolerates lower temperatures than *P. vulgata* and *P. depressa*. For a higher range of temperatures (16°C to 28°C), the HTT₅₀ of survival was 25.3°C for *P. ulyssiponensis*, 24.3°C for *P. vulgata* and 24.8°C for *P. depressa* (Figure 10b). Therefore, *P. ulyssiponensis* presented a higher thermal limit than the other two species – *P. vulgata* and *P. depressa*.

This research was only carried out for temperature ranges between 6°C and 28°C, however other authors reported experiments for the same species at higher temperatures. Vinagre *et al* (2019) studied the thermal limits of temperate and tropical organisms for seven days and suggested 38.85°C and 37.45°C for *P. vulgata* and *P. depressa*, respectively. While according to Evans (1948) limpets from the British Islands survive temperatures superior to 40°C. This last study showed a lethal temperature of 42.8°C for *P. vulgata*, 43.3°C for *P. depressa* and 41.7°C for *P. athelica* (now called *P. ulyssiponensis*) (Evans, 1948). In future studies, a wider range of temperatures should be considered to fully understand the thermal limits for survival of these species in Portugal.

4.4 Species distribution models

The recruitment of sessile and mobile marine species, particularly those with a planktonic larval stage is largely influenced by hydrogeographic conditions (e.g. temperature, salinity, pH, coastal water movements, wind speed and direction, upwelling frequency and intensity) and by physical barriers (Helmuth *et al.*, 2006).

Species Distribution Models (SDMs) of the four target species reinforced the idea that seawater temperature is probably the main driver of the distribution of marine organisms, including intertidal species, as reported by Jenkins *et al* (2001) and Moore *et al* (2011). Indeed, other authors have found similar results (Lima *et al.*, 2006; Seabra *et al.*, 2015; Seabra *et al.*, 2016). Changes in seawater temperature have proven to have strong effects on metabolism, growth, behaviour, reproduction, larval development and consequently affect the distribution of the species (Southward *et al.*, 1995; Helmuth *et al.*, 2006; Hawkins *et al.*, 2009; Mieszkowska & Lundquist, 2011). Helmuth *et al* (2006) suggested most of the stages, from gametogenesis to the adult stage, are controlled by sea temperature. This effect is expected to have an impact on the reproductive output, leading to changes in abundance of intertidal organisms (Helmuth *et al.*, 2006). Also, sea surface temperature might be a major determinant of *Patella rustica* reproductive success and, consequently, its dispersal potential (Lima *et al.*, 2006). These authors have also observed an expansion phenomenon of this species, which recolonised a historical gap at the Northern end of its distribution on the Portuguese coast, during the late 1990s (Lima *et al.*, 2006; 2007). In the Northern co-occurrence zones of *Patella vulgata* and *Patella depressa*, sea surface temperatures have been increasing throughout the recent decades (Vega, 2018). *P. depressa* at favourable seawater temperature and closest to its optimum, has great growth activity, more reproductive output and, ultimately, recruitment (Moore *et al.*, 2011). Possibly, this factor could contribute to increasing this species dispersal potential, as observed for *P. rustica*. *P. vulgata* is especially susceptible to increasing temperatures and its activity decreases under temperatures above 27.5°C (Seabra *et al.*, 2016), despite being able to survive temperatures up to 42.8°C (Evans, 1948). On the other hand, salinity has also appeared to be important for the distribution of *P. vulgata* and *P. rustica*. This might be explained by the positive relationship between water salinity and *Patella* survivors (Denny & Gaines, 2007). Exposure to freshwater or low levels of salinity can be extremely stressful for limpets (Seabra *et al.*, 2016). Little *et al* (1991) observed reduced levels of activity in limpets after rainfall and, at low salinities in laboratory conditions, activity completely stopped. In the intertidal zone, *P. vulgata* and *P. rustica* can be found in the upper-shore (Boaventura *et al.*, 2002a; Lima *et al.*, 2006) - a zone where the variability in salinity is

typically higher than in low-shore (Denny & Gaines, 2007). Further studies are needed to understand the relation between each species and levels of water salinity.

The predicted distribution of the four target species is in line with previously described distribution ranges (Guerra & Gaudencio, 1986; Southward *et al.*, 1995; Boaventura *et al.*, 2002a; Kendall *et al.*, 2004; Lima *et al.*, 2006; 2007; Borges *et al.*, 2015). Although, models have predicted the presence of the four species in North America and *P. rustica* in the Red Sea, there are no records of these species presence in such areas. Despite such results, there is confidence in models' predictions as values of accuracy are high (TSS > 0.70). Models have predicted suitable conditions for the occurrence of these species in North America and Red Sea, because they meet the environmental conditions for occurrence of these species. Indeed, the genus *Patella* is historically restricted to the North-eastern Atlantic and Mediterranean rocky shores (Henriques *et al.*, 2012). The colonisation of the Western Atlantic and the Red Sea is biologically unfeasible due to the long distance to source populations. The life cycle of these species is characterised by a planktonic larval stage and a benthic adult stage, and large-scale movements are exclusive to the planktonic larval stage (Orton *et al.*, 1956). The distance travelled in the ocean current is dependent on the planktonic larval stage duration (Sponaugle *et al.*, 2002). For *Patella* spp., the planktonic larval stage duration was reported by Ribeiro (2008), ranging between 2.8 - 13.7 days in *P. ulyssiponensis*, 5.7 - 14.6 days in *P. vulgata* and 3.7 - 14 days in *P. depressa*. The distance required for the planktonic larvae to travel from the Eastern Atlantic to the Western Atlantic (or to the Red Sea), is greater than the number of days of planktonic larval stage making it impossible to survive until finding suitable substratum to settle.

All target species were predicted to shift their range towards the North. According to RCP8.5, there will be an increase in temperature in the future (~ 1.5°C) (IPCC 2018). Therefore, if temperature influences distribution of target species, it is expected that they will expand northwards. Global warming is leading to a physiological adaptation of these species to the new conditions or changing their distribution range to locations where the temperatures are more favourable to survive (Doney *et al.*, 2012). Distribution shifts have been predicted to happen in the future for several marine organisms in response to global climate change (Thompson *et al.*, 2002; Hawkins *et al.*, 2009; Firth *et al.*, 2009). For example, changes in assemblage composition and distribution of seaweed have been observed in Europe with advances of Northern limit of Southern species and retraction of the Southern limit of Northern species (Jueterbock *et al.*, 2013; Assis *et al.*, 2016). Such studies have predicted the potential northward shift of intertidal seaweed along temperate North-Atlantic rocky shores, in the future (Jueterbock *et al.*, 2013; Assis *et al.*, 2016). The same predictions have also been made for *Chathamalus* spp., under different

climate scenarios (Hawkins *et al.*, 2008). For *Semibalanus balanoides*, some predictions indicate that the species will disappear in Southwest England, due to climate warming by the 2050s (Poloczanska *et al.*, 2008). *S. balanoides* has already disappeared from the coast of northern Spain and shifted their range towards the North (Wetthey *et al.*, 2008). In conclusion, predictive models are a valuable tool for studying the distribution of limpets under future climate change scenarios.

5. Final remarks

The increase in ocean temperature is probably the most evident effect of climate change. It alters patterns of distribution and phenology of marine organisms, by modifying the physiological processes that allow them to adapt and survive to specific temperature ranges (Harley *et al.*, 2009). The present study provided information about the effect of temperature in oxygen consumption in four species that occur in the rocky shores of Portugal. This work provided new information about the thermal limits for three *Patella* spp. from mainland Portugal and can be used as a starting point for future studies. Additionally, in a future perspective it would be important to extend the temperature ranges to better understand this relationship.

Under climate change scenarios, temperatures are expected to rise globally. With it, the effects of limpet's grazing of seaweed assemblages will probably intensify, causing a disruption in the balance of intertidal seaweed assemblages. Increasing temperatures will be responsible for overcoming the grazing metabolic threshold, leading to shifts in community regimes, from a top-down (herbivore-regulated) to a bottom-up (seaweed or nutrient-regulated) system (Sampaio *et al.*, 2017). The Metabolic Theory of Ecology has been used to predict increases in top-down control of seaweed assemblages (O'Connor, 2009), with limpets grazing being an excellent example of exerting top-down control of seaweed assemblages in the intertidal. This study contributed to increase the knowledge concerning the influence of temperature on oxygen consumption rate for *Patella* spp. thereby providing insights for using limpets as models to test those predictions.

The predicted current models allowed to identify the environmental variables that most contribute to *Patella* spp. distribution - sea surface temperature and salinity. Understanding which variables are most important in a species ecology and distribution is fundamental before predicting futures changes, especially considering climate change. Future prediction models for *Patella* spp. in the Northern Atlantic Ocean suggested changes in the distribution of the species due to climate warming. Changes in their range towards the North urge the application of effective conservation measures, not only to protect these species, but also to protect the species that already inhabited the sink localities.

The development of coastal engineering structures offers an opportunity to increase habitat complexity in marine habitats and to manage the biodiversity loss (Bulleri & Chapman, 2010; Martins *et al.*, 2010; Firth *et al.*, 2014). Artificial structures in the shore provide important habitat for marine organisms and have showed to promote the recruitment, increase the populations, and reduce the mortality (Firth *et al.*, 2014). For limpets, these engineering structures have been studied in the Portuguese islands,

revealing themselves to be effective in promoting the stock recovery of exploited species (Martins *et al.*, 2010). In these islands some measures, such as minimum catch sizes, areas where limpet harvesting is interdicted and closed seasons, were implemented to guarantee the conservation of the species. Marine Protected Areas (MPAs) emerge as a solution to contribute to maintaining biodiversity, recovering stocks and improving habitat quality (Abecasis *et al.*, 2013). Over the last decades, MPAs have gained much importance as conservation and management tools to restore stocks of exploited marine organisms (Abecasis *et al.*, 2013; Diogo *et al.*, 2016). Despite the implementation of MPAs contributing as a measure to conserve limpet populations in the islands, monitoring programs should also be designed to better understand spatial and temporal changes of these populations and better protect them (Abecasis *et al.*, 2013; Sousa *et al.*, 2019).

With species changing their distributions, it is important to consider when new species enter an established community. Upon their introduction, they will compete with pre-existing species, creating a complex network of interactions that might be difficult to manage. It is crucial to understand species interactions and predict distributional shifts, so that effective management measures can be applied. If the correct measures are applied in time, the disappearance of species might be avoided. This allows to preserve not only their ecological value, but also their future potential for biotechnological applications.

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7. Appendix

Appendix I

Table 3: Percentage of correct classification rate (%CCR) of models for each algorithm and each species.

	% CCR			Mean
	GLM	GAM	Maxent	
<i>Patella ulyssiponensis</i>	98	93	99	96.6
<i>Patella vulgata</i>	99	92	99	96.6
<i>Patella depressa</i>	99	97	99	98.3
<i>Patella rustica</i>	87	56	97	83.3

Appendix II

Table 4: Initial dataset, final dataset and Nearest Neighbour Index (NNI).

	Initial dataset			Final dataset	NNI	p-value	Validate dataset	
	OBIS	GBIF	Total				NNI	p-value
<i>Patella ulyssiponensis</i>	280	2 287	2 567	89	0.710	1.66x10 ⁻⁰⁷	0.085	1.02x10 ⁻¹⁹
<i>Patella vulgata</i>	2 000	10 000	12 000	127	0.730	6.93x10 ⁻⁰⁹	0.08	0.9x10 ⁻¹⁹
<i>Patella depressa</i>	153	882	1 035	98	0.713	5.70x10 ⁻⁰⁸	0.169	7.15x10 ⁻³⁰
<i>Patella rustica</i>	491	257	748	45	0.733	6.12x10 ⁻⁰⁷	0.229	4.81x10 ⁻⁶³

Appendix III

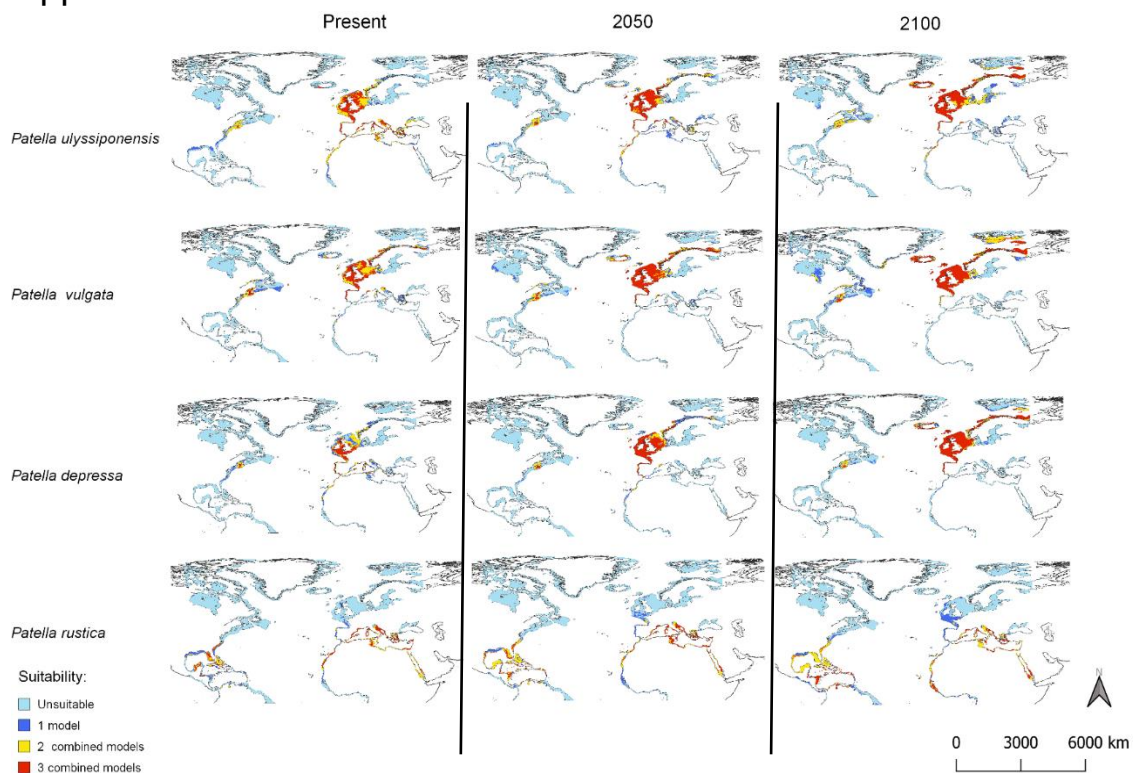


Figure 12: Consensus map of the predicted suitable areas of the for target species in current conditions and projections for 2050 and 2100 under the RCP8.5 scenario. a) *Patella ulyssiponensis*, b) *Patella vulgata*, c) *Patella depressa* and d) *Patella rustica*.

Appendix IV

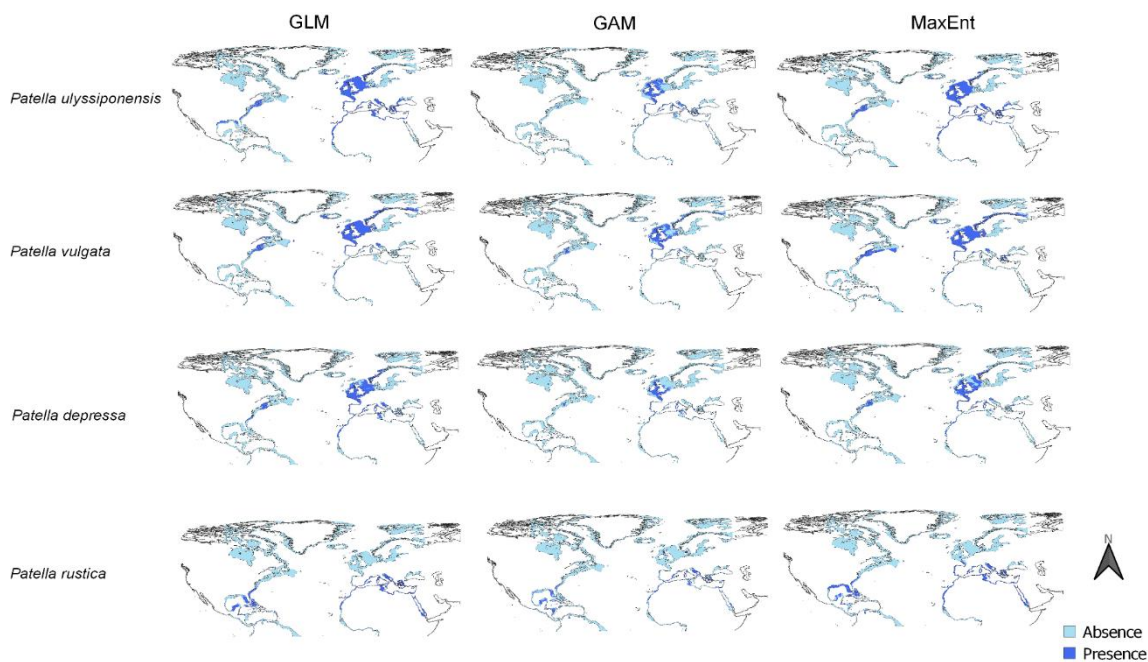


Figure 13: Predicted suitable areas of the for target species in current conditions for each model. a) *Patella ulyssiponensis*, b) *Patella vulgata*, c) *Patella depressa* and d) *Patella rustica*

Appendix V

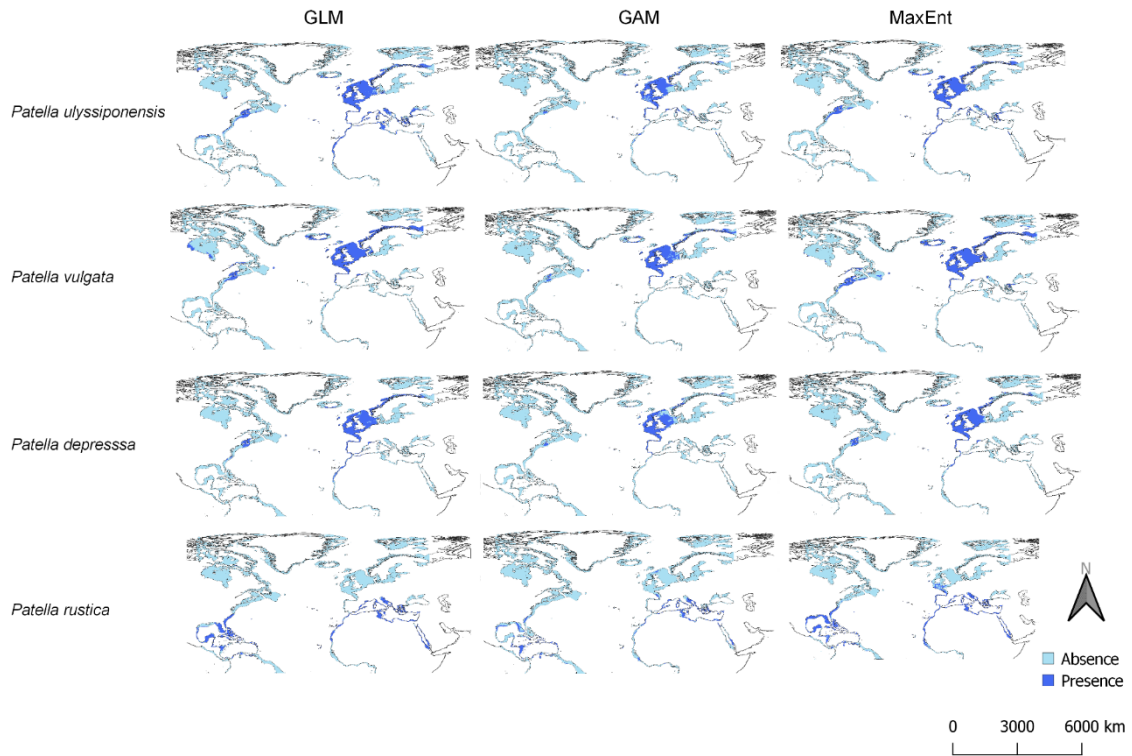


Figure 14: Projection of suitable areas of the for target species for 2050 under the RCP8.5 scenario. a) *Patella ulyssiponensis*, b) *Patella vulgata*, c) *Patella depressa* and d) *Patella rustica*.

Appendix VI

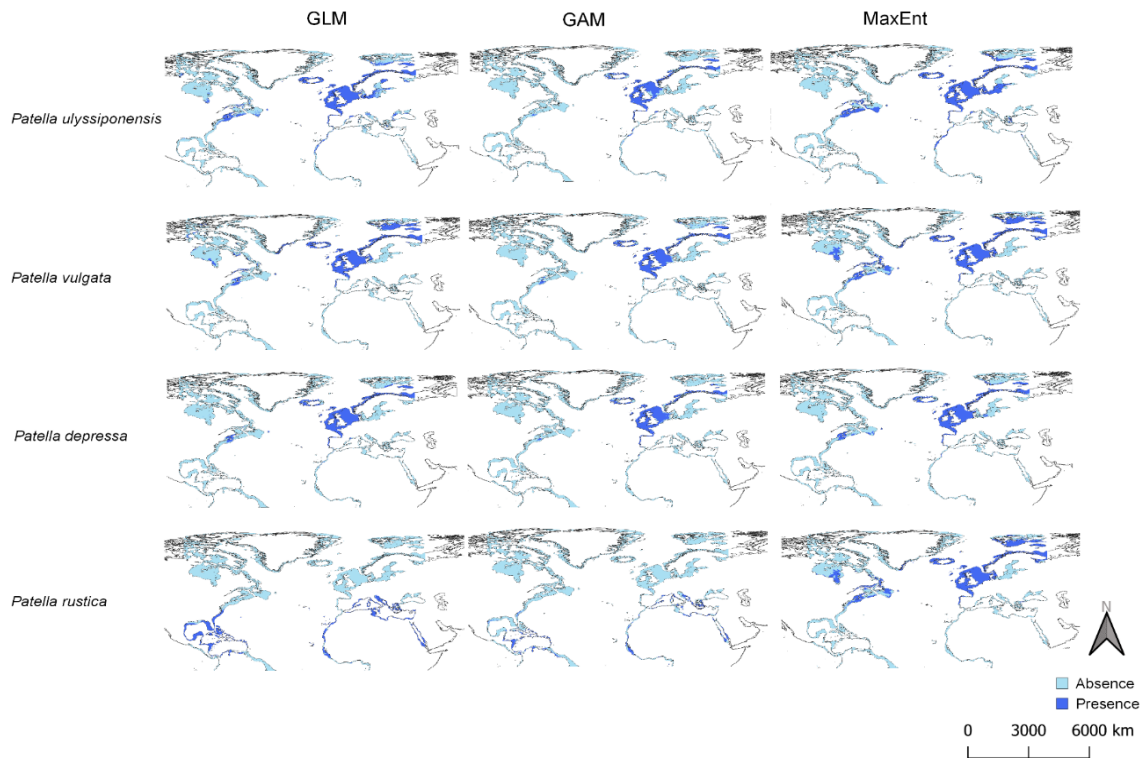


Figure 15: Projection of suitable areas of the for target species for 2100 under the RCP8.5 scenario. a) *Patella ulyssiponensis*, b) *Patella vulgata*, c) *Patella depressa* and d) *Patella rustica*.

