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**Living at the edge: Ecology of Patella species in Britain**

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## **Living at the edge: Ecology of *Patella* species in Britain**

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Submitted in accordance with the requirements for the degree of Doctor of Philosophy

**November 2018**

## SUMMARY

Climatic fluctuations over the last 120 years have been well described in northern Europe, showing alternation of colder (1910s to 1920s, 1960s to 1980s) and warmer (1930s to 1950s) periods upon which recent anthropogenic warming has been superimposed. Biological manifestation of such changes in climate may be determined by examination of shifts in species distribution and performance traits. In Britain, shifts in biogeographic ranges of species have been well documented because of the biogeographical boundary, which crosses the British Isles featuring the overlapping geographical distributions of cold- and warm-water species. Patellid limpets have been proposed as climatic indicators and they are considered a keystone species on exposed- and semi-exposed rocky shores in the British Isles. Changes in demographic attributes across the distributional range will therefore have consequences on intertidal communities. This PhD thesis has studied two patellid species: the warm-water species *Patella depressa*, which reaches its northern limit in Britain and its congener, and putative competitor, the cold-water species *Patella vulgata*. The overall question was addressed towards what processes at individual and population levels are setting both poleward range limits of *P. depressa* distribution. Thus, in order to determine how geographical distribution in relation to range edge affects individual and population traits, the southern limpet *P. depressa* was studied in detail at two poleward range limits in Britain (North Wales [N-Wales] and South-east [S-East] England) and at more central populations in South-west (S-West) England. Comparisons based on both historical and current abundances, size, growth, mortality and competition were made with its sibling species *P. vulgata*, which is at its centre of distribution in Britain.

Results showed that shifts in the two-poleward limits of *P. depressa* have occurred in different ways over the past decades, evidenced by historical records in Britain (1950s). The current range edge of *P. depressa* in N-Wales has not fully recovered to that occupied in the warm 1950s after the cooler 1960s to early 1980s. Nowadays, breeding populations reach the northern edge of Cardigan Bay and have not re-extended around the Llyn Peninsula. Scattered individuals are no longer found on Anglesey as in the early 1980s. In contrast, in the English Channel, its abundance was higher in the warm 1950s than the cooler early 1980s, but its range has now extended to the east of the Isle of Wight, forming a breeding population at Southsea. Further, long-term comparisons (1980-2016) have indicated that *P. depressa* has different abundance patterns towards the two leading edges in Britain. *P. depressa* has been much less abundant in N-Wales when compared with populations in S-East England in the last 35 years. Furthermore, a significant fraction of individuals of juvenile *P. depressa* (less than 15 mm in length) were found in S-East England, indicating much more consistent recruitment when compared to N-Wales.

Based on Brown (1984), I have explored the Abundant-Centre Hypothesis (ACH) to understand the mechanisms that determine patterns of growth and mortality rates across a species range. I found that growth and mortality - both variables measured by marking limpets in the field - do not differ substantially

between *P. depressa* and *P. vulgata* across regions in Britain. However, growth and mortality rates of both limpet species were higher at the range edge of *P. depressa* in S-East England, when compared with populations in the range edge in N-Wales and in central populations in S-West England. Surprisingly, *P. vulgata*, which may be considered at the centre of its range of distribution in the British Isles, showed patterns very similar to *P. depressa*. Hence, these patterns of growth and mortality of both *Patella* species do not support the ACH.

Further investigation of growth patterns through analysis of inner growth lines visible in shell sections have showed that populations of *P. depressa* nearer to their poleward edge in N-Wales are characterized by older individuals, when compared to populations in S-East England. Growth performance calculated by using annual lines on shells supported the results of limpet growth obtained by marking limpets; similar growth performance values were obtained by using both approaches. Furthermore, I also found that *P. depressa* growth patterns were influenced by density-dependent effects over different spatial scales. Thus, across locations, high limpet density does not necessarily lead to a reduction in growth rates in *Patella* species. In contrast, at a local quadrat-scale, I found a localised effect of limpet density on growth performance of *P. depressa*. These patterns suggest that growth rates in limpet species are highly variable, subject to drivers and limitations at various levels of geographical scale, with local processes being important.

Competitive interactions between both limpet species were explored by determining the biological and physical factors, which are setting the leading edges of *P. depressa* at poleward populations. Individuals of *P. depressa* were strongly affected by inter-specific competition at its range edge in N-Wales, particularly in mixed plots with *P. vulgata* under shading treatments. By contrast, *P. vulgata* was affected by intra-specific competition in no-shading plots, particularly in central populations in S-West England. These results suggest that both biological and physical factors are modulating the poleward range of *P. depressa* in populations in N-Wales. Therefore, a better understanding of the differences in competitive ability between *Patella* species over a large spatial scale will improve our understanding of the role of competition in determining the performance of range edge individuals and hence range limits of populations.

Finally, as the British Isles are affected by different weather conditions, limpets performance traits may be vary leading to regional variations irrespective of the species. Limpet competitive interactions and local physical conditions must be considered as important local drivers within a large geographical scale. My results do not support the ACH in populations at the northern fraction of *P. depressa* distribution. As *Patella* species have been proposed as climate indicator species, the effects of climate must be considered in terms of both limpet life-history traits and the interaction between the ultimate and a multitude of local proximate factors.



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## **CHAPTER 1:**

### **Climate warming and its consequences on marine ecosystems: Comparisons between range edges and central populations of marine species**



### 1.1. Global Warming in Northern Europe: A Case Study

Globally, species have shown strong shifts in distribution and abundance in response to anthropogenic climate change (Parmesan, 2006; Poloczanska *et al.*, 2013; Burrows *et al.*, 2014; Hawkins *et al.*, 2016; Poloczanska *et al.*, 2016). Nowadays climatic records and forecasts are alarming, highlighting the increase in global temperatures of  $\sim 1^\circ\text{C}$  over the last century (Poloczanska *et al.*, 2016), and predicting an overall warming of  $1.5^\circ\text{C}$  between 2030 and 2052 (IPCC, 2018). Recently attention has focused on predicting changes in species distribution in relation to the velocity of climate change (Parmesan & Yohe, 2003; Helmuth *et al.*, 2006; Parmesan, 2006; Sorte *et al.*, 2010; Poloczanska *et al.*, 2013; Burrows *et al.*, 2014; Brito-Morales *et al.*, 2018). Threats to global biodiversity from climate variability make it important to identify which species have already responded to recent warming (Poloczanska *et al.*, 2013; Brown *et al.*, 2016; Poloczanska *et al.*, 2016; Brito-Morales *et al.*, 2018) and what will be the consequences for ecosystem functioning at both large and small spatial and temporal scales (*e.g.*, Crisp 1964; Southward *et al.*, 1995; Herbert *et al.*, 2003; Hiscock *et al.*, 2004; Kendall *et al.*, 2004; Mieszkowska *et al.*, 2005; Southward *et al.*, 2005; Mieszkowska *et al.*, 2006; Herbert *et al.*, 2007; Mieszkowska *et al.*, 2007; Hawkins *et al.*, 2008, 2009; Herbert *et al.*, 2009; Wetthey *et al.*, 2011; Hawkins *et al.*, 2016; Herbert *et al.*, 2016).

I have chosen the benthic intertidal habitat as a tractable test system, and specifically patellid limpet species as model organisms to explore what sets the range edges of species in the North-east Atlantic. I have focused on the warm-water species *Patella depressa*, which reaches its northern limit in northern Europe and its congener, and putative competitor, the cold-water species *Patella vulgata*. Brown's (1984) Abundant-Centre Hypothesis (hereafter ACH) has been explored; understanding what sets range edges provides insight into the processes driving species range extensions. Advantage has been taken of the multiple range edges of *P. depressa* in the British Isles, specifically comparing limpet populations at two poleward limits of *P. depressa* (*i.e.*, the central-east part of the English Channel and North Wales), with those in South-west England where *P. depressa* makes up around 50% or more of all patellid limpets.

In the remainder of this introductory chapter, I review climate change in marine systems, processes driving species range distribution, recent shifts in biogeographical ranges of intertidal species, the Patellidae family and distributional changes observed in *Patella* species, the

ecological interaction between *P. depressa* and *Patella vulgata*, and finally about performance traits on species range distributions. I conclude this chapter by describing the rationale of the thesis, my overall aims and specific objectives.

### 1.2. Climate Change and Consequences on Marine Species

The influence of recent changes in climate is being increasingly recognised, with changes in abundance and geographical ranges of species (Southward *et al.*, 1995; Hampe & Petit, 2005; Hawkins *et al.*, 2008, 2009; Sorte *et al.*, 2010; Birchenough *et al.*, 2015; Poloczanska *et al.*, 2016) as well as alterations to phenological traits of various species (Parmesan & Yohe, 2003; Moore *et al.*, 2011; Poloczanska *et al.*, 2013; Brown *et al.*, 2016). Marine ecosystems seem to be more susceptible than terrestrial systems to climatic variations (Parmesan & Yohe, 2003; Sorte *et al.*, 2010; Moore *et al.*, 2011). For example, global warming-related to range shifts of marine species (on average 19 km/year; Sorte *et al.*, 2010) exceed those of terrestrial species by an order of magnitude (0.6 km/year; Parmesan & Yohe, 2003). Distributional shifts have been found for several components of marine ecosystems such as: plankton (Beaugrand & Ibanez, 2004; Hays *et al.*, 2005; Beaugrand *et al.*, 2008), zooplankton (Beaugrand & Ibanez, 2004; Pitois & Fox, 2006), fish (Genner *et al.*, 2004; Perry *et al.*, 2005), offshore benthic organisms (Hiscock *et al.*, 2004) and intertidal species (Herbert *et al.*, 2003, 2007, 2009; Helmuth *et al.*, 2006; Hawkins *et al.*, 2008, 2009).

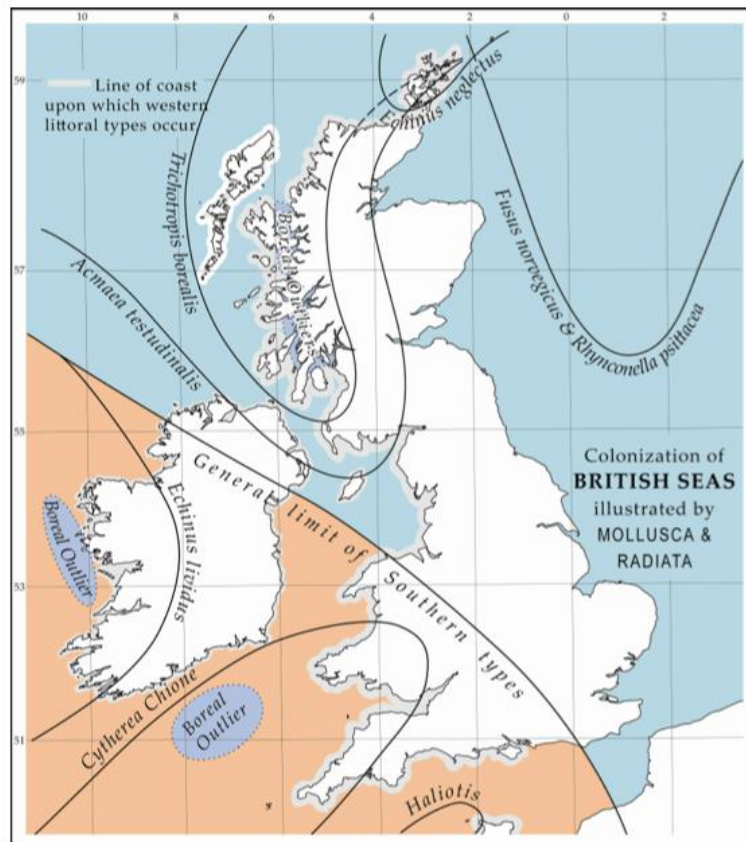
Phenological changes in response to climate warming have been recorded in several species (Root *et al.*, 2003; Helmuth *et al.*, 2006; Kordas *et al.*, 2011; Pacifici *et al.*, 2017). Quantitative comparisons across broad taxonomic and functional groups have indicated that amphibians show a phenological shift of between 12 and 34 days per decade compared with other taxonomic groups (*e.g.*, butterflies, birds, herbs and shrubs; Parmesan & Yohe, 2003; Parmesan, 2007). However, the magnitude of changes in phenology in marine systems is greater than terrestrial communities, possibly indicating a greater sensitivity of marine species to climatic variation (Root *et al.*, 2003; Edwards & Richardson, 2004; Sorte *et al.*, 2010; Moore *et al.*, 2011; Brown *et al.*, 2016). In marine species, such phenological shifts have been observed in plankton (Edwards & Richardson, 2004), nekton (Sims *et al.*, 2001, 2004), echinoderms (Kirby *et al.*, 2007; Ling *et al.*, 2008), bivalves (Honkoop & van der Meer, 1998; Philippart *et al.*, 2003) and intertidal gastropods (Moore *et al.*, 2011). For example, in the North Atlantic, Edwards &

Richardson (2004) showed that the timing of seasonal peaks of plankton occurred 27 days earlier during warmer periods, based on a 45-year study period. Moreover, changes in the timing of gametogenesis and spawning of the urchin *Echinocardium cordatum* have been observed in relation to rising sea temperature in the North Sea (Kirby *et al.*, 2007). Rising sea temperature also reduces reproductive output as well as delaying the spawning of intertidal bivalve species (*i.e.*, more eggs are produced at lower than at higher water temperatures; Honkoop & van der Meer, 1998, Philipart *et al.*, 2003). Furthermore, in marine populations that are already depressed, due to overharvesting, environmental changes are more likely to have a larger impact, in part because they have reduced reproductive output and therefore limited capacity for genetic and/or phenotypic variation (Fenberg & Rivadeneira, 2011; Sumaila *et al.*, 2011).

On the other hand, in North-east Atlantic, climatic conditions are influenced by the extension of the Gulf Stream drift (Hiscock, 1998; Thornalley *et al.*, 2018). The Gulf Stream, together with its northern extension, the North Atlantic Drift, is a powerful, warm, and swift Atlantic Ocean current that originates in the Gulf of Mexico (Thornalley *et al.*, 2018). Its exit to cross the Atlantic Ocean is through the Strait of Florida, reaching the European shelf at around 50 °N (*i.e.*, ~ English Channel) and flowing north-eastwards into the Norwegian Sea (Hiscock, 1998). It influences allows milder winter conditions, forming a mosaic of distributions between warm- and cold-water species in the southern half of the British Isles (Lewis, 1964; Hiscock, 1998 for details). The extent of both species distribution and the persistence or relative abundance of their populations vary widely between species, suggesting different tolerances to different environmental factors (Lewis, 1964).

The first description of the distributional limits of certain marine species, including a delineation of the general limit of Lusitanian southern species was prepared by Edward Forbes in 1858 (Figure 1.1). Thus, Britain and Ireland straddle a biogeographic boundary between cold boreal northern species and warmer Lusitanian southern species meaning that many intertidal species reach their southern or northern limits of distribution in/or close to the British Isles (Figure 1.1; Forbes, 1858; Lewis, 1964; Hiscock *et al.*, 2004). However, although warm-water species extends strictly to the entrance to the English Channel, many species of the Mediterranean-Atlantic flora and fauna extend their poleward edge to the south-western and western coasts of the British Isles (Hiscock, 1998; Hiscock *et al.*, 2004). This has created a natural laboratory in which the consequences and effects of climate variability on species can be

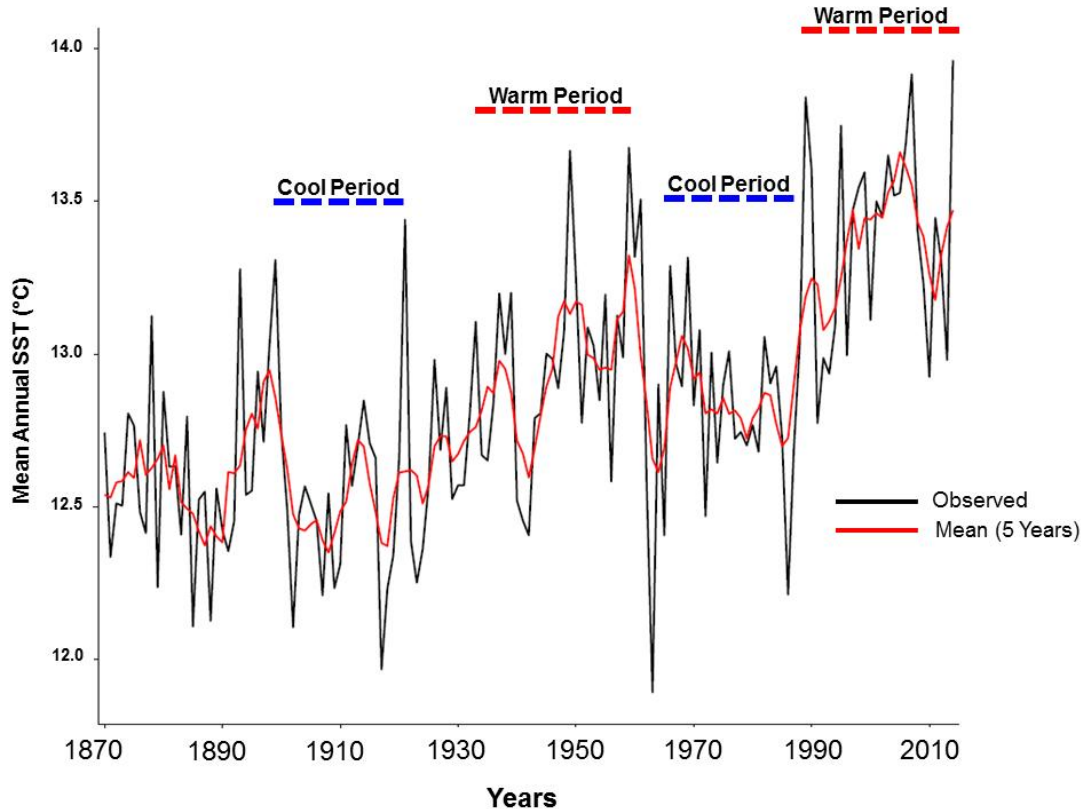
studied. In general, cold-water species are decreasing in abundance and retreating poleward, while warm water species are increasing in abundance and advancing northwards (Southward *et al.*, 1995; Hawkins *et al.*, 2003; Mieszkowska *et al.*, 2005; Simkanin *et al.*, 2005; Mieszkowska *et al.*, 2006, 2007; Hawkins *et al.*, 2008, 2009). Surveys conducted by the Marine Biodiversity and Climate Change project (<http://www.mba.ac.uk/marclim/>, MarClim®) have shown range extensions of several southern intertidal species, which has highlighted the importance of the historical, broad-scale and quantitative as well as semi-quantitative time series available for rocky shores around the British Isles (Mieszkowska *et al.*, 2005, 2006, 2007, 2014).



**Figure 1.1.** Biogeographical characteristics of the coast of the British Isles, including the range limits of some species (*e.g.*, Fishes, Molluscs and Radiata). Redrawn from Forbes (1858) and including absence of the Isle of Anglesey as in the original publication (Figure adapted from Hiscock *et al.*, 2004).

Marine ecosystems appear to already be affected by climate change in most European seas and temperature increase has generally been higher in northern than southern Europe (Philippart *et al.*, 2011; Poloczanska *et al.*, 2013, 2016). For example, the North Atlantic has been a region of high net heat accumulation compared to other regions (see Palmer *et al.*, 2007 for details), and some of the most notable changes in species distributions as a consequence of climate warming (Poloczanska *et al.*, 2016), have been seen on the rocky shores of northern Europe (Southward *et al.*, 1995; Hawkins *et al.*, 2003; Herbert *et al.*, 2003; Mieszkowska *et al.*, 2005; Simkanin *et al.*, 2005; Mieszkowska *et al.*, 2006; Herbert *et al.*, 2007; Mieszkowska *et al.*, 2007; Hawkins *et al.*, 2008, 2009; Herbert *et al.*, 2009). In the British Isles, from the 1920s onwards there was a period of warming marked by high inter-annual fluctuations (Figure 1.2), until the 1960s when the extreme cold winter between 1962 and 1963 caused high mortality of many species (Crisp, 1964; Southward *et al.*, 2005; Hawkins *et al.*, 2003; Mieszkowska *et al.*, 2014). Since then, the conditions were generally much cooler until the mid-1980s (Figure 1.2), after which rapid warming has been observed (Hawkins *et al.*, 2003; Southward *et al.*, 2005; Mieszkowska *et al.*, 2014; Brito *et al.*, 2018). In fact, recent paleoclimatic studies have shown that the northern hemisphere has warmed more since the 1980s than at any other time during the last 2000 years (Mann & Jones, 2003; Moberg *et al.*, 2005). From the 1990s to the present day, conditions have become much warmer (Hiscock *et al.*, 2004; Southward *et al.*, 2005; Hawkins *et al.*, 2008, 2009; Mieszkowska *et al.*, 2014). This is typified by milder winters, due to the prevalence over much of the period of both the positive North Atlantic Oscillation (hereafter NAO) and the Atlantic Multi-decadal Oscillation (hereafter AMO) index, with predominantly westerly winds bringing warm and moist air during the winter across northern Europe, and colder/drier conditions in the Mediterranean and southern Europe (Hawkins *et al.*, 2003; Broitman *et al.*, 2008a; Mieszkowska *et al.*, 2014). An exception to this occurred over the period 1990-1995 when high local Sea Surface Temperature (hereafter SST) records are not reflected by extreme AMO values; see Mieszkowska *et al.* (2014) for details.

The distributional limits of a species are a consequence of the interaction between geographical variation in the environment and the physiological tolerances and the adaptability of each species (Caughley *et al.*, 1988; Parmesan, 2006; Gaston, 2009) as well as biological interactions (Leonard, 2000; Poloczanska *et al.*, 2008; Firth *et al.*, 2009). The literature concerning biogeographic response to climate has tended to focus on long-term trends, like pole-



**Figure 1.2.** Mean annual Sea Surface Temperature (SST) 1870-2014 off Plymouth, UK (Met Office Hadley Centre). Black line indicates annual mean temperature; red line indicates 5-year running average (Adapted from Hawkins *et al.*, 2016).

ward progression of species boundaries (*e.g.*, Parmesan, 2006; Helmuth *et al.*, 2006; Hawkins *et al.*, 2009). As a result, current predictions of ecological responses to climate change and the design of experiments conducted to understand underlying mechanisms, are too often based on broad-scale trends (Helmuth *et al.*, 2014). Climate proxies (*e.g.*, NAO, AMO or SOI, El Niño–Southern Oscillation Index) are useful indicators of broad-scale oceanographic and atmospheric variability, but the relationship between these proxies and benthic communities is sometimes not consistent and may be influenced by local environmental conditions (Helmuth *et al.*, 2006; Broitman *et al.*, 2008a; Helmuth *et al.*, 2014; Mieszkowska *et al.*, 2014; Birchenough *et al.*, 2015). Therefore, organismal scale habitat variation can be overlooked when investigating large-scale averages of key factors, such as temperature, and the conditions that organisms experience

often depends strongly on local small-scale habitat effects and interactions (Helmuth *et al.*, 2002, 2006, 2014; Mota *et al.*, 2014). To understand the dynamics of how the ranges of species are shifting on a broad-scale, various studies have attempted to link climatological, biophysical and demographic models/processes. This aims to produce a more refined understanding of how temperature changes influence the distribution and abundance of species (Lima *et al.*, 2007ab; Cheung *et al.*, 2009; Kearney & Warren, 2009; Fordham *et al.*, 2013; Jueterbock *et al.*, 2013).

### 1.3. Physical and Biological Processes as Drivers of Range Distributions

Species ranges are highly variable, often shifting, expanding and contracting over time and are generally correlated with a large number of abiotic and biotic factors (Brown *et al.*, 1996; Helmuth *et al.*, 2006; Sexton *et al.*, 2009; Helmuth *et al.*, 2014). Theoretical and empirical evidence shows that demographic parameters (*i.e.*, immigration, birth, death and emigration) can have a strong influence on geographic distribution of species (Guo *et al.*, 2005; Gaston, 2009). Thus, dispersal between populations located at the centre and those at the range edge of a species distribution is a key process required for the persistence of those populations and their capacity to adapt to local conditions (*e.g.*, birth or mortality rates; Guo *et al.*, 2005; Gaston, 2009; Bates *et al.*, 2014; Chuang & Peterson, 2016). When the ranges expand, the individuals at the limits will tend to have better dispersal abilities and if some component of this dispersal ability is heritable (Bates *et al.*, 2014; Chuang & Peterson, 2016), then the offspring of individuals at the range limit will also tend to have higher dispersal ability (Gaston, 2009; Sexton *et al.*, 2009). Consequently, long-distance dispersal is crucial because it may control the demography of marine populations established far away from central populations, in addition to the dynamics of colonization, range expansion, and genetic exchange (Gaylord & Gaines, 2000; Kinlan & Gaines, 2003). Hence, variations in population dynamics across the distributional range of species must reflect geographical variation and connection between populations, but further local experimentation is needed to understand the underlying mechanisms that operate on species ranges dynamics on both large and small spatio-temporal (Gaston, 2009; Araujo *et al.*, 2014).

Under conditions of large-scale environmental perturbation, expansion or contraction of species' ranges is likely to be a complex process (Chuang & Peterson, 2016), which depends on the mean dispersal scale and the relative importance of long or short-distance dispersal events (Kinlan & Gaines, 2003). For example, in marine ecosystems the dispersal scales of macroalgae

are more restricted than those of fish and invertebrates that tend to disperse over wider spatial scales (Kinlan & Gaines, 2003). In fact, low population differentiation and high gene flow are commonly reported in marine invertebrates with planktonic development (*e.g.*, gastropods; Eckert *et al.*, 2008; Coulson *et al.*, 2011; Fenberg & Rivadeneira, 2011) whereas low levels of gene flow and sharp genetic differences between nearby populations at small geographic scale, have been described for macroalgal species (*e.g.*, *Mazzaella laminarioides*; Montecinos *et al.*, 2012). One example of low population differentiation between invertebrate populations can be seen in the distribution of the limpet *Patella rustica*, where not even a 280 km gap in its range is an effective barrier to gene flow between populations (Lima *et al.*, 2006, 2007). Levels of differentiation between individuals on the edges of ranges are low, suggesting that currents flowing along the Atlantic coast of Iberia could be responsible for maintaining connectivity between the borders of this gap (Lima *et al.*, 2006; Ribeiro *et al.*, 2010). Therefore, it is likely that species with long-dispersal distances are less susceptible to constraints on their distributional limit than algae, given their high dispersal potential that supplies propagules from populations at the core to those at the edge.

Range extensions are driven by increased abundance and reproductive success of populations within the range (Ling *et al.*, 2008), which provide the propagules for successful recruitment at the edges of a species range (Kinlan & Gaines, 2003; Chuang & Peterson, 2016; see also Box 1.1). Thus, recruitment processes are considered to be key determinants in the establishment of new populations at range limits, along with sufficient levels of self-recruitment within edge populations (Lewis, 1964; Kinlan & Gaines, 2003; Navarrete *et al.*, 2005; Bates *et al.*, 2014; Chuang & Peterson, 2016; Box 1.1). For example, the absence of small individuals at range edges can indicate sporadic or limited recruitment, whereas absence of large individuals can reveal post-recruitment mortality, or lack of growth as a result of unfavourable environmental conditions (Bowman & Lewis, 1977; Kendall & Lewis, 1986; Gilman, 2006a; Hidas *et al.*, 2010; Coulson *et al.*, 2011; Shanks *et al.*, 2014; Borges *et al.*, 2015). Nonetheless, the recruitment of sessile and mobile marine benthic species, particularly those with a planktonic larval stage are influenced largely by hydrographic conditions (*e.g.*, temperature, salinity, pH, coastal water movements, wind speed and direction, upwelling frequency and intensity) and by physical barriers (*e.g.*, peninsulas) and both of these may be used to approximately predict particular species limits (Kinlan & Gaines, 2003; Broitman *et al.*, 2005; Pfaff *et al.*, 2011;



Adams *et al.*, 2014). For example, Southward (1991) showed that *Semibalanus balanoides* abundance within its southern range is strongly negatively correlated with SST. Therefore, in a climate-warming context it is likely that many southern *S. balanoides* populations will experience sustained levels of low recruitment, eventually contracting its southern margin (Svensson *et al.*, 2005). However, model simulations indicate that populations of *S. balanoides* in the Isle of Man (in the Irish Sea, northern Europe) are quite resistant to relatively high frequencies of low recruitment and recruitment failure, indicating tolerance to changes in climate (Svensson *et al.*, 2005; Poloczanska *et al.*, 2008).

Box 1.1		
Concept	Definition	Paper for details
<b>Population:</b>	Individuals of a single species.	Leibold <i>et al.</i> , (2004)
<b>Settlement:</b>	Process in planktonic larvae of benthic invertebrates, which generally dependent on whether metamorphosis is included. Generally includes the contact with the substratum, exploratory behaviour, orientation and metamorphosis into a new habitat.	Jenkins <i>et al.</i> , (2009)
<b>Post-Settlement:</b>	The period immediately following settlement, which involve the transition from a pelagic to benthic state.	Jenkins <i>et al.</i> , (2009)
<b>Recruitment:</b>	Defined as the number of settlers remaining at the end of the short period of settlement. It reflects a combination of settlement and a post-settlement period of arbitrary length, determined by the length of time before the settler is counted by an observer.	Jenkins <i>et al.</i> , (2009)
<b>Mortality:</b>	The loss of individuals in a population through death can be defined in terms of the percentage of individuals that survive (survival rate) over a particular time interval, or the percentage that die. Many factors in the marine environment act to reduce the chances of survival of individuals in a population. These include adverse conditions, lack of food, competition and predation, etc.	King <i>et al.</i> , (2007)

An index of large-scale atmospheric and oceanic activity, like NAO, has been correlated with recruitment variability of rocky intertidal invertebrates in the North Atlantic (Broitman *et al.*, 2008a; Mieszkowska *et al.*, 2014). The NAO is a measure of the meridional (*i.e.*, north-south) oscillation in atmospheric mass arising from variations in atmospheric pressure conditions during winter in the northern hemisphere, and the immediate expression of NAO index are shifts in weather patterns and atmospheric flow (Trigo *et al.*, 2002; Broitman *et al.*, 2008a; Mieszkowska *et al.*, 2014). For example, in the topshell *Gibbula umbilicalis* (re-named as *Steromphala umbilicalis*; Affenzeller *et al.*, 2017) and invasive barnacle *Austrominius modestus*, both warm-water species, recruitment has been positively associated with NAO3 (*i.e.*, an average of the NAO over periods of three months; Broitman *et al.*, 2008a). This suggests that the milder

winter atmospheric conditions associated with positive values of NAO index may favourably affect the recruitment of both species. Similar to its association with NAO3, *A. modestus* recruitment shows a significant positive association with NAO6 (*i.e.*, an average of the NAO over periods of six months; Broitman *et al.*, 2008a). Therefore, *A. modestus* recruitment appears to be affected both by atmospheric influences on the survival of newly settled recruits during winter and spring due to warmer sea and air temperatures, and by oceanic currents during the dispersive larval phase (Broitman *et al.*, 2008a). Whether

Some intertidal organisms with larval planktonic development may be highly susceptible to climatic variability such as temperature variations (Broitman *et al.*, 2005; Jones *et al.*, 2012; Mislan *et al.*, 2014). Sea temperature during the larval stage can influence larval survival, and hence abundance, by reducing the time spent in the plankton, a period characterised by high mortality (Rumrill, 1990; Kirby *et al.*, 2007). Some analyses suggest that SST is an important factor influencing *Echinocardium cordatum* larval abundance and the per capita egg production of the bivalve *Macoma balthica* (Beukema *et al.*, 1998 and Philipart *et al.*, 2003 for *M. balthica*; Kirby *et al.*, 2007 for *E. cordatum*). Furthermore, harsh winters are often followed by high densities of intertidal bivalve recruitment, generating a negative relationship between winter temperatures and recruitment on a large geographic scale (500 km coastline; Beukema *et al.*, 1998; Strasser *et al.*, 2003). In fact, a higher bivalve recruitment in the 1970s and 1980s than in the 1990s has been related to the near absence of severe winters since 1987 (Strasser *et al.*, 2003). Hence, the likelihood of range extensions will be determined by a combination of climate-drivers and life history traits, which have the potential to influence dispersal and settlement capabilities (Kinlan & Gaines, 2003; Gaines *et al.*, 2007).

### 1.4. Shifts in Range Distributions of Intertidal Species in North-West Europe

Physical and biological changes offshore can have a major influence on the shoreline, given the prevalence of pelagic early life-stages in most intertidal species (Southward *et al.*, 2005; Hawkins *et al.*, 2008, 2009). Moreover, intertidal species may respond more rapidly to environmental changes than their terrestrial counterparts, because they usually have a shorter life span (Southward *et al.*, 2005; Moore *et al.*, 2011). Therefore, the intertidal zone can be considered a proxy for broad-scale changes caused by climate warming in near-shore waters (Lima *et al.*, 2006, 2007a; Hawkins *et al.*, 2009; Mieszkowska *et al.*, 2014). In fact, many

intertidal species, such as limpets, barnacles, trochids and macroalgae have been proposed as possible climate indicators (Mieszkowska *et al.*, 2005; Southward *et al.*, 2005; Hawkins *et al.*, 2008, 2009).

Ecological studies on the impacts of climate generally focus on the relationship between a species' thermal tolerance limits and its distribution (Helmuth *et al.*, 2002, 2006; Pearson *et al.*, 2009, Sunday *et al.*, 2012; Mota *et al.*, 2014; Birchenough *et al.*, 2015). Temperature is one of the most fundamental determinants of biological patterns and process, and many natural history traits are triggered by temperature-related cues (Helmuth *et al.*, 2002; Stillman, 2003; Helmuth *et al.*, 2006; Kordas *et al.*, 2011). There is considerable evidence that both cold-water species and warm-water species distributions are being affected by shifts in sea-water temperature (Southward *et al.*, 1995; Mieszkowska *et al.*, 2005; Simkanin *et al.*, 2005; Mieszkowska *et al.*, 2006, 2007; Hawkins *et al.*, 2008, 2009; Yesson *et al.*, 2015). For example, the boundary zone that straddles the British Isles (as mentioned above) creates an overlapping zone between cold-water northern species and warm-water southern species (Crisp & Southward, 1958; Lewis, 1964; Hawkins *et al.*, 2003; Hiscock *et al.*, 2004). This region has seen some major changes in distribution in response to warming from the early 1990s onwards (Figure 1.2), with warm-water species extending their northern range poleward and by contrast, northern cold-water species decreasing in abundance and retreating poleward (Lima *et al.*, 2007ab; Hawkins *et al.*, 2009; Mieszkowska *et al.*, 2014). Work done by Hawkins *et al.* (2003, 2008, 2009), Herbert *et al.* (2009), Mieszkowska *et al.* (2005, 2006, 2007), Simkanin *et al.* (2005) and Yesson *et al.* (2015) show the best documented range changes for northern and southern species along the European coast in response to climate variability, with particular emphasis on the British Isles and Ireland. Examples of the best-documented range shifts in response to climate warming are detailed below:

### 1.4.1. Macroalgae

Changes in assemblage composition and distribution of macroalgae have been observed in Europe with advances of the northern limit of southern species and retraction of the southern limit of northern species (Lima *et al.*, 2007b; Jueterbock *et al.*, 2013; Yesson *et al.*, 2015). In northern Spain, recent distributional declines have also been reported for fucoid species (Viejo *et al.*, 2011; Martinez *et al.*, 2012; Ferreira *et al.*, 2014). Over the past 30 years, the southern range

edge of *Fucus vesiculosus* has contracted, from northern Morocco to southern Portugal, with a northward latitudinal shift of approximately 1250 km, coupled with the loss of its genetic background (Nicastro *et al.*, 2013). In fact, a prediction based on niche models, investigating the potential northward shift of intertidal canopy-forming macroalgae indicated that *F. serratus* and *Ascophyllum nodosum* will be extinct in the East-Atlantic from Portugal up to Brittany, by 2100, under all possible climate change scenarios (*i.e.*, around 50° N; Jueterbock *et al.*, 2013). For kelp species, like *Saccorhiza polyschides*, *Laminaria hyperborea*, *Laminaria ochroleuca* and *Saccharina latissima*, SST warming is a major factor in their ongoing decline and westward displacements at their borders (Muller *et al.*, 2009; Fernández, 2011; Viejo *et al.*, 2011; Martinez *et al.*, 2012). For example, *Alaria suciculenta* populations were badly impacted by the last warm period (1950s) in the western English Channel and did not recolonize the area during the colder 1960s-1980s (Mieszkowska *et al.*, 2005, 2007; Hawkins *et al.*, 2009). By contrast, the calcareous brown alga *Padina pavonica* at its northern limit on the south coast of England seems to be affected by increasing temperatures because of climate warming, but vegetative stages during its life cycle have potentially enabled its persistence over centuries in Britain (Herbert *et al.*, 2016).

### 1.4.2. Barnacles

*Chthamalus* spp. have increased in abundance and their boreo-arctic counterpart, *Semibalanus balanoides* has declined after the 1990s (Southward & Crisp, 1954, 1956; Southward, 1967, 1991; Southward *et al.*, 1995, 2005; Hawkins *et al.*, 2008; Mieszkowska *et al.*, 2014). For *S. balanoides* populations, some predictions made under different climate scenarios indicate that it will disappear in South-west England by the 2050s (Poloczanska *et al.*, 2008). In fact, *S. balanoides* has already disappeared from the coast of northern Spain (Wethey & Woodin, 2008). Poloczanska *et al.* (2008) examined how temperature mediated competition between the competitively dominant cold-water *S. balanoides* and warm-water *Chthamalus* spp. The outcome showed that interspecific competition between fast growing juvenile *S. balanoides* is important in regulating chthamalid density (Poloczanska *et al.*, 2008). In addition, temperature was the main driver in recruitment of *S. balanoides* with higher recruitment in cooler years. Furthermore, in warm years there is no direct effect of temperature on *Chthamalus* spp., but they were released from competition with faster growing *S. balanoides* (Poloczanska *et al.*, 2008; Mieszkowska *et al.*, 2014). Nonetheless, Simkanin *et al.* (2005) reported an increase in abundance of *S. balanoides* in Ireland between 1958 and 2003. However, this difference has been attributed to

methodological error and not due to anthropogenic reasons (*i.e.*, operator error in ‘ACFOR’ abundance scale; Crisp & Southward, 1958; Simkanin *et al.*, 2005).

The border of *C. montagui*, has extended by no more than 8 km along the southern coast England since 1970 (Herbert *et al.*, 2009). *Chthamalus* species have not yet reached beyond the Isle of Wight and compared to other southern species (Herbert *et al.*, 2003, 2009) changes in their abundance have been relatively minimal in the English Channel (Herbert *et al.*, 2007, 2009). In contrast *C. stellatus* has been found on the Isle of Man and there has been some spread of *C. montagui* along the North Wales coast to the Wirral (Hawkins *et al.*, 2009, Mieszkowska *et al.*, 2014). The range of the southern barnacle *Perforatus perforatus* has extended on both sides of the English Channel by 120-190 km, with a trend of decreasing abundance eastward in the English Channel (Crisp & Southward, 1958; Herbert *et al.*, 2003, 2009).

Wetthey & Woodin (2008) found that between 1872 and 2006 the distribution of *S. balanoides* shifted northward by 300 km along the European coast. They examined three alternative hypotheses for this change: 1) The summer heat death hypothesis (Hutchins, 1947) postulated that adult survival is restricted at the southern geographic limit by high temperatures; 2) the day-length hypothesis (Davenport *et al.*, 2005) postulated that reproduction is dependent upon shortening day length, and that there is geographic variation in response; and 3) the winter cold limitation of reproduction hypothesis postulated that reproduction fails if temperatures remain above 10°C during winter months (Wetthey & Woodin, 2008). Thus, Wetthey & Woodin (2008) concluded that changes in the southern limit of *S. balanoides* in Europe are due to intolerance of winter body temperatures above 10° C leading to reproductive failure. This change in distribution is similar to that proposed by Jones *et al.* (2012) for *S. balanoides* in the Atlantic coast of the United States (350 km), but the mechanism causing the change is different compared with the European coast. Whilst the summer heat death hypothesis is possible on the Atlantic coast of North America, Therefore, the differences between mechanisms controlling distribution along the western and eastern Atlantic could be due to regional variations in thermal tolerance (Sorte *et al.*, 2011).

### 1.4.3. Trochids

Trochids such as *Osilinus lineatus* (re-named as *Phorcus lineatus*; Affenzeller *et al.*, 2017) and *Steromphala umbilicalis* have increased in abundance and their ranges have extended

to northern Scotland, Ireland, Wales and the eastern English Channel (Mieszkowska *et al.*, 2006, 2007). The range of *P. lineatus* retracted following the extremely cold winter between 1962 and 1963 (Crisp, 1964). The recovery and recolonization of *P. lineatus* were hindered predominantly by colder weather, but in recent years it has breached the barrier of the Llyn Peninsula in North Wales (Mieszkowska *et al.*, 2007; Hawkins *et al.*, 2009). In the case of *S. umbilicalis*, its northern range distribution has extended along the north-east coast of Scotland by over 55 km and by 125 km along the eastern English Channel since the 1980s. Nowadays, it reaches Kent (East of England), an eastward extension of over 240 km beyond the Isle of Wight (Mieszkowska *et al.*, 2005; Hawkins *et al.*, 2009).

### 1.5. Patellidae Family

Limpets are common inhabitants of seashores throughout the world oceans from tropical to polar regions (Ridgway *et al.*, 1998; Nakano & Ozawa, 2007). The Patellidae are one of the most successful families of gastropods that inhabit from higher to lower levels on intertidal rocky shores (Hayward & Ryland, 1995) and contains most of the common limpets in cold and temperate regions such as Mediterranean Sea (Ridgway *et al.*, 1998), North and South-east Atlantic (Jenkins *et al.*, 2001; Espinosa & Rivera-Ingraham, 2017), New Zealand (Creese *et al.*, 1990), Pacific Central-east coast (Espinosa & Rivera-Ingraham, 2017) and South Africa (Branch, 1975, 1976, 1981). Physical conditions of intertidal habitats are extremes, particularly in term of temperature, wave exposure and desiccation (Raffaelli & Hawkins, 1999), which makes limpets species an ideal model to understand their morphological and biological adaptations to these harsh environments (Henriques *et al.*, 2017). As a consequence of their accessibility and ecological significance, many aspects of the biology of patellid limpets, including behaviour, diet, life history and physiology, have been thoroughly studied (reviews by Branch, 1981; Fretter & Graham, 1994; Espinosa & Rivera-Ingraham, 2017; Henriques *et al.*, 2017).

The Patellidae family of the North-east Atlantic form a single clade, *Patella* (Ridgway *et al.*, 1998). In Britain, it is mainly represented by *Patella vulgata*, *Patella depressa* and *Patella ulyssiponensis* (Ridgway *et al.*, 1998). Ridgway *et al.* (1998) have shown that members of the clade *Patella* tend to be morphologically rather uniform in the North-west of Europe (except for the genus *Helcion*; Ridgway *et al.*, 1998). Although, the three *Patella* species are genetically and morphologically distinct (Koufopanou *et al.*, 1999), both *P. depressa* and *P. vulgata* are

genetically closely related, and *P. ulyssiponensis* has a different genetic origin when compared with both *P. depressa* and *P. vulgata* (Koufopanou *et al.*, 1999).

### 1.5.1. Changes in Distribution of *Patella* Species

The northern limpet *Patella vulgata* and the southern limpet *Patella depressa* have overlapping distributions across the British Isles with the leading range edge of *P. depressa* occurring in North Wales and South-east England. These limits have been established through its expansion northward over the last 30 years associated with a period of climate warming (see Kendall *et al.*, 2004; Hawkins *et al.*, 2009). In North Wales, the range of *P. depressa* has not extended in great numbers beyond the Llyn Peninsula (Kendall *et al.*, 2004; Hawkins *et al.*, 2008, 2009; also personal observations). Its eastern range limit in the English Channel, has extended 30 km east from the Isle of Wight to Hayling Island (Kendall *et al.*, 2004; Mieszkowska *et al.*, 2005; Hawkins *et al.*, 2008, 2009). In South-west England, *P. depressa* is now much more common (Hawkins *et al.*, 2008). Indeed, on the North coasts of Devon and Cornwall, *P. depressa* now comprises up to 80% of the limpet populations and by contrast, the relative proportions of the northern limpet *P. vulgata* have reduced since 1980s (Mieszkowska *et al.*, 2006; Hawkins *et al.*, 2008, 2009). In addition, the range of *P. ulyssiponensis* has extended eastwards in the English Channel 120 km further from Bembridge in the Isle of Wight, where only isolated individuals had originally been found in the 1980s (Mieszkowska *et al.*, 2005).

Others limpet species have also shown changes in distribution over the last decades (Mieszkowska *et al.*, 2005). The southern limpet *Patella rustica* has expanded into northern Iberia (Mieszkowska *et al.*, 2005; Hawkins *et al.*, 2009). In the late 1990s, the historic gap in the distribution of *P. rustica* towards northern Portugal was bridged (280 km) because of a relaxation of cold-water upwelling and combination of several climatic events (see Lima *et al.*, 2006, 2007a for details). A bioclimatic model performed by Lima *et al.* (2007a) suggests that changes in distribution of *P. rustica* along the European Atlantic coast can be explained by air and sea temperature patterns; the model excluded *P. rustica* from areas of cold water upwelling, where temperatures were too low. By contrast, in locations characterized by warmer temperatures (*i.e.*, the southern Portuguese coast and the Bay of Biscay), the model predicted high densities of *P. rustica* (Lima *et al.*, 2007a).

### 1.5.2. Relation between *Patella vulgata* and *Patella depressa* in North-West Europe

Limpets are an important component of intertidal assemblages worldwide and their grazing is known to play a key role in the ecology of these habitats (Hawkins & Hartnoll, 1983b; Hawkins *et al.*, 1992; Poore *et al.*, 2012; Aguilera *et al.*, 2013). In the North of Europe, some limpet species, such as *Patella vulgata* and *Patella depressa* show considerable geographic differences in their distribution at large scales (Kendall *et al.*, 2004; Lima *et al.*, 2016). This is because in the British Isles there is a biogeographic boundary between warm-water species, such as *P. depressa*, which extends through Portugal, Spain, to southern England and Wales; and boreal, cold-water species, such as *P. vulgata*, which extends from Norway, throughout the British Isles to the North of Portugal, where it is less abundant and/or rare (Guerra & Gaundencio, 1986; Boaventura *et al.*, 2002ab, 2003; Ribeiro *et al.*, 2009; Lima *et al.*, 2016). Although both *Patella* species differ in their geographic range, they can coexist at smaller spatial scales and both have been proposed as suitable indicator species to help monitor and predict future climate change and potential shifts in marine biodiversity throughout the British Isles (Southward *et al.*, 1995; Mieszkowska *et al.*, 2005, 2006; Hawkins *et al.* 2008, 2009).

The vertical zonation of *Patella vulgata* is less restricted than *Patella depressa*, but both limpet species are influenced by local environmental conditions (Evans, 1947; Orton & Southward, 1961). Generally, *P. vulgata* extends from Mean Low Water Spring tides (MLWS) to Mean High Water Spring (MHWS) (Evans, 1947). *P. depressa* has a restricted vertical range and is usually most abundant between Mean High Water Neap (MHWN) and Mean Tide Level (MTL) (Orton & Southward, 1961). In morphological terms, *Patella* species traits are variable, some are remarkably constant, and yet others are intermediate in their variability (Bowman, 1981). The shell of *P. vulgata* is circular/oval, a little flattened and its inner surface is grey-green and nacreous (Evans, 1947; Bowman, 1981). They are very conical with a central apex (Bowman, 1981; Hayward & Ryland, 1995). The largest specimens grow up to 70 mm in length (Hayward & Ryland, 1995). *P. depressa*, shells are usually very flat compared to *P. vulgata*, with fine radiating ribs and distinctive orange-brown marginal rays on its inner surface (Evans, 1947; Bowman, 1981; Hayward & Ryland, 1995). Shells have either a markedly oval or a triangular shape and never grow as large as *P. vulgata* (Evans, 1947) with a maximum length of between 30 and 40 mm (Bowman, 1981). Generally, it has a darker coloured foot and its pallial tentacles are chalky-white (Bowman, 1981). In contrast, *P. vulgata* has a grey-brown coloured



foot with translucent pallial tentacles and more extended on the border mantle (Evans, 1947; Bowman, 1981; Hayward & Ryland, 1995).

The reproductive behaviour of both limpet species is well understood and it is thought the initiation of gonad development, for both species, is driven by temperature (Orton *et al.*, 1956, Orton & Southward, 1961; Lewis, 1986). In general, there is a latitudinal trend consisting of progressively longer reproductive seasons, with spawning occurring later in the year towards the south (Guerra & Gaudencio, 1986; Lewis, 1986; Ribeiro *et al.*, 2009). *Patella vulgata* exhibits a single synchronous spawning event during the late autumn and winter with gonads developing during the autumn (Orton *et al.*, 1956; Lewis, 1986). Spawning occurs earlier in northern Britain than further south, with spawning thought to be stimulated when the SST falls below 12 °C (Lewis, 1986). In contrast, *Patella depressa* differs because the potential for multiple spawning events and re-development is much stronger than *P. vulgata*, and gonad activity may last from March/June to August/November, with little predictability in the time of spawning (Orton & Southward, 1961; Guerra & Gaudencio, 1986; Lewis, 1986; Ribeiro *et al.*, 2009; Moore *et al.*, 2007b). There is strong evidence of changes in the reproductive cycles of *P. depressa* and *P. vulgata*, possibly driven by climate warming (Moore *et al.*, 2011). For example, a comparison between both limpet species shows important differences between decades (1940s/2000s) in terms of reproductive development (Moore *et al.*, 2011). For example, the population proportion with mature reproductive stages for *P. depressa* has advanced by 10.2 days per decade since the 1940s, compared to *P. vulgata* that has shown a delay by 3.3 days per decade over the same period. *P. depressa* has experienced an increase in the proportion of the population in advanced reproductive states and multiple periods of spawning and gonad re-development during its reproductive season have been recorded (Ribeiro *et al.*, 2009; Moore *et al.*, 2011).

Additionally, sex change in limpets is widely known (Orton, 1928; Blackmore, 1969; Borges *et al.*, 2015). Earlier works reported high percentages of males in small-size classes of *Patella vulgata* (*i.e.*, 65% to 86%), at lengths from 15 to 21 mm (Orton, 1928). *Patella vulgata* sex change usually occurs in longer individuals (*i.e.*, >30mm in length). However, this pattern is not present at its equatorial range edges (*i.e.*, Portugal; Borges *et al.*, 2015). Thereby, individuals are male at first sexual maturity and a differential rate of growth between both sexes could be expected (Orton, 1928). Conversely, *Patella depressa* is considered a gonochoristic species in Britain, but some individuals may show protandry, particularly close to its centre range in

Portugal (Orton & Southward, 1961; Boaventura *et al.*, 2003; Borges *et al.*, 2015). Thus, these reproductive differences coupled with a series of warming and cooling phases due to climatic variability, can produce noticeable shifts in their distributional range as well as their phenological features, which might have an impact on growth rates of both *Patella* species on the British coasts (Crisp & Southward, 1958; Lewis, 1964).

The gastropod limpets, *Patella vulgata* and *Patella depressa* have different biogeographical ranges but occupy similar niches (Hawkins *et al.*, 1989, 2009). The radulae of *P. vulgata* and *P. depressa* are virtually identical and both species can exploit similar food resources (Hawkins *et al.*, 1989; Thompson *et al.*, 2000). Individuals of closely related species usually overlap greatly in the resources they require, and will presumably compete where they coexist (Branch, 1975, 1981). However, different trends in relation to competition for resources between and within *Patella* species have been found. The standing stock of epilithic microalgae, the principal food resource of patellid limpets, shows a general decline from Isle of Man to South-west of Portugal and could be related to the increase of limpet species from the northern to the southern coast of Europe (Jenkins *et al.*, 2001). Nonetheless, there is no clear evidence that the exploitation of microalgae (*i.e.*, standing stock) is the direct reason for inter and intra-specific competitive interactions in *Patella* species (Thompson *et al.*, 2000; Boaventura *et al.*, 2002b, 2003; Marzinelli *et al.*, 2012). By contrast, Underwood (1984) and Lasiak & White (1993) have demonstrated that the intensity of competition could vary in space and time depending on the densities and the makeup of grazer species and according to the availability of microalgal food.

Competitive interactions between invertebrates have been studied in rocky intertidal communities, including competition for space between sessile invertebrates (Connell, 1961; Dayton, 1971) and intertidal herbivores (Branch, 1975, 1976; Underwood, 1978, 1984; Boaventura *et al.*, 2002b, 2003). There is strong evidence that intraspecific competition in *Patella* species is stronger than interspecific competition and manipulative experiments have quantified the strength of intra and inter-specific interactions along the northern Europe coast (Thompson *et al.*, 2000; Boaventura *et al.*, 2002b, 2003; Moore *et al.*, 2007b; Firth *et al.*, 2008, 2009, 2010). For example, a manipulative experiment to test the effect of inter and intra-specific competition in *Patella depressa* and *Patella vulgata* was conducted on the northern Portuguese coast, where both limpet species co-occur at similar densities (equatorward range edge of *P.*

*vulgata*; Boaventura *et al.*, 2002b). The effect on mortality and growth of *P. depressa* by the addition of *P. vulgata* does not differ from the effect on mortality and growth of *P. vulgata* when *P. depressa* is added. In addition, Boaventura *et al.* (2002b) found that both species at low intra-specific densities show higher survivorship, length, weight and gonad development. By contrast, an increase in mortality, reduction in length and weight, and a reduced gonadal development were recorded in high intra-specific densities (Boaventura *et al.*, 2002b). They also found that *P. depressa* was most susceptible to intraspecific competition, whilst *P. vulgata* showed less negative density dependence. This is in contrast to other experiments performed by Thompson *et al.* (2000), where a high density of limpets resulted in increased mortality of *P. vulgata*.

The consequences of limpet grazing on macroalgal abundance will depend on latitude. For example, Moore *et al.* (2007b) compared grazing activity between *Patella vulgata* and *Patella depressa* and its effect on the development of canopy-forming algae in South-west Britain. They found that *P. vulgata* showed more grazing activity than *P. depressa*, especially during the spring and summer, when *P. depressa* populations had fully mature gonads, which has been shown to reduce the grazing activity of limpets (Jenkins & Hartnoll, 2001; Moore *et al.*, 2007b). Consequently, *Fucus vesiculosus* was able to grow to a size at which it escaped grazing by *P. depressa*, resulting in mature individuals of *F. vesiculosus* (Moore *et al.*, 2007b). In contrast, further south in Portugal, *P. depressa* has an important role in structuring *Fucus* spp. populations (Boaventura *et al.*, 2002ab, 2003); in this area *P. depressa* dominates and *Fucus* spp. grow when limpets are excluded (Boaventura *et al.*, 2002ab, 2003). Recent distributional declines of *Fucus* species towards northern Europe because of climate warming have been reported and loss of habitat-forming *Fucus* spp. caused by high temperature could modify limpet behaviour (Moore *et al.*, 2007ab; Viejo *et al.*, 2011; Martinez *et al.*, 2012; Jueterbock *et al.*, 2013; Nicastro *et al.*, 2013). For example, the northern limpet *P. vulgata* preferentially aggregates under *Fucus* spp. canopy, but when *Fucus* spp. is removed, it increases the mortality of *P. vulgata*. In contrast, its congener *P. depressa*, does not aggregate under *Fucus* spp. and is therefore not affected in terms of mortality by loss *Fucus* spp. (Moore *et al.*, 2007a). Given the different temperatures during low tide, between exposed rock (26°C) and beneath the canopy of *Fucus* spp. (21°C), this suggests that *P. depressa* has low tolerance to cool temperatures and conversely *P. vulgata* has low tolerance to warm temperatures at small spatial scales (Moore *et al.*, 2007ab). Similar relationships between intertidal patellid species, which also overlap their

distribution range and canopy-forming algae have been reported along the Chilean coast (*i.e.*, *Scurria viridula* and *S. zebrina*, and the red algae *Mazzaella laminarioides*; Aguilera *et al.*, 2013). In the overlap zone, the northern limpet *S. viridula* (analogous with the southern limpet *P. depressa*) uses flat rock platforms while resting, and its congener *S. zebrina* (analogous with the northern limpet *P. depressa*) is commonly seen resting under *M. laminarioides* canopy (Aguilera *et al.*, 2013). Hence, if warming continues, the local persistence of many species may become more dependent on the presence of others, and shifts, as consequences of higher temperature, could be magnified where biological habitats are lost or reduced (Moore *et al.*, 2007ab; Schiel & Lilley, 2011; Jueterbock *et al.*, 2013).

### 1.6. Patch Dynamics between Limpet and Algae Species

In the intertidal landscape of the British Isles, there are complex direct and indirect interactions among northern/boreal species, such as *Patella vulgata*, *Semibalanus balanoides* and *Fucus* spp. (Lewis, 1964; Hawkins & Hartnoll, 1983ab; Hawkins *et al.*, 1992). These interactions have allowed novel approaches to investigating patch dynamics, especially on exposed and semi-exposed rocky shores. As a consequence (Johnson *et al.*, 1997, 2008), the study of these interactions has created a better understanding of the underlying processes that structure intertidal communities in northern Europe at both small and large scales (Hawkins & Hartnoll, 1983ab; Hartnoll & Hawkins, 1985; Johnson *et al.*, 1997; Burrow & Hawkins, 1998; Johnson *et al.*, 1998ab; Raffaelli & Hawkins, 1999; Jenkins *et al.*, 2001, 2005; Coleman *et al.*, 2006; Johnson *et al.*, 2008).

The classic scheme used to explain these interactions starts with settlement of *Fucus* spp. in areas of low grazing activity (Hartnoll & Hawkins, 1985). Small recruits are more likely among dense patches of barnacles, in particular *S. balanoides* (Hawkins, 1981, 1983). Areas with low limpet abundance and high barnacle recruitment facilitate escapes of *Fucus* spp., while places with high limpet abundance and poor barnacle recruitment inhibit algae escapes (Hartnoll & Hawkins, 1985). New settlement of barnacles under *Fucus* spp. clumps is prevented by the sweeping of algal fronds (*i.e.*, whiplash effect) but predation and limpet bulldozing may also be important factors (Hawkins, 1983; Hartnoll & Hawkins, 1985). Groups of limpets can thrive under *Fucus* spp. clumps and may persist for some time after the algae disappear. Nonetheless, in some cases limpets increase the vulnerability of fucoid fronds to wave-induced breakage

(Davies *et al.*, 2007). A manipulative experiment confirmed that the limpet *P. vulgata* preferentially aggregates under *Fucus* spp. patches (Moore *et al.*, 2007a). If these patches of *Fucus* spp. are removed, significant numbers of *P. vulgata* relocate their home scars beneath new fucoid patches or die (Moore *et al.*, 2007a). This allows new *Fucus* spp. clumps to form in areas of lower grazing pressure between limpet patches (Hartnoll & Hawkins, 1985). These areas tend to have high densities of barnacle that also reduces the effectiveness of limpet grazing (Hawkins, 1981, 1983). Finally, dense *S. balanoides* settlement promotes *Fucus* spp. escapes in subsequent years (Hawkins, 1981, 1983; Hartnoll & Hawkins, 1985). The strength or direction of these interactions will depend on the fluctuations of extrinsic and intrinsic factors in space and time (Hawkins *et al.*, 1992). Spatial statistics and models have examined these patterns, which highlight the importance of the aggregative behaviour of *P. vulgata* under patches of fucoid canopy in determining the mosaic patterns of the intertidal landscape (Burrows & Hawkins, 1998; Johnson *et al.*, 1998ab). However, while numerous studies point to the important role of patellid limpets on moderately exposed rocky shores, they have a more limited role in structuring intertidal communities of sheltered shores of the British Isles (Jenkins *et al.*, 1999abc; Davies *et al.*, 2008).

Manipulative experiments have been conducted to identify the roles of *Patella vulgata*, *Semibalanus balanoides* and *Fucus* spp. on intertidal communities, especially in the North Atlantic (*i.e.*, British Isles: Scotland, Isle of Man and SW England; North Spain and Portugal). At small scales, work done by Jenkins *et al.* (1999c) on the Isle of Man, suggests that the effect of *F. serratus* canopy removal on the understory community depends on the presence/absence of *P. vulgata*. Although the density of *P. vulgata* decreases after canopy removal, grazing activity remains high enough to prevent new recruitment to open substrate. On the other hand, canopy removal together with the absence of limpets produces a strong change in community structure (Jenkins *et al.*, 1999c). On the west coast of Scotland, Marzinelli *et al.* (2012) suggests strong competitive interactions between size-classes of *P. vulgata* in the presence of *Fucus* spp. They found higher survival rates of small limpets than large ones in the presence of *Fucus* spp., but large limpets appear to influence the survival of smaller limpets as well. In fact, in growth terms the presence of *Fucus* spp. plus the addition of large limpets, significantly reduced the growth and proportional shell-weight of small limpets. However, small limpets do not seem to affect the growth and survival of large limpets (Marzinelli *et al.*, 2012). These results are similar to those

found for *P. depressa* in Portugal, where a strong negative effect of large limpets on small has been shown (Boaventura *et al.*, 2002ab, 2003).

Over a regional scale, the effect of limpet grazing is not homogenous along the British Isles coastline (Ballantine, 1961; Jenkins *et al.*, 2001, 2005) when compared with some experimental manipulations of limpets made further south in the Mediterranean Sea (Benedetti-Cecchi *et al.*, 2000, 2001). For example, limpet removal produced different community responses on the Isle of Man compared to shores in South-west England. In the Isle of Man, local scale removal of limpets leads to rapid and spatially consistent development of fucoids, whereas in South-west England the response is weak and variable (Jenkins *et al.*, 2005). On a large scale, both species richness and total species density of limpets increases from the North (*i.e.*, Isle of Man) to south of Europe (*i.e.*, South-west Portugal) with a decline in microalgal abundance (Jenkins *et al.*, 2001). In fact, from the Isle of Man to South-west Portugal, there is latitudinal gradient of grazing activity with a clear seasonal trend, increasing from northern to southern Europe (except for northern Spain; see Jenkins *et al.*, 2001; Coleman *et al.*, 2006). This seasonal trend can be explained by the strong relationship between mean SST and grazing activity (Thompson *et al.*, 2000; Jenkins *et al.*, 2001). Hence, if SST continues rising like it has in the last decades (Mieszkowska *et al.*, 2014; Birchenough *et al.*, 2015), grazing pressure will progressively increase northward (Southward *et al.*, 1995; Jenkins *et al.*, 2001; Davies *et al.*, 2007; Hawkins *et al.*, 2008).

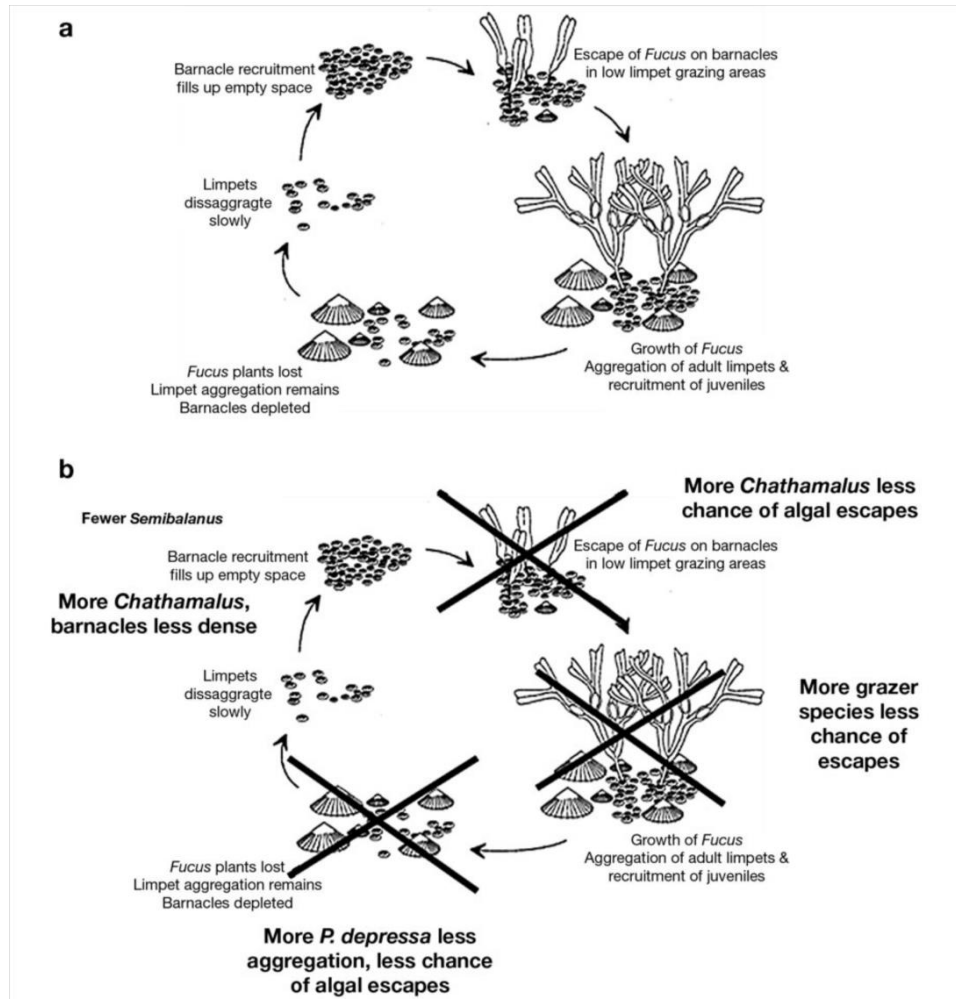
Changes in the strength or direction of species interactions could fundamentally alter assemblage composition with strong consequences for ecosystem functioning (Hawkins *et al.*, 1992). On the rocky shores of Europe, the patch dynamics among limpets, barnacles and fucoid species could be modified in different ways within the context of climate warming (Hawkins *et al.*, 2008, 2009). For example, a decrease in biological habitats produced by loss of fucoid canopy could affect the assemblage composition of species on exposed and semi-exposed rocky shores in northern Europe (Davies *et al.*, 2007; Lima *et al.*, 2007b; Moore *et al.*, 2007a; Jueterbock *et al.*, 2013). Results from a manipulative experiment show important geographical differences in fucoid recruitment in the presence/absence of limpets (*i.e.*, central range *vs.* edge range; North Wales and Portugal, respectively; Ferreira *et al.*, 2015). In the absence of limpets, northern fucoid populations (central range; *i.e.*, North Wales) had higher numbers of recruits than southern ones (edge range; *i.e.*, Portugal), but in the presence of limpets fucoid recruitment

was similar in both regions (Ferreira *et al.*, 2015). This suggests that fucoid species have lower recruitment success in areas close to their range edge, which is a possible reason for the decline in algal abundance in southern Europe (Lima *et al.*, 2007b; Viejo *et al.*, 2011; Martínez *et al.*, 2012; Jueterbock *et al.*, 2013; Ferreira *et al.*, 2014). Therefore, if the abundance of *Fucus* species continue decreasing in their southern limit (Jueterbock *et al.*, 2013), it is probably that the aggregative behaviour of *P. vulgata* under *Fucus* spp. canopy will not occur, increasing its mortality (Hawkins *et al.*, 2008). Similarly, for the northern/boreal barnacle *S. balanoides* some predictions under different climate scenarios indicate that it may go extinct in South-west England by the 2050s (Poloczanska *et al.*, 2008). This could result in an eventual replacement of *S. balanoides* by *Chthamalus* spp., which in turn could affect the probability of *Fucus* spp. escapes, given the small size and slow growth of *Chthamalus* spp. (Figure 1.2; Hawkins *et al.*, 2008). Hence, these results indicate that species roles could change in response to climate warming, depending on the position within their own distribution range, generating considerable impacts on ecosystem functioning.

### 1.7. Performance Traits on Species Range Distributions

The impacts of climate change on species traits will vary across different positions within their own range distribution (Bates *et al.*, 2014). The biological performance of species close to their biogeographic boundaries is of great interest in a period of climate variability and can be used to help predict future patterns of species distribution (Helmuth *et al.*, 2006; Fredston-Hermann *et al.*, 2018). The classic view is that performance attributes (*e.g.*, growth, survival and reproductive) will gradually decline with increasing distance from the core towards a range's edge, often with a reduction in size and densities of marginal populations, which are more fragmented than central populations (Brown, 1984; Caughley *et al.*, 1988; Guo *et al.*, 2005). In general, as the edge populations tend to be small, less diverse genetically and more sensitive to changes in the environment than centre populations, they may compromise local adaptability (Eckert *et al.*, 2008; Pearson *et al.*, 2009; Nicastro *et al.*, 2013; Mota *et al.*, 2014). However, evidence of a decrease in abundance and fitness is lacking (Sagarin & Gaines, 2002ab; Gilman, 2005, 2006ab; Sexton *et al.*, 2009; Hidas *et al.*, 2010; Coulson *et al.*, 2011; Herbert, 2011). For example, on the western coast of the United States, only 2 of 12 intertidal marine invertebrates have abundant-centre distributions (Sagarin & Gaines, 2002a). This suggests that the underlying assumptions of the Abundant-Centre Hypothesis (ACH; see Box 1.2 for details) may conflict

with specific characteristics of the life histories and patterns of environmental variation across the ranges of marine species (Gilman, 2005; Gaston, 2007; Helmuth *et al.*, 2006; Gaston, 2009; García-Molinos *et al.*, 2017; Fredston-Hermann *et al.*, 2018).



**Figure 1.3.** Sequence of events on patchy, moderately exposed shore over several years. (a) Shores dominated by *P. vulgata* and *Semibalanus balanoides*, (b) shores dominated by *P. depressa* and *Chthamalus* spp (Figure from Hawkins *et al.*, 2008).



Box 1.2		
Concept	Definition	Papers for details
<b>Abundant-Centre Hypothesis (ACH)</b>	Formalised by Brown (1984), assumes that environmental suitability is spatially auto-correlated such that species abundance is greatest where the environment is most favourable: at the species range-centre. Thus, in terms of population dynamics, central populations are sources and edge populations are sinks. This hypothesis has also been applied to test others species traits such growth, reproduction and mortality along their distribution.	Brown, (1984) Brown <i>et al.</i> , (1996) Sagarin & Gaines, (2002ab) Gilman, (2005) Sagarin <i>et al.</i> , (2006) Gilman, (2006ab)

Intertidal species have been the focus of many experiments designed to test the change performance attributes across ranges (e.g., Williamson & Kendall, 1981; Lewis *et al.*, 1982; Kendall & Lewis, 1986; Kendall, 1987; Herbert *et al.*, 2003; Gilman, 2005, 2006ab, Herbert *et al.*, 2007; Ling *et al.*, 2008; Herbert *et al.*, 2009; Hidas *et al.*, 2010; Araujo *et al.*, 2011; Coulson *et al.*, 2011; Viejo *et al.*, 2011; Oppliger *et al.*, 2012, 2014; Shanks *et al.*, 2014). For example, Herbert *et al.* (2009) examined growth and reproduction in the barnacle *Chthamalus montagui* in the central English Channel, one of its poleward limits around the British Isles. A gradient in growth was not apparent from its core distribution towards its range limits and gonads appear to develop normally but with faster gonadal development close to the range edge compared to central populations (Herbert *et al.*, 2009). Similarly, in the limpet *Collisella scabra*, populations at the range edge show higher growth and lower mortality than higher density populations in more central parts of its distribution and there is also little evidence that fecundity at marginal populations is reduced (Gilman, 2006b).

In macroalgae, the range edge of two related kelp species can be explained by differential responses of the vital rates of the haploid microscopic stage along the Chilean coast (*i.e.*, gametophyte) and by different reproductive strategies in relation to temperature (Oppliger *et al.*, 2012). For example, gametophytes of the northern species (*i.e.*, *Lessonia berteroa*) are more tolerant to higher temperatures than gametophytes from the southern species (*i.e.*, *Lessonia spicata*) together with a shorter vegetative growth phase during its haploid microscopic stage (Oppliger *et al.*, 2012). In *Laminaria digitata*, populations located at the range edge are still maintained mostly by sexual reproduction despite the expected tendency of geographical parthenogenesis in marginal populations (Oppliger *et al.*, 2014). On the another hand, in fucoid species, such as *Fucus serratus* and *Ascophyllum nodosum* there are evident differences in reproductive and morphological traits between central and marginal populations within their

ranges along the European coast (Araújo *et al.*, 2011; Viejo *et al.*, 2011). Edge populations of *A. nodosum* have higher reproductive output, fertility and density, but attain smaller sizes in relation to centre populations (Araújo *et al.*, 2011). In contrast, differences between marginal and central populations are not as evident for *F. serratus* and populations do not differ between central and border locations (Araújo *et al.*, 2011). However, Viejo *et al.* (2011) found that for *F. serratus* the threshold size of reproduction and reproductive capacity decreases at the range margin in relation to central populations. Likewise, the stochastic population growth rate differs between fucoid species at different localities of their range distribution (Araújo *et al.*, 2014). The stochastic population growth rate of *A. nodosum* is lower and more variable in the centre of its distribution than in southern sites (*i.e.*, edge range), whilst for *F. serratus* the opposite trend is seen, with growth rate much lower and more variable in southern (*i.e.*, edge range) than in central populations (Araújo *et al.*, 2014). However, manipulative field experiments found that the response of *F. serratus* exposed to acute stress is not different between the marginal and central populations of the Atlantic coast (Martinez *et al.*, 2012). This does not exclude the possibility of differential adaptive responses of *F. serratus* to withstanding the extreme stress conditions at its distributional limits (Pearson *et al.*, 2009; Martinez *et al.*, 2012). Therefore, the question is, why the strategy for local persistence differs between the two species, as they are functionally, phylogenetically, and ecologically similar (Viejo *et al.*, 2011). To determine if reproduction is the demographic cause of range limits, it is necessary to study spatial and temporal variation in all of the demographic parameters (Gaston, 2009).

In terms of recruitment, the persistent discontinuity of the barnacle *Chthamalus montagui* on the south coast of England (*i.e.*, range edge) is considered to be due to recruitment limitation (Herbert *et al.*, 2009; Keith *et al.*, 2011). Similarly, for the limpet *Lottia gigantea*, its northern limit is probably controlled by recruitment limitation, resulting in sparsely populated sites that consist almost solely of adults (Fenberg & Rivadeneira, 2011). In the South-east of Australia, the population structure of the barnacle *Tessieropora rosea* suggests a decline in the frequency of recruitment events at its range limit (Hidas *et al.*, 2010). Hidas *et al.* (2010) found that both the densities of adults and recruits for the whelk *Morula marginalba* were lower in the range edge than centre populations. By contrast, Coulson *et al.* (2011) found no evidence for a significant decline of *M. marginalba* recruits from core to edge range, suggesting a considerable variation in density that occurs among sites, principally by presence or absence of its potential competitor

(i.e., the whelk *Haustorium vinosum*). For the limpet *Lottia scabram* (on the west coast of the United States), recruitment also declines from centre to edge range populations, but this can be associated with differences in microhabitats, as centre populations are close to areas dominated by the giant kelp *Macrocystis pyrifera*, which facilitates recruitment in marine invertebrates (Shanks *et al.*, 2014). Hence, these studies suggest that multiple factors may act to set range limits.

In physiological performance terms, fucoid species differ between populations located in the core and edge of their range distributions. For example, along Atlantic European shores, the southern edge populations of *Fucus serratus* are less resilient to desiccation and heat shock than central populations and this contrasts with both *Fucus vesiculosus* and *Fucus spiralis* (Pearson *et al.*, 2009; Ferreira *et al.*, 2014). For *F. vesiculosus*, there is no evidence of physiological divergence in heat shock response (Pearson *et al.*, 2009). According to Ferreira *et al.* (2014), the photosynthetic system of specimens from northern populations of *F. vesiculosus*, exposed to abiotic stress were more affected than those from southern populations. However, that result contrasts with physiological studies that show no regional differentiation in physiological response of *F. vesiculosus* (Pearson *et al.*, 2009; Zardi *et al.*, 2013). These contradictory results may be explained by the nature of the stress used in the different experiments (Pearson *et al.*, 2009; Zardi *et al.*, 2013; Ferreira *et al.*, 2014).

### 1.8. Rationale of Thesis, Overall Aim and Specific Objectives

#### 1.8.1. Rationale of Thesis

Marine ecosystems are being affected by global warming leading to changes in abundance and shifts in distribution of species (Southward *et al.*, 1995; Hawkins *et al.*, 2008, 2009; Poloczanska *et al.*, 2013; Burrows *et al.*, 2014; Birchenough *et al.*, 2015; Poloczanska *et al.*, 2016). Paleoclimate and long-term studies have shown that the northern hemisphere has warmed more since the late 1980s than at any other time during the last 2000 years (Mann & Jones, 2003; Moberg *et al.*, 2005). In addition, mean SST has been higher in northern than southern Europe in the last decades (Mann & Jones, 2003; Moberg *et al.*, 2005; Philippart *et al.*, 2011). As consequence, changes in geographic ranges of marine species have been seen on rocky shores in North-west Europe (Southward *et al.*, 1995; Hawkins *et al.*, 2003; Herbert *et al.*, 2003; Mieszkowska *et al.*, 2005; Simkanin *et al.*, 2005; Mieszkowska *et al.*, 2006, 2007; Hawkins *et al.*, 2008; Hawkins *et al.*, 2009). In the last two decades, range shifts have been recorded in species of macroalgae (Southward *et al.*, 1995; Yesson *et al.*, 2015), barnacles (Southward *et al.*, 1995; Herbert *et al.*, 2003, 2007; Mieszkowska *et al.*, 2014), trochids (Southward *et al.*, 1995; Mieszkowska *et al.*, 2005, 2006, 2007) and limpets (Southward *et al.*, 1995; Lima *et al.*, 2007ab; Hawkins *et al.*, 2008, 2009), although in some cases boundaries have remained static (Herbert *et al.*, 2009).

Britain and Ireland straddle a biogeographic boundary between cold boreal northern species and warmer Lusitanian southern species (Forbes, 1858; Lewis, 1964; Hiscock *et al.*, 2004). Over the last century, considerable fluctuations in climate have been recorded with consequences for marine ecosystems (Southward, 1980; Southward *et al.*, 1995; Hiscock *et al.*, 2004; Southward *et al.*, 2005). Either side of the First World War (1910-1920s) there was a cold period. This was followed by a period of warming until the late 1950s – early 1960s. Following the extremely cold winter of 1961/1963, there was a cooler period until the 1980s. Since the mid-1980s, the climatic conditions have become much warmer around the British Isles (Figure 1.2); typified by milder winters due to the prevalence of both the NAO and AMO index (Broitman *et al.*, 2008; Hawkins *et al.*, 2008, 2009; Mieszkowska *et al.*, 2014). In this context, changes in the abundance and geographic range of northern as well as southern species' distribution have been correlated with climate change (Herbert *et al.*, 2003; Mieszkowska *et al.*, 2005, 2006; Herbert *et al.*, 2009).

*al.*, 2007; Mieszkowska *et al.*, 2007; Broitman *et al.*, 2008; Hawkins *et al.*, 2008, 2009; Mieszkowska *et al.*, 2014; Herbert *et al.*, 2016). In general, the abundances of Lusitanian species have increased and northern species have declined after the 1990s (Mieszkowska *et al.*, 2005, 2006, 2007; Hawkins *et al.*, 2008, 2009; Mieszkowska *et al.*, 2014; Yesson *et al.*, 2015). Responses to climatic changes offshore are reflected on the seashore and given the prevalence of pelagic early life-stages of most intertidal species (*e.g.*, molluscs and crustaceans), the intertidal zone can be considered a proxy for broad-scale changes caused by climate variability (Southward *et al.*, 2005; Hawkins *et al.*, 2008, 2009). Hence, the seashore provides a natural laboratory in which the consequences and effects of climate warming on species have been extensively studied around the British coast (Southward *et al.*, 1995; Hiscock *et al.*, 2004; Mieszkowska *et al.*, 2005; Southward *et al.*, 2005; Mieszkowska *et al.*, 2006, 2007; Hawkins *et al.*, 2008, 2009, 2016).

In the intertidal landscape of the British Isles, the complex direct and indirect interactions among northern/boreal species such as *Patella vulgata*, *Semibalanus balanoides* and *Fucus* spp. have allowed novel approaches to investigating patch dynamics, especially on exposed and semi-exposed rocky shores (Lewis, 1964; Hawkins *et al.*, 1992, Burrows & Hawkins, 1998; Johnson *et al.*, 1998ab). However, these patch dynamics may be modified in different ways considering the changes in abundance of species reported over recent decades on North Atlantic coasts (Southward *et al.*, 2005; Hawkins *et al.*, 2008, 2009). For example, the recent increased abundance of the southern species *P. depressa* now exceeds levels during the last warm period (1950s) in South- and South-west England (Southward *et al.*, 1995; Kendall *et al.*, 2004; Hawkins *et al.*, 2008). Replacement of *P. vulgata* by *P. depressa* could have a strong impact on intertidal assemblages of the British coast (Moore *et al.*, 2007ab; Hawkins *et al.*, 2008; Firth *et al.*, 2009; Hawkins *et al.*, 2009). In addition, both *Patella* species have been categorized as climate indicator species (Southward *et al.*, 1995; Mieszkowska *et al.*, 2005, 2006), which makes both limpets a good model to test hypotheses about performance traits across distributional ranges of species.

Biological performance of species close to their biogeographic boundaries is of great interest in a period of climate warming (Helmuth *et al.*, 2006). The classic view is that performance attributes will gradually decline with increasing distance from the core towards the edge of a species range (Brown, 1984; Caughley *et al.*, 1988; Guo *et al.*, 2005). However,

evidence of a decrease in abundance and performance attributes is lacking (Sagarin & Gaines, 2002ab; Sexton *et al.*, 2009). Intertidal organisms have been the focus of many studies designed to test differences in performance attributes from central populations towards range edges (*e.g.*, Gilman, 2005, 2006ab; Herbert *et al.*, 2009; Hidas *et al.*, 2010; Araujo *et al.*, 2011; Coulson *et al.*, 2011; Herbert, 2011; Viejo *et al.*, 2011; Oppliger *et al.*, 2012, 2014; Shanks *et al.*, 2014; Lima *et al.*, 2016; Seabra *et al.*, 2016). Several of these studies have challenged the ACH (Abundant-Centre Hypothesis; Gilman, 2005; 2006ab; Hidas *et al.*, 2010; Araujo *et al.*, 2011; Coulson *et al.*, 2011; Viejo *et al.*, 2011; Oppliger *et al.*, 2012, 2014; Shanks *et al.*, 2014), emphasizing the primacy of small-scale differences in temperature over-riding latitudinal trends (Helmuth *et al.*, 2002; Sagarin & Gaines, 2002ab; Helmuth *et al.*, 2006; Chapperon *et al.*, 2016; Lima *et al.*, 2016; Seabra *et al.*, 2016). Despite numerous observations of shifts in species distribution along the northern European coast because of climatic variability, little is known about the changes in performance attributes (*e.g.*, survival, reproduction and growth) in northern/southern intertidal species under current climate warming scenarios in northern Europe.

### 1.8.2. Overall Aims and Specific Objectives

Limpets are an important component of intertidal assemblages worldwide and their grazing is known to play a key role in the ecology of these habitats (Hawkins & Hartnoll, 1983b; Hawkins *et al.*, 1992; Poore *et al.*, 2012; Aguilera *et al.*, 2013). *Patella vulgata* and *Patella depressa* have been proposed as suitable indicator species to help monitor and predict future climate change and potential changes in marine biodiversity throughout the British Isles (Southward *et al.*, 1995; Mieszkowska *et al.*, 2005, 2006). Thus, the overall aim of my thesis was to evaluate the processes at individual and population levels occurring in the warm-water limpet *P. depressa* at both poleward (*i.e.*, leading edges) range limits of its distribution in the British Isles, in North Wales and the South-eastern English Channel. A comparative approach was taken by comparing processes at range edges with those in more central populations in South-west England, where *P. depressa* reaches over 50% of the limpet populations at mid-shore levels in the intertidal zone (Kendall *et al.*, 2004; Moore *et al.*, 2007; Hawkins *et al.*, 2008, 2009). In addition, comparisons were made with its cold-water congener *P. vulgata* in terms of abundance, size, growth, mortality. Competition between these co-occurring species was also investigated. Thus, I explored the processes setting the range edge of *P. depressa* and those involved in

determining the level of competition and patterns of co-existence of *P. depressa* with its congener *P. vulgata*.

My overall aim was to distinguish what are the ultimate and proximate factors (see Box 1.3 for details) determining both range limits of *Patella depressa* in the British Isles. The following specific objectives were developed in the next five chapters:

In Chapter 2, a long-term comparison of distribution and abundance of *P. depressa* at both of its range edges in Britain was made. In addition, physical variables were related with a short-term estimation of abundance and sizes at well-established population of both *Patella* species and at both poleward edges of *P. depressa* in the British Isles.

In Chapter 3, individual growth and population mortality of *P. depressa* and *P. vulgata* were evaluated as a measure of species performance traits at different places in their distributional range in Britain. Further, the influence of local limpet density (i.e., at site-scale) on individual growth performance of *P. depressa* was also examined.

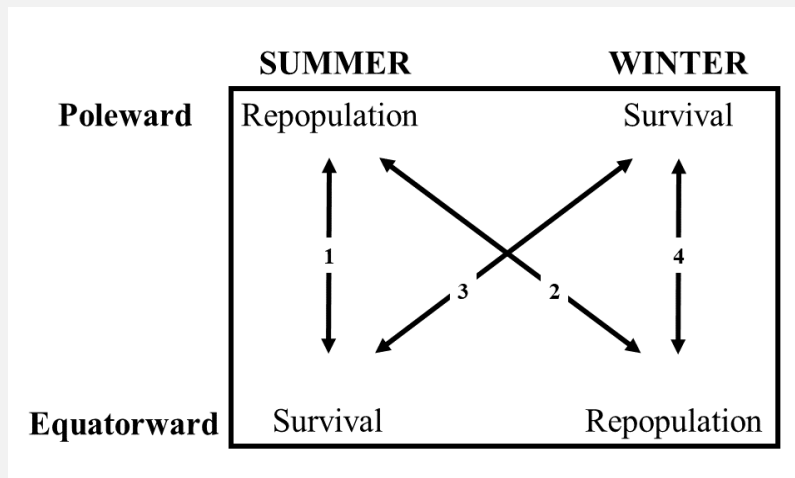
In Chapter 4, age and growth patterns of individuals of *P. depressa* were estimated using inner growth lines in shells from different locations of its range distribution in Britain. Further, the influence of local limpet density (i.e., habitat patch or quadrat-scale) on individual growth performance of *P. depressa* was also evaluated.

In Chapter 5, competition between both conspecific limpets in well-established populations for both *Patella* species and at the range edges of *P. depressa* in North Wales were experimentally evaluated. In addition, in order to assess if temperature can modify this competitive interaction, an experimental shade was added in the field.

Finally, in Chapter 6, an overview of the main findings is given and my results put into a broader context. Limitations of my work and suggestions for further research are made.

**Box 1.3**

**Ultimate Factor** Defined as the fundamental driver factor in species distribution. In marine ecosystem, Hutchins (1947) distinguished the role of sea water temperature on reproduction and recruitment in setting species distributions. Temperature can operate through four ways explained in Figure 1.3. The simplest type is that in which the extreme temperatures for survival of the individuals are critical both north and south. This involves a winter temperature toward the pole and summer temperature toward the equator. Type 2, is the exact converse of Type 1, and covers distributions bounded at both ends by temperatures required for repopulation (*i.e.*, summer temperatures) toward the poles and winter temperatures toward the equator. Type 3 and 4 are combination types, one boundary in each case depending on survival tolerances, and the other on reproductive requirements.



**Figure 1.3.** Diagram of the four basic types of zonation showing for each the season providing the critical poleward and equatorward conditions (Adapted from Hutchins, 1947).

**Proximate Factor** Defined as the following driver factor in species distribution. In marine species, immediately after the temperature effects on survival and reproduction of species, proximate factors play a secondary role acting through stress *e.g.*, air temperature, tides, wave action, competition, etc (see Helmuth, 2006 for details).



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## Chapter 1: Climate warming and its consequences on range edges and central populations

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## **CHAPTER 2:**

# **Comparisons of historical abundance and consequences of extreme temperatures at poleward range edges of the warm-water limpet, *Patella depressa* Pennant**

## 2.1. INTRODUCTION

Marine ecosystems have long been known to respond to climate fluctuations (Poloczanska *et al.*, 2013; Burrows *et al.*, 2014; Brito *et al.*, 2018). A wide range of observations in different marine ecosystems have shown significant responses to anthropogenic climate change (Bates *et al.*, 2014; Brown *et al.*, 2016; Poloczanska *et al.*, 2016). In our understanding of marine species responses to changes in climate, it is necessary to consider the relationship with their historical shifts in the past, when scientific records have begun in earnest (Crisp, 1959). There have been both warming and cooling periods over the last 100 years particularly in the North-east Atlantic region (Southward *et al.*, 1995; Hawkins *et al.*, 2003; Luterbacher *et al.*, 2004; Southward *et al.*, 2005; Lima & Wetthey 2012). Moreover, such fluctuations and the general upward trend in temperature has been punctuated by extreme weather - both warm (Luterbacher *et al.*, 2004; Lima & Wetthey, 2012; Oliver *et al.*, 2017, 2018) and cold events (Crisp, 1964; Southward *et al.*, 1995; Stachowicz *et al.*, 2002; Wetthey *et al.*, 2011; Firth *et al.*, 2015). As a consequent, these climate variations may have an impact on marine species distribution (Hutchins, 1947).

Species distributions (Poloczanska *et al.*, 2016) and phenological traits (Brown *et al.*, 2016) are responding to climatic change (Poloczanska *et al.*, 2013; Burrows *et al.*, 2014; Brito *et al.*, 2018). Intertidal species are one of the most studied groups exhibiting both shifts in geographic range (Southward *et al.*, 1995; Herbert *et al.*, 2003; Mieszkowska *et al.*, 2005, 2006, Herbert *et al.*, 2007; Mieszkowska *et al.*, 2007; Hawkins *et al.*, 2008, 2009), as well as phenology (Moore *et al.*, 2011; Brown *et al.*, 2016). Extreme weather may have positive or negative effects on intertidal species (Crisp, 1964; Stachowicz *et al.*, 2002; Firth *et al.*, 2011), particularly on the survival of newly settled recruits and hence on their population structure (Lewis & Bowman, 1975; Bowman & Lewis, 1977; Kendall & Lewis 1986; Beukema *et al.*, 1998; Wetthey *et al.*, 2011). Intertidal species must be able to cope with a wide range of temperatures over a tidal cycle (Lima *et al.*, 2016). Therefore, exposure to the varying temperatures of water and air appear to be primary drivers in the success of distinct populations (Lewis & Bowman, 1975; Bowman & Lewis, 1977; Lima *et al.*, 2006, 2007; Broitman *et al.*, 2008; First *et al.*, 2011; Wetthey *et al.*, 2011; Lima & Wetthey, 2012; Seabra *et al.*, 2016). Species distribution breaks often occur in regions with the widest thermal range between winter and summer temperatures (Hutchins, 1947; Crisp & Knight-Jones, 1954; Lewis, 1964; Hiscock, 1998). Therefore, populations at their marginal borders could



be strongly affected since climate change is expected to increase the frequency and intensity of severe weather events (Stachowicz *et al.*, 2002; Francis & Vavrus, 2012; Vasseur *et al.*, 2014).

Species range edges may be limited both toward the poles and toward the equator by tolerances or requirements, which can be attributed to summer or winter seasonal conditions (Hutchins, 1947; Crisp & Knight-Jones, 1954). Winter conditions appear to be primary drivers in the success of southern marine species at northern high latitudes (Crisp & Knight-Jones, 1954; Crisp & Southward, 1958; Crisp, 1964; Wethey *et al.*, 2011; Bates *et al.*, 2014; Firth *et al.*, 2015). In Britain, the widest range of temperatures can be seen in the east of the English Channel punctuated by extreme cold winters and hot summers (Crisp & Southward, 1958; Robinson *et al.*, 2017). This region coincides with one of the poleward limits for several southern lusitanian marine species (Crisp & Southward, 1958; Mieszkowska *et al.*, 2005, 2006, 2007; Hawkins *et al.*, 2008, 2009). The gradient from west to east along the Channel can be considered as analogous to a poleward gradient (Herbert *et al.*, 2009). The eastern English Channel contains the most climatically-continental places in the British Isles because it is affected by the tropical continental air mass from Africa, which brings hot and dry weather in summer, and also by a polar continental mass bringing cold air, snow and freezing conditions from central Europe in winter (Crisp & Southward, 1958; Hiscock, 1998; Robinson *et al.*, 2017). Both air and sea temperatures are influenced by the inflow of water eastwards through the English Channel, which produces a marked temperature gradient from the western half towards the eastern half (Crisp & Southward, 1958; Lewis, 1964; Hiscock, 1998). In contrast, regions such as North Wales and South-west England have similar thermal range since both are affected by a tropical maritime air mass from the Atlantic sea, which transports moist air and mild weather (Crisp & Knight-Jones, 1954; Lewis, 1964). Consequently, summer temperatures fall progressively from south to north, but in winter the west coast is generally warmer than the east side of Britain (Crisp & Southward, 1958; Lewis, 1964; Hiscock, 1998; Hiscock *et al.*, 2004). These combined effects can produce noticeable differences in the range of both air and sea temperature values, which might be expected to have an impact on the distribution of southern intertidal species on the coasts of the British Isles (Hutchins, 1947; Crisp & Knight-Jones, 1954; Crisp & Southward, 1958; Lewis, 1964).

Britain and Ireland straddle a biogeographic boundary for lusitanian southern species with their northern limit around the South-east England, North Wales and North Ireland (Forbes, 1858; Crisp & Southward, 1958; Lewis, 1964; Hiscock, 1998). Cold-water northern species

overlap this region, creating a natural laboratory in which comparisons among species with differing biogeographical distributions can be made (Crisp & Southward, 1958; Southward, 1967; Southward *et al.*, 1995; Hawkins *et al.*, 2003; Hiscock *et al.*, 2004; Hawkins *et al.*, 2008, 2009). There is considerable evidence that both the distributions of cold-species and warm-species are being affected by shifts in seawater temperature (Southward, 1967; Southward *et al.*, 1995; Hawkins *et al.*, 2003; Hiscock *et al.*, 2004; Mieszkowska *et al.*, 2005; Southward *et al.*, 2005; Hawkins *et al.*, 2008, 2009; Mieszkowska *et al.*, 2014; Herbert *et al.*, 2016). For example, *Osilinus lineatus* (re-named as *Phorcus lineatus*; Affenzeller *et al.*, 2017), an intertidal warm-water species disappeared from North Wales (*i.e.*, its northern limit) following the cold winter of 1962/63 (Crisp, 1964). Nowadays, with much warmer conditions this species occurs beyond Anglesey in North Wales (Mieszkowska *et al.*, 2006, 2007). Surveys conducted by the Marine Biodiversity and Climate Change project (MarClim®) have shown range extensions of several southern intertidal species, when compared to the historical, broad-scale and quantitative time series available for rocky shores around the British Isles including the English Channel (Herbert *et al.*, 2003; Mieszkowska *et al.*, 2005, 2006, 2007; Hawkins *et al.*, 2008, 2009; Herbert *et al.*, 2009; Mieszkowska *et al.*, 2014).

Shifts in species distribution because of global warming have stimulated research examining species performance traits close to their biogeographic boundaries (Caughley *et al.*, 1988; Hampe & Petit, 2005; Helmuth *et al.*, 2006; Parmesan, 2007; Herbert *et al.*, 2009; Bates *et al.*, 2014; Bennett *et al.*, 2015; Chuang & Peterson, 2016). The classic view about species attributes is that they will gradually decline from the centre of distribution towards the edges, which is explained by the Abundant-Centre Hypothesis (hereafter ACH; Brown, 1984). In general, edge populations tend to be small, fragmented, less genetically diverse and more sensitive to climatic variability than central populations (Hellberg *et al.*, 2001; Guo *et al.* 2005; Eckert *et al.*, 2008; Nicastro *et al.*, 2013). Nevertheless, along a species distributional range it must be recognized that there are two different types of edge populations (Hampe & Petit, 2005; Bennett *et al.*, 2015; Chuang & Peterson, 2016). The rear edge is located at low and warm latitudes (Hutchins, 1947), ultimately controlled by high temperatures, especially in the summer (Bates *et al.*, 2014). The leading edge occurs at higher and colder latitudes (Hutchins, 1947), ultimately being controlled by low temperatures, especially in winter (Bates *et al.*, 2014). Both range edges are modulated by opposite mechanisms and therefore they have different population dynamics (Bates *et al.*, 2014).

Whilst populations at their rear edge are suffering lower abundance and hence poleward contraction, populations at their leading edge are increasing in abundance leading to range extension (Bates *et al.*, 2014). Benthic organisms have been the focus of many studies to investigate how abundance and performance features vary between central and marginal populations (Kendall & Lewis, 1986; Gilman, 2005; Rivadeneira & Fernandez, 2005; Gilman, 2006ab; Mieszkowska *et al.*, 2007; Herbert *et al.*, 2009; Ling, 2008; Ling *et al.*, 2008, 2009; Hidas *et al.*, 2010; Herbert, 2011; Coulson *et al.*, 2011; Shanks *et al.*, 2014). For example, Herbert *et al.* (2009) examined growth and reproduction traits in the barnacle *Chthamalus montagui* (*i.e.*, a warm-water species) between populations in centre and east of the English Channel. Although a small reduction in growth can be identified towards its range limits, against expectation gonads had faster development in populations closest to its border. Similar patterns have been found in the urchin *Centrostephanus rogersii* in eastern Tasmania, with a greater reproductive investment at its leading edge compared to central populations (Ling *et al.*, 2008, 2009). Likewise, the limpet *Collisella scabra* shows higher growth and lower mortality in populations located at its range edge than central individuals, but there is also some evidence that fecundity is reduced at marginal populations (Gilman, 2006a). Therefore, the underlying assumptions of the ACH (Brown, 1984) may conflict with specific species life histories and local climatic conditions across rear, central and leading populations (Sagarin & Gaines, 2002ab; Gilman, 2005; Rivadeneira & Fernandez, 2005; Helmuth *et al.*, 2006; Sagarin *et al.*, 2006) as well as density dependent processes (Kendall & Lewis, 1986; Guo *et al.*, 2005; Jenkins *et al.*, 2005; Coulson *et al.*, 2011).

Other proximate factors, rather than the ultimate factor of temperature (Hutchins, 1947; Crisp & Knight-Jones, 1954) could also play a major role in determining the geographic range limits of species, such as hydrographic barriers to connectivity (Crisp & Southward, 1958; Gaylord & Gaines, 2000; Keith *et al.*, 2011; Adams *et al.*, 2014) and habitat quality (Herbert & Hawkins, 2006; Ling, 2008; Herbert *et al.*, 2009). Climate change may also have indirect effects by modulating biological interactions (Poloczanska *et al.*, 2008; Firth *et al.*, 2009; Coulson *et al.*, 2011; Kordas *et al.*, 2011; Shanks *et al.*, 2014). Theoretical and empirical evidence shows that demographic parameters (*i.e.*, immigration, birth, death and emigration) can also have a strong influence on species ranges (Guo *et al.*, 2005; Gaston, 2009). Thus, dispersal from central populations towards marginal populations is a key process required to maintain existing and establish new populations in new habitats (Kinlan & Gaines, 2003; Bates *et al.*, 2014; Chuang &

Peterson, 2016). Low abundances and absence of small individuals near range limits can suggest sporadic or limited recruitment (Bowman & Lewis, 1977; Kendall & Lewis, 1986; Gilman, 2006a; Herbert *et al.*, 2009; Hidas *et al.*, 2010; Coulson *et al.*, 2011; Shanks *et al.*, 2014; Borges *et al.*, 2015). For example, for many intertidal species their bounds are controlled by recruitment processes, resulting in sparsely populated sites which consist almost entirely of adults, *e.g.*, see Kendall & Lewis (1986) for *Gibubula umbilicalis* (re-named as *Steromphala umbilicalis*, Affenzeller *et al.*, 2017), Herbert *et al.* (2009) for *Chthamalus montagui*, Hidas *et al.* (2010) for *Morula marginalba*, Fenberg & Rivadeneira (2011) for *Lotia gigantea*, and Shanks *et al.* (2014) for *Lottia scabram*. Hence, the likelihood of range extension or contraction will be determined by an interaction between physical drivers and life-history traits of species, influencing their survival, reproductive output and population persistence (Hutchins, 1947).

*Patella* species are considered a keystone species because they control algal vegetation and determine patch dynamics on exposed and semi- exposed rocky shores (Jones, 1948; Southward & Southward, 1978; Branch, 1981; Hawkins, 1981; Hawkins & Hartnoll, 1983; Hartnoll & Hawkins, 1985; Jenkins *et al.*, 2005; Coleman *et al.*, 2006). In the North-west of Europe, limpet species such as the lusitanian southern warm-species *Patella depressa* and the boreal northern cold-species *Patella vulgata* show considerable geographic differences in their distribution (Figure 2.1. A). *P. depressa* is distributed from North Wales (Crisp & Knight-Jones, 1954; Kendal *et al.*, 2004) to North Africa (Fischer-Piette, 1936, 1948; Orton & Southward, 1961; Guerra & Gaudencio, 1986). *P. depressa* never colonized Ireland when it expanded northwards at the end of the last ice age (Crisp & Southward, 1953). Its congener *P. vulgata* is distributed from Norway to southern Portugal (Fischer-Piette, 1936; Guerra & Gaudencio, 1986; Southward *et al.*, 1995; Ribeiro *et al.*, 2009; Lima *et al.*, 2016) and is at the centre of its distribution throughout Britain (Lima *et al.*, 2016) where it coincides with both poleward borders of *P. depressa*, in the North-west of Wales and in the South-east England (Figure 2.1. A). *Patella* species have been proposed as climate indicator species (Southward *et al.*, 1995; Mieszkowska *et al.*, 2005), with *P. depressa* more abundant during the 1950s (a warm period) than during the cold period 1980/1984 (Crisp & Knight-Jones, 1954; Kendal *et al.*, 2004) and showing increased abundance in the last 30 years in Britain (Hawkins *et al.*, 2008). For instance, in the South-west of England *P. depressa* accounts for up to 50% of total limpets and in some places this figure is closer to 80% (*e.g.*, north coasts of Devon and Cornwall; Mieszkowska *et al.*, 2005; Hawkins *et al.*, 2008). Nevertheless, the current

leading edge of *P. depressa* in North Wales has not fully recovered to the full extent occupied in the 1950s, when it was categorised as “Common” by Crisp & Knight-Jones (1954) using the Crisp & Southward (1958) abundance scale on the west coast of Anglesey. Some relict population were still present in the north of the Llyn peninsula, recorded as occasional species at Nefyn in 1980s (Hawkins, unpublished), but by this time *P. depressa* was very rare on the Isle of Anglesey (Kendall *et al.*, 2004; Hawkins, unpublished). On the other hand, the range of *P. depressa* has extended its limit from the east of the Isle of Wight along the English Channel (Fischer-Piette, 1936, 1948; Crisp & Southward, 1958; Kendall *et al.*, 2004; Keith *et al.*, 2011), forming a breeding population at Southsea with scattered individuals beyond (Hawkins, unpublished).

Opposite mechanisms are affecting both *Patella* species at their rear versus leading edge (Crisp & Knight-Jones, 1954; Crisp & Southward, 1958; Lima *et al.*, 2006, 2007; Moore *et al.*, 2007; Lima *et al.*, 2016). For *Patella vulgata*, it has been suggested that its rear edge in Portugal is set by summer conditions (Chappon *et al.*, 2016; Lima *et al.*, 2016; Seabra *et al.*, 2016). For *Patella depressa*, winter conditions are modulating both of its leading edges in Britain (Crisp & Knight-Jones, 1954; Crisp & Southward, 1958). For instance, Lima *et al.* (2016) have indicated that there is a negative relationship between the number of days with temperatures above 27.5 °C and the abundance of *P. vulgata*. Thus, different types of microhabitats (thermal refuges) could be affecting the equatorial edge of boreal species (Chappon *et al.*, 2016; Lima *et al.*, 2016; Seabra *et al.*, 2016). On the other hand, the loss of cold microhabitats such as fucoid patches may be allowing the expansion of warm-water species northwards (Moore *et al.*, 2007). Climate warming has produced distributional declines of *Fucus* spp. in North west Europe (Jueterbock *et al.*, 2013). At small scales, *P. vulgata* can be found usually under *Fucus* spp. canopy (cold microhabitats), which provide an excellent nursery for recruitment (Lewis & Bowman, 1975; Hartnoll & Hawkins, 1985; Moore *et al.*, 2007). When these patches are removed, *P. vulgata* relocate their home scars or just die (Moore *et al.*, 2007). In contrast, *P. depressa* does not aggregate under *Fucus* spp. (Moore *et al.*, 2007). Since temperatures during low tide are higher in exposed rock than beneath *Fucus* spp. canopy, this suggests that *P. depressa* has higher tolerance to warm temperatures and does not need to aggregate under *Fucus* to keep cool (Moore *et al.*, 2007). Conversely, *P. vulgata* has lower tolerance to high temperatures and benefits from the cooler temperatures under fucoid clumps (Moore *et al.*, 2007).

*Patella* species are susceptible to fluctuations in aerial conditions and sea surface temperature, and therefore both species are considered indicators of climatic variability (Mieszkowska *et al.*, 2005; Lima *et al.*, 2006, 2007; Broitman *et al.*, 2008; Hawkins *et al.*, 2008, 2009; Lima *et al.*, 2016; Seabra *et al.*, 2016). The greatest effects of climate variability on marine species distribution may be due to changing maximum and minimum temperatures rather than annual means (Stachowicz *et al.*, 2002, Helmuth *et al.*, 2006; Francis & Vavrus, 2012; Helmuth *et al.*, 2014; Vasseur *et al.*, 2014). To understand the role of extreme temperature values on populations of a warm/lusitanian limpet species positioned at its poleward limits (leading edges), I tested a simple mechanistic geographic hypothesis (Hutchins, 1947; Lewis, 1964). I postulate that northern geographic range limits of *P. depressa* are set by extreme winter conditions (minimum winter temperatures of both sea surface and air) reflected by low abundances and by large individuals at both of its leading range edges in Britain (North Wales and South-east English Channel) compared to central populations (South-west England). Specifically, the combination of warm-summertime from the late 1980s to the mid-2000s, followed by more recent cold-winters (2005 onward; see Figure 1.1, Chapter 1) allows the separation and comparison of opposite latitudinal trends across the British Isles (Crisp & Knight-Jones, 1954; Crisp & Southward, 1958; Lewis, 1964). This hypothesis was tested by using a historical limpet data-set (Hawkins, unpublished; MarClim® project archives) to compare the abundance patterns between both *P. depressa* and the cold/boreal species *P. vulgata* from 1980 to 2016 around Britain. Furthermore, temporal and spatial shifts in the historical abundance of *P. depressa* at both of its leading boundaries were also analysed, using data from the 1950s compiled by Prof S.J. Hawkins from Crisp & Southward (1958) and by Crisp & Knight-Jones (1954) and published in Kendall *et al.* (2004). The alternative hypothesis that the range edges of *P. depressa* are set by a combination of poor reproductive output (Moore *et al.*, 20011), coupled with poor dispersal (Crisp & Southward 1958; Keith *et al.*, 2011) was also considered, but not formally tested.

## 2.2. MATERIALS AND METHODS

### 2.2.1. *Patella vulgata* and *Patella depressa* around Britain

Vertical zonation of *P. vulgata* is less restricted than *P. depressa*, but both limpet species are influenced by local environmental conditions (Evans, 1947; Orton & Southward, 1961). Generally, *P. vulgata* extends from Mean Low Water Spring tide level (MLWS) to Mean High Water Spring (MHWS) (Evans, 1947), whereas *P. depressa* has a more restricted vertical range in the British Isles and is usually most abundant between Mean High Water Neap (MHWN) and Mean Tide Level (MTL) (Orton & Southward, 1961). *P. vulgata* exhibits a single synchronous spawning event during the late autumn and winter with gonads developing during autumn (Orton *et al.*, 1956; Lewis, 1986). In southern England, females are larger than males, indirectly indicating the occurrence of protandry (Orton *et al.*, 1956; Borges *et al.*, 2015; see Box 2.1), confirmed by biopsy (Le Quesne & Hawkins, 2006). This pattern is not present at its equatorial range edges (*i.e.*, Portugal; Borges *et al.*, 2015). In contrast, *P. depressa* is a summer spawner in Britain, with gonad development commencing in the spring with its peak reproductive recorded in the late summer in the 1940s and 1950s (Orton & Southward, 1961). Further south in Portugal, the reproductive season is extended and multiple spawning events occur, followed by gonad redevelopment (Guerra & Gaudencio, 1986; Ribeiro *et al.*, 2009). In recent years, reproductive activity of *P. depressa* has extended from spring to autumn (Moore *et al.*, 2011). In addition, *P. depressa* is considered a gonochoristic species in Britain (Orton & Southward, 1961; Moore *et al.*, 2011; Borges *et al.*, 2015), but some individuals may show protandry particularly close to the centre of its range (Boaventura *et al.*, 2002, 2003; Borges *et al.*, 2015; see Box 2.1).

Box 2.1		Papers for details
<b>Gonochoristic</b>	Those species with sexes separate, the male and female reproductive organs being in different individuals, as opposed to hermaphroditic, gynogenetic, and hybridogenetic.	Orton <i>et al.</i> , (1956)
<b>Protandry</b>	Sequential hermaphroditism in which an individual transforms from male to female. Hermaphroditism refers to have both sexes in the same individual, either at the same time (synchronous hermaphrodite) or at different times (successive hermaphrodite). When the male form occurs first, this is referred to protandrous hermaphroditism.	Orton & Southward, (1961) Moore <i>et al.</i> , (2011) Borges <i>et al.</i> , (2015)

### 2.2.2. Historical data-set of *Patella* Species Abundances

A total of 69 locations were used to compare the abundance patterns of *Patella depressa* and *Patella vulgata* from 1980 to 2016 around Britain (Figure 2.1. B). Data from 1980 to 2001 were obtained from the notebooks of Prof S.J. Hawkins. A subset of this data on *P. depressa* abundance recorded during a cold period between 1980 and 1984 by Prof S.J. Hawkins, as well as summary of information collected by Crisp & Knight-Jones (1954) and by Crisp & Southward (1958) in the 1950s has already been published by Kendall *et al.* (2004). Data from 2002 to 2016 were taken from MarClim® archives ([www.marclim.co.uk](http://www.marclim.co.uk)) with data primarily being collected by Prof S.J. Hawkins, N. Mieszkowska and P. Moore.

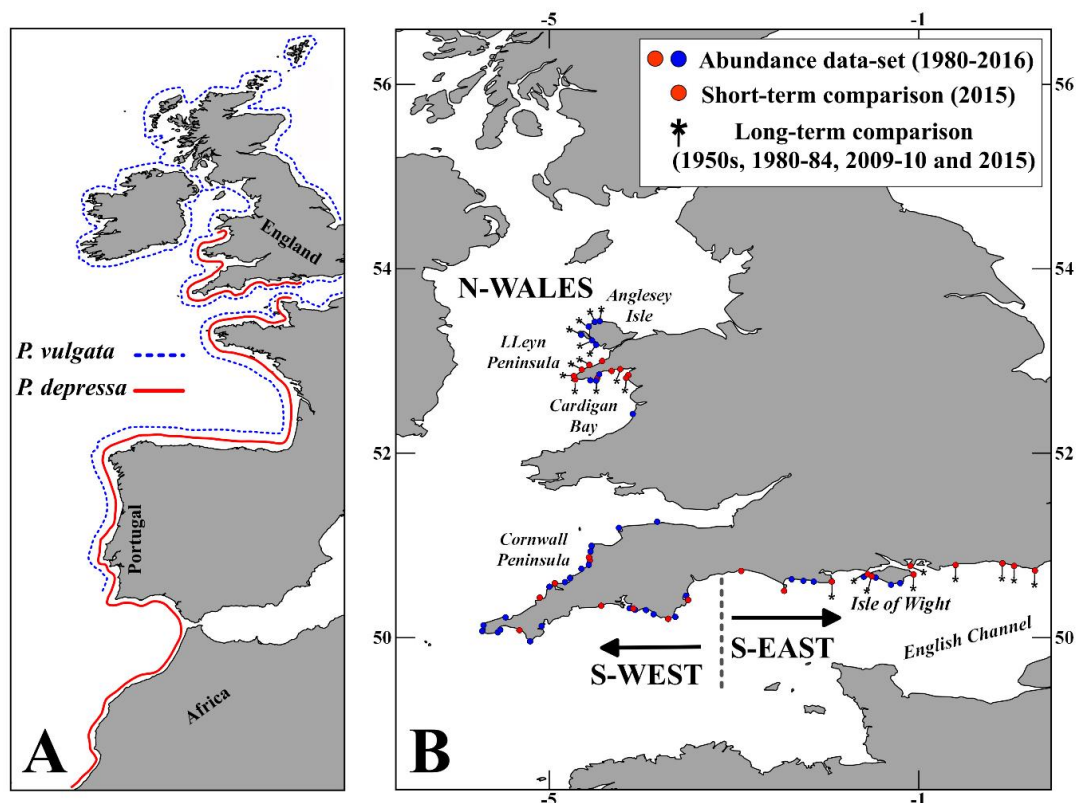
Locations were divided by region (Figure 2.1. B): 1) North Wales, hereafter N-Wales - from north Anglesey southwards to the northern edge of Cardigan Bay; 2) South-west England, hereafter S-West - from north of the Cornwall Peninsula following the coastline eastwards into the English Channel to Torquay; and 3) South-east England, hereafter S-East - from Lyme Regis to Eastbourne in the eastern English Channel (Figure 2.1. B).

### 2.2.3. Long-Term Comparison of *Patella depressa* Abundance and Distribution

Due to the unbalanced numbers of quadrats used to quantify limpet abundance in the historical database (1980/2016; Figure 2.2), *P. depressa* abundance was compared semi-quantitatively. In order to examine temporal and spatial shifts in the historical abundance of *P. depressa* at both of its northern limits in Britain, a total of 12 locations in N-Wales and 9 locations in S-East England were selected (Figure 2.1. B). To extend the temporal scale comparison, abundances recorded by Crisp & Southward (1958) and Crisp & Knight-Jones (1954) during the 1950s (compiled by Prof S.J. Hawkins) reported by Kendall *et al.* (2004) were included. Consequently, locations were compared among distinct periods: 1) 1950s (data from Kendall *et al.*, 2004) 2) 1980/1984 (data from Prof S.J. Hawkins) 3) 2009/2010 (data from MarClim® archives) and 4) 2015 (data obtained from this work). This long-term comparison was made using the semi-quantitative “ACFOR” scale (*i.e.*, Abundant, Common, Frequent, Occasional and Rare; Crisp & Southward, 1958) adapted from Kendall *et al.* (2004) for the periods 1950s and 1980/1984. Locations and spatial scales were also chosen following Kendall *et al.* (2004) and according to the current distribution of *P. depressa* at both of its leading edges (*i.e.*, N-Wales and



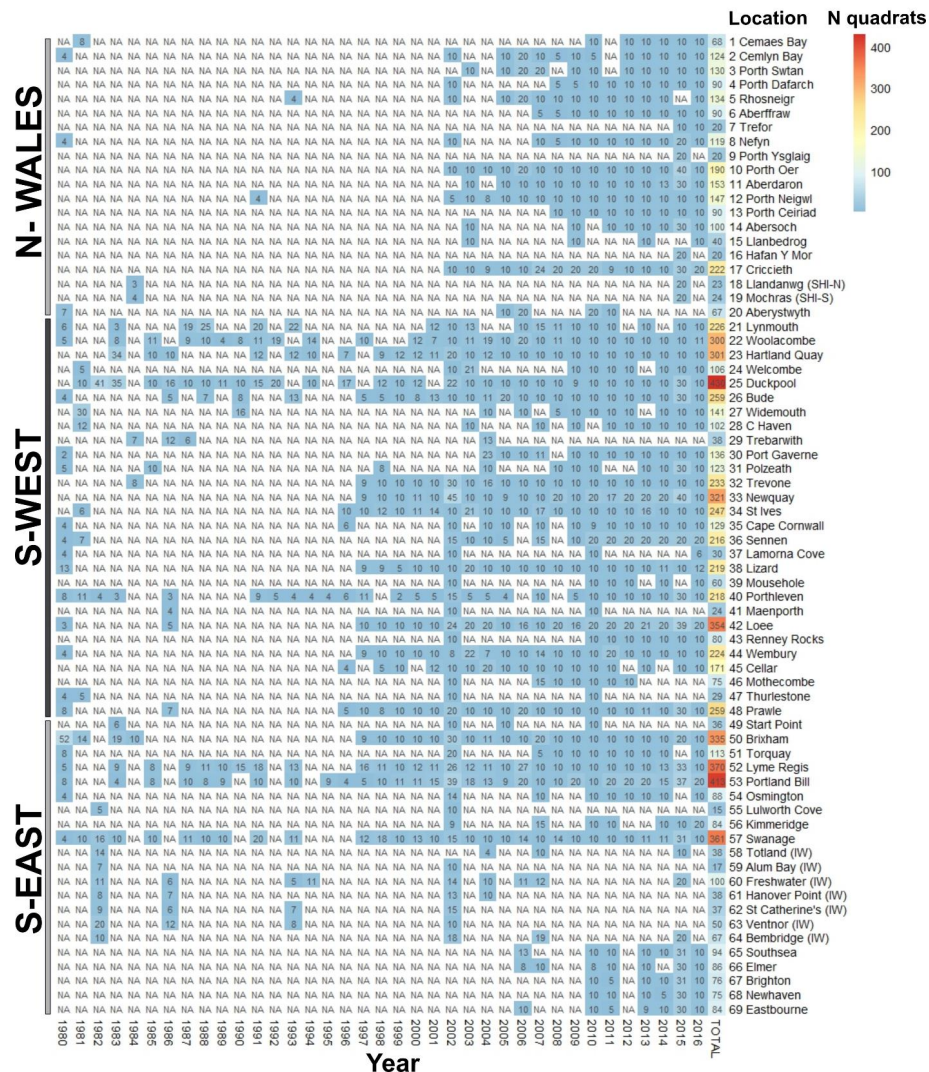
S-East England; Mieszkowska *et al.*, 2005; Hawkins *et al.*, 2008, 2009; Keith *et al.*, 2011; Borges *et al.*, 2015).



**Figure 2.1.** (A) Distributional range of *P. depressa* (red) and *P. vulgata* (blue) in the North West of Europe. (B) Locations in blue and red (total=69) were used to compare abundances (1980/2016) of both *Patella* species between N-Wales, S-West and S-East of England. Some locations in red colour (n=30) were used to determine the role of summer and winter temperatures (2014/2015) on the abundance and size of *P. depressa* (short-terms comparison). Locations with \* were used to compare both temporal and spatial shifts in the historical abundance of *P. depressa* at both leading edges in Britain: N-Wales and S-East England (long-term comparison).

#### 2.2.4. Short-Term Comparison of *Patella depressa* Abundance and Sizes

In order to determine the abundance and size distributions of *P. depressa*, a total of 30 locations (exposed- or semi-exposed shores) were sampled between September and late October 2015 around Britain (Figure 2.1. B). Surveys were conducted within the barnacle zone at three distinct levels defined by the dominant organisms of each region: 1) High zone - located between *Pelvetia* spp. band and the upper limit of the barnacle distribution; 2) Mid zone - situated in the



Each location was divided into two sites, separated by ~ 50-100 meters. In each vertical zone, ten 0.25 m<sup>2</sup> quadrats were deployed along a transect parallel to the coastline, ~ 1 m apart. In each quadrat, the total number of individuals of *P. depressa*, *P. vulgata* and *P. ulysiponensis* was recorded. For size measurements, four sub-samples (0.016 m<sup>2</sup>) were used in each quarter of the quadrat. The maximum length of each individual of *P. depressa* and *P. vulgata* contained in each sub-sample was measured with calipers to a resolution of 0.1mm. Locations were sampled at low water during spring tides to allow for an adequate estimate of lower shore species abundances. All quadrats were placed on open rock, but avoiding crevices, canopy-forming algae and rock pools.

#### **2.2.5. Maximum and Minimum Temperatures of both Sea Surface and Air**

Sea Surface Temperature (hereafter SST) and Air Temperature (hereafter AT) were obtained from different sources. SST was obtained from the Atlantic European North West Shelf Ocean, Odyssey Sea Surface Temperature Analysis (2007-present) - provided by the Monitoring Service Marina Copernicus (<http://marine.copernicus.eu/>) and based on a re-analysis of satellite data from both infra-red and micro-wave radiometers, with a spatial resolution of 0.02° (latitude) and 0.02° (longitude) and a daily temporal resolution. AT was taken from the Environmental Information Platform of the Centre for Ecology & Hydrology (<https://www.ceh.ac.uk/>) - based on an Atmospheric Evaporative Demand model, which is determined by meteorological variables with a spatial resolution of 1 km<sup>2</sup> and a daily temporal resolution (see Robinson *et al.*, 2017 for details). Both SST and AT for winter 2014/2015 (December 2014 - February 2015) and summer 2015 (June - August 2015) were downloaded. Then, daily minimum winter temperature (2014/2015) and daily maximum summer temperature (2015) of both SST and AT for each location were selected.

### **2.3. STATISTICAL ANALYSIS**

#### **2.3.1. Short-Term Comparison of *Patella depressa* Abundance and Sizes**

To determine whether *P. depressa* size structure differed between regions (late summer - early autumn 2015), size distributions were compared using a Kolgomorov-Smirnov test ( $\alpha = 0.05$ ). Subsequently cumulative size-frequency data were plotted by species and region.

In order to determine the relationship between temperature and abundance as well as size of *P. depressa* recorded in 2015, a set of extreme temperature values from different locations (daily

minimum 2014/2015 and daily maximum 2015 of SST and AT) were used. General Additive Models (hereafter GAMs) were used in which the dependent variable was modelled as the additive sum of various covariates (Zuur *et al.*, 2010). GAMs use a link function to establish a relationship between the mean of the response variable (*i.e.*, abundance and size) and a ‘smoothed’ function of the explanatory variables (Guisan *et al.*, 2002). The strength of GAMs is their ability to deal with highly non-linear and non-monotonic relationships between the response and the set of explanatory variables (Zuur *et al.*, 2009). Furthermore, GAMs have been extensively used to determine the nature of the relationship between the response and a set of explanatory variables rather than assuming some form of parametric relationship (Yee & Mitchell, 1991; Guisan *et al.*, 2002). Variance Inflation Factor (hereafter VIF) values (see Box 2.2), Pearson correlation matrices and scatterplots, which allow for the visualisation of the relationships among the complete set of variables and the characterisation of their correlation structure, were useful to avoid complications of multi-collinearity among explanatory variables (Zuur *et al.*, 2009, 2010). Explanatory variables with VIF values over 3 were excluded (Zuur *et al.*, 2010; see Box 2.2). The best model was considered the one with the lowest Akaike Information Criterion (AIC), highest explained deviance, highest adjusted  $R^2$  and lowest Un-biased Risk Estimator (UBRE) (Guisan *et al.*, 2002; Zuur *et al.*, 2009, 2010; Ortega-Garcia *et al.*, 2015; see Box 2.2). Diagnostic plots (*i.e.*, histograms of residuals and residuals vs. linear predictor) were used to evaluate model fitness and statistical assumptions of residuals. All statistical analyses were done using CRAN R project (R Development Core Team 2014). For Kolmogorov-Smirnov the STATS package (*i.e.*, The R Stats Package) was used and all GAMs were built with the package MGCV (*i.e.*, Mixed GAM Computation Vehicle with Automatic Smoothness Estimation).

The proportion of *P. depressa* out of the total number of individuals of all limpet species has been widely used as an index of abundance (Mieszkowska *et al.*, 2005; Hawkins *et al.*, 2008; Keith *et al.*, 2011). This proportional measure has been useful when comparing abundance of *P. depressa* with the cold-boreal limpet *P. vulgata* on the South west coast of England over the last 50 years (Southward *et al.*, 1995; Mieszkowska *et al.*, 2005; Hawkins *et al.*, 2008). This approach was adopted here. Therefore, in order to establish the relationship between *P. depressa* abundance and extreme temperatures values, the mean of *P. depressa* proportion per location was determined. Thus, once the VIF values were calculated for each variable, *i.e.*, both daily minimum winter and maximum summer 2014/2015 of SST/AT, a base model was used to explain the mean proportion

of *P. depressa* comprising of the following variables: 1) daily minimum winter SST (hereafter, SST min winter), 2) daily maximum summer SST (hereafter, SST MAX summer) and 3) daily minimum winter AT (hereafter, AT min winter).

In order to determine which variables affect the size of *P. depressa*, the mean size of *P. depressa* for each location was calculated. Consequently, a second model was used based on extreme temperature variables, as well as biological variables. Because previous studies have highlighted that *Patella* species show stronger intra-specific competition than inter-specific competition (Thompson *et al.*, 2000; Boaventura *et al.*, 2002, 2003; Moore *et al.*, 2007; First *et al.*, 2009; Firth & Crowe, 2010), the mean density of *P. vulgata* and *P. depressa* were also included. Finally, once VIF values were calculated for each temperature variable and for each biological variable, the base model included the following explanatory variables: 1) Mean *P. depressa* density, 2) Mean *P. vulgata* density, 3) SST min winter, 4) AT min winter and 5) daily maximum summer of AT (hereafter AT MAX summer).

Box 2.2		References
<b>Variance Inflation Factor</b>	The question behind this concept is: Is there collinearity among the covariates? Collinearity is the existence of correlation between covariates. The problem of multicollinearity can be analyzed by looking at variance inflation factors. The Variance Inflation Factor (VIF) quantifies the severity of multicollinearity in an ordinary least squares regression analysis. One strategy for addressing this problem is to sequentially drop the covariate with the highest VIF, recalculate the VIFs and repeat this process until all VIFs are smaller than a pre-selected threshold. Some authors use a value of 10, but Zuur <i>et al.</i> (2010) suggest a more stringent approach to use values as low as 3.	Yee & Mitchell, (1991) Guisan <i>et al.</i> , (2002) Zuur <i>et al.</i> , (2009) Zuur <i>et al.</i> , (2010) Ortega-Garcia <i>et al.</i> , (2015)
<b>Akaike information Criteria (AIC)</b>	It is a fined technique based on in-sample fit to estimate the likelihood of a model to predict/estimate the future values. A good model is the one that has minimum AIC among all the other models. The following equation is used to estimate AIC: $-2 * \ln L + 2 * K$ ; where L is the value of the likelihood, N is the number of recorded measurements, and K is the number of estimated parameters.	
<b>Un-biased Risk Estimator</b>	Smoothing parameter estimation method in General Additive Models (GAMs). The prediction error criteria use are Generalized (Approximate) Cross Validation (GCV or GACV) when the scale parameter is unknown or an Un-Biased Risk Estimator (UBRE) when it is known. When UBRE is the smoothness selection method this will give the same result as comparing by AIC.	

## 2.4. RESULTS

### 2.4.1. Historical data-set of *Patella* Species Abundances

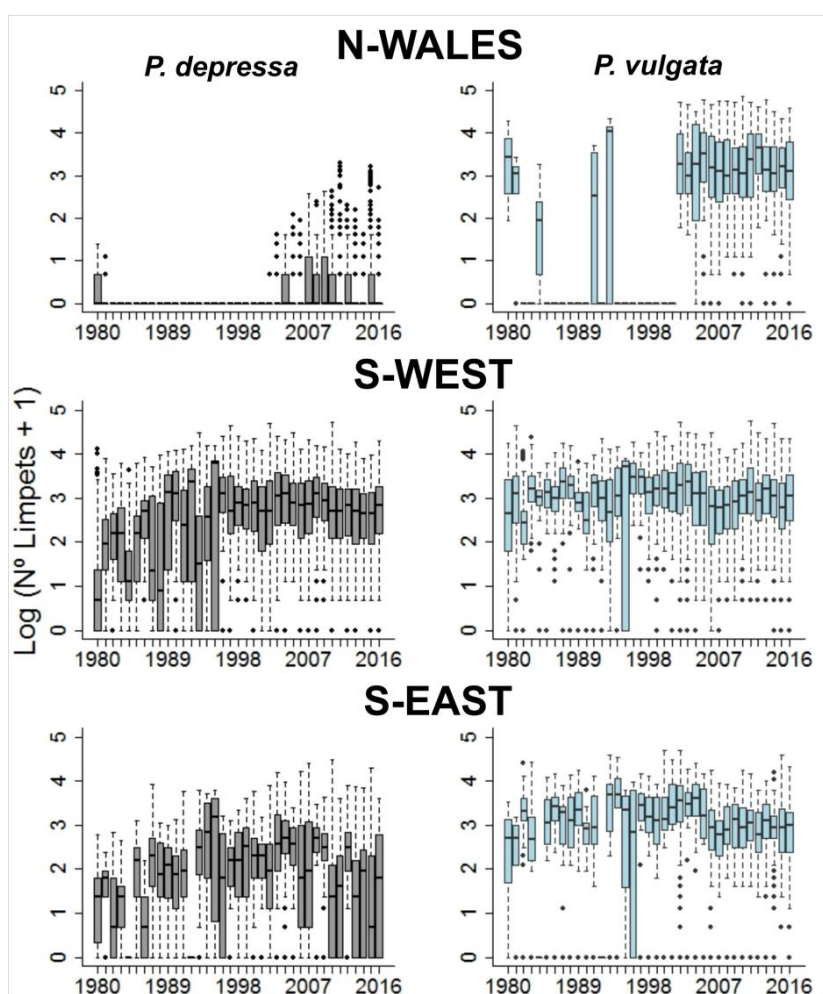
Prior to 2002, the majority of surveys were focused in S-West and S-East England (Figure 2.2). Intermittent surveys were made in N-Wales before 2002 by Prof S.J. Hawkins (Figure 2.2). After 2002, sampling effort has increased throughout all regions (Figure 2.2). Further, the limpet abundance dataset (1980/2016) indicated that *P. depressa* has different abundance patterns at its two leading edges in Britain (Figure 2.3). In N-Wales, its abundance has been much lower than S-East England over the last 35 years (Figure 2.3). In S-East England, *P. depressa* abundance has increased from the 1980s to 1990s, but also seems to show a recent dip in the late 2010s (Figure 2.3). Both *Patella* species tend to have equivalent patterns of abundance over the last two decades in S-West England (Figure 2.3). In this region, it appears that during the earliest period for which data are available *P. depressa* abundances were lower. However, its density shows a slight increase over the period 1980-1990 in this region (Figure 2.3).

### 2.4.2. Long-term Comparison of *Patella depressa* Abundance and Distribution

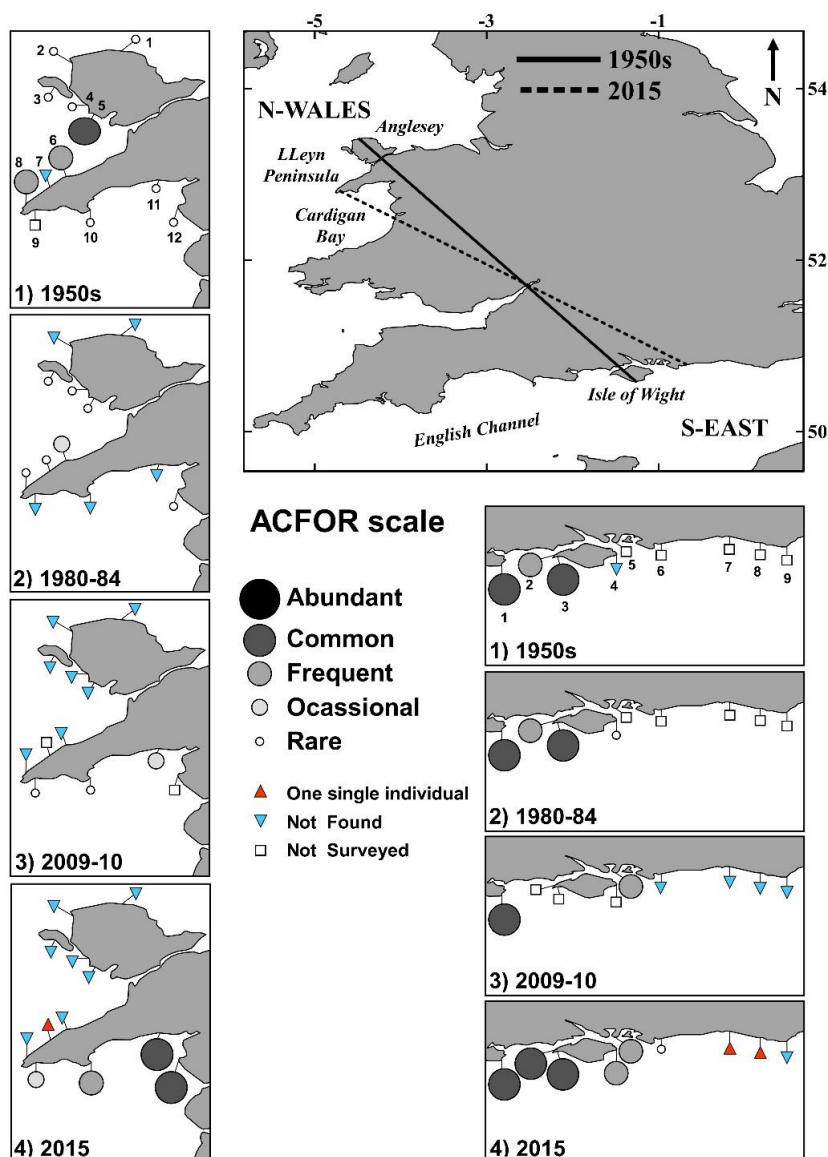
Long-term comparisons showed opposite patterns in shifts in *P. depressa* abundances at the two leading edges in Britain (Figure 2.4). In N-Wales, based on data from Kendall *et al.* (2004), *P. depressa* occurred on the north side of the Lleyn peninsula up to its northern limit on the north coast of Anglesey in the warmer 1950s, being recorded as “Common” species at some locations (e.g., Rhosneigr) by Crisp & Knight-Jones (1954). Scattered occasional and rare individuals were still present in the early 1980s, at the end of the cold spell which started after the extremely cold winter of 1962/63 (Hawkins, pers. comm.), and largely disappeared from north of the Lleyn and Anglesey by the mid-1980s (Hawkins, pers. comm.). In recent years, *P. depressa* has rarely been found on the north coast of the Lleyn Peninsula and not at all on the Isle of Anglesey (Figure 2.4). Nevertheless, a little further south of the Lleyn Peninsula in Cardigan Bay, *P. depressa* has become much more abundant than in the 1980s, exceeding values found in the 1950s and occurring in densities that constitute a breeding population (Figure 2.4). In fact, at the northern edge of Cardigan Bay, Kendall *et al.* (2004) reported *P. depressa* as a “Rare” species during both the 1950s and 1980s periods, but surveys made in 2015 showed that *P. depressa* has become a “Common” species (Figure 2.4).



On the other hand, in S-East England, *P. depressa* abundance showed a different shift in pattern (Figure 2.4). In recent years, the distributional range of *P. depressa* has extended beyond the Isle of Wight in the English Channel when compared with the Kendall *et al.* (2004) records for 1950s and 1980s (Figure 2.4) and now occurs as east as far as Newhaven, but not in sufficient numbers to form a breeding population (Figure 2.4). The last breeding population is at Southsea (Hawkins, pers. comm.), which represents a very small extension from the previous range edge recorded in the 1950s and 1980s on the Isle of Wight (Figure 2.4; Kendall *et al.*, 2004).



**Figure 2.3.** Box-plot of both *P. depressa* (left) and *P. vulgata* (right) densities (number of limpets per 0.25 m<sup>2</sup>) throughout N-Wales, S-West and S-East England from 1980 to 2016. Densities are expressed in Log (x + 1). Data between 1980 and 2001 were obtained from Prof S.J. Hawkins personal notebooks. Data from 2002 to 2016 were taken from MarClim® archives. Quadrats surveyed in this study (late summer - early autumn 2015) were also included.



**Figure 2.4.** Abundance comparison between both leading edges of *P. depressa* in Britain for the periods 1) 1950s, 2) 1980-84, 3) 2009-10 and 4) 2015. Abundances are expressed in ACFOR scale adapted from Crisp & Southward (1958) and reported by Kendall *et al.* (2004). **Top right:** Solid line and dashed black lines indicate its leading borders at N-Wales and S-East reported by Kendall *et al.* (2004) during 1950s and by this work for summer 2015, respectively. **Left side:** Locations in N-Wales are from north Anglesey southwards to the north of Cardigan Bay: 1) Cemaes Bay, 2) Porth Swtan, 3) Trearddur Bay, 4) Rhosneigr, 5) Aberffraw, 6) Nefyn, 7) Porth Ysglaig, 8) Porth Oer, 9) Aberdaron, 10) Abersoch, 11) Criccieth and 12) Shell Island. **Bottom right:** Locations in S-East England are towards the east through the English Channel: 1) Swanage, 2) Totland (Isle of Wight), 3) Freshwater (Isle of Wight), 4) Bembridge (Isle of Wight), 5) Southsea, 6) Elmer, 7) Brighton, 8) Newhaven and 9) Eastbourne.



### 2.4.3. Short-Term Comparison of *Patella depressa* Abundance and Sizes

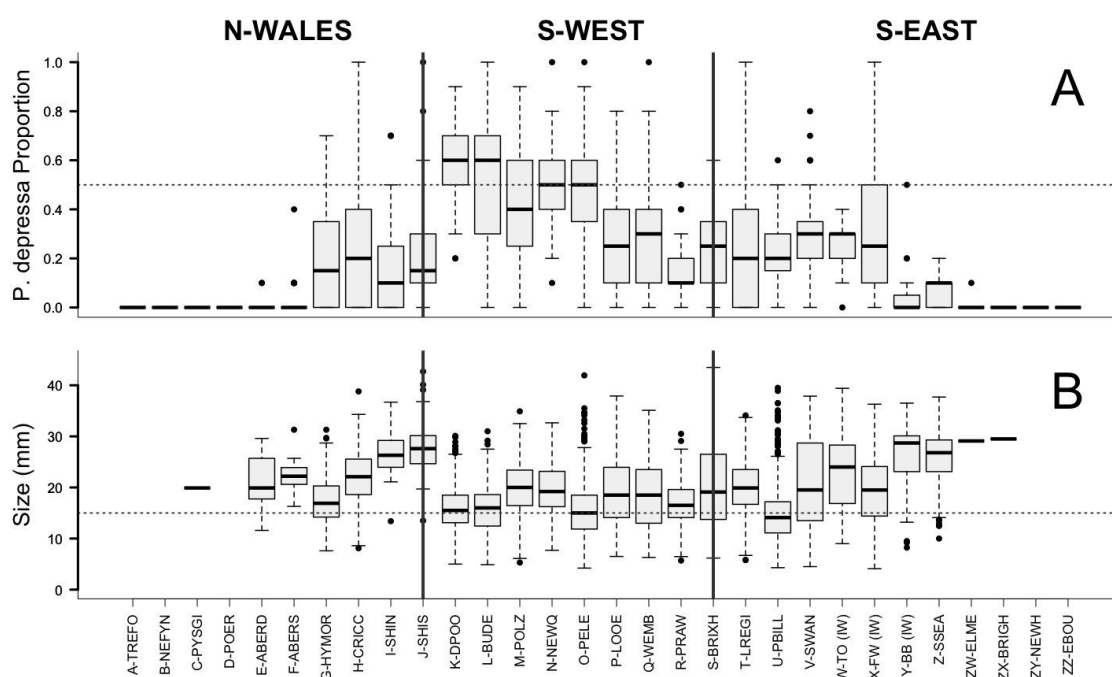
In terms of abundance, short-term surveys during late summer 2015 showed that *P. depressa* proportions did not reach more than 50% of total limpets in most locations in N-Wales and S-East England (Figure 2.5. A). In N-Wales, the highest proportions of *P. depressa* were found on the north coast of Cardigan Bay (from Hafan y Môr to Criccieth; Figure 2.5. A). Just a single individual was found on the north coast of the Llyn Peninsula (Porth Ysgaden; Figure 2.5. A). In S-East England, the highest proportions of *P. depressa* were found from Lyme Regis to the east side of the Isle of Wight (*i.e.* Freshwater; Figure 2.5. A). Further, reasonably dense numbers of *P. depressa* individuals were found beyond the east of the Isle of Wight at Southsea on the mainland (Z-SSEA; Figure 2.5. A), in the east of the Isle of Wight. Towards the eastern end of the English Channel, a single individual of *P. depressa* was found at locations such as Brighton, Newhaven (note: this last individual was found outside the sampled quadrats; Figure 2.5. A) and Eastbourne (Hawkins, unpublished). In contrast, the proportion of *P. depressa* reached more than 50% of all limpets in some locations in S-West England, predominantly in the north of Cornwall (Figure 2.5. A).

In terms of sizes, *P. depressa* individuals below 15mm in length indicating recent recruitment were more frequent at locations in S-West and S-East England when compared with locations in N-Wales (Figure 2.5. B and Figure 2.6). However, Kolmogorov-Smirnov tests detected no difference in the size distribution of *P. depressa* from N-Wales and S-East England ( $P > 0.05$ ). In fact, at both leading edges, *P. depressa* exhibited a similar range of the median length values among locations, which varied from 17 mm to 28 mm, and between 14 mm to 28 mm in N-Wales and S-East of England, respectively (Figure 2.6). By contrast, the range of median length values was narrower at locations in S-West England, where median length values varied between 15 to 20 mm (Figure 2.6). A similar range of median length values for *P. vulgata* when compared with *P. depressa* in N-Wales was found (from 18 mm to 28.5 mm; Figure 2.6). Nevertheless, cumulative size-frequency curves showed a wider range of the median length values for *P. vulgata* than *P. depressa* in locations at S-West and S-East England (Figure 2.6).

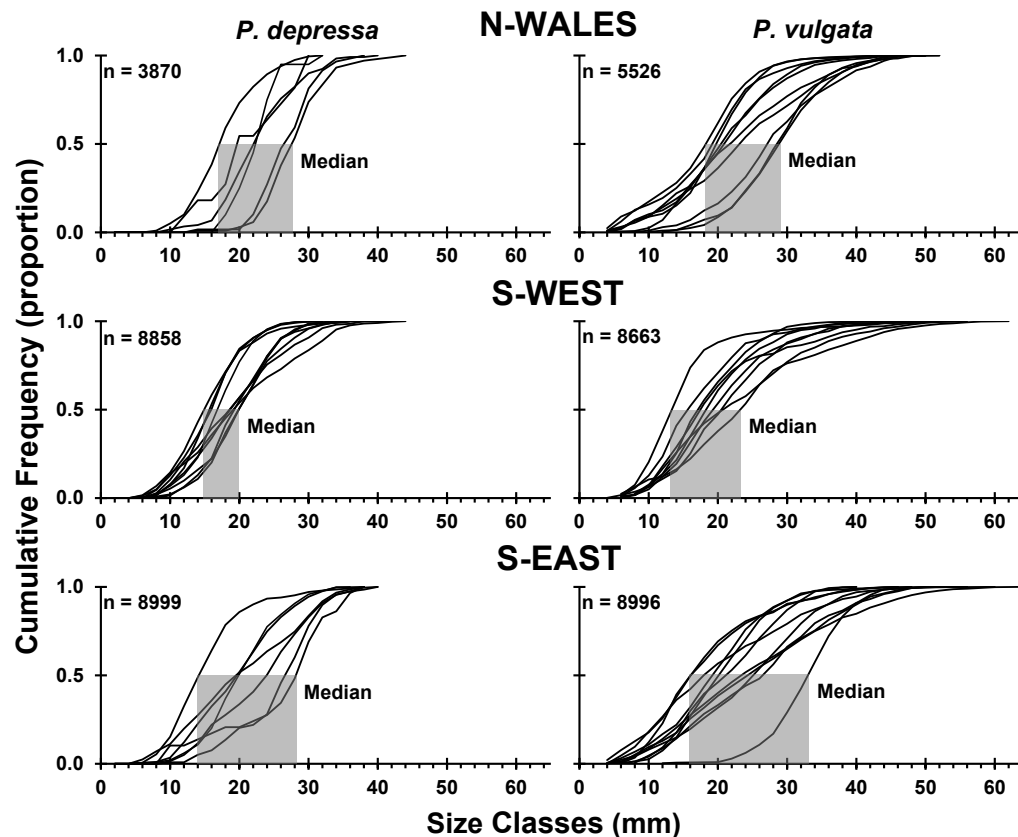
### 2.4.4. Maximum and Minimum Temperatures of both Sea Surface and Air

For winter temperatures (2014/2015), daily minimum SST values were higher than daily minimum AT values throughout all regions (Figure 2.7). By contrast, summer daily AT values

(2015) were warmer than daily SST (Figure 2.7). The widest difference in SST between summer and winter was found at locations in N-Wales and S-East England, especially at the northern edge of Cardigan Bay and towards the east of the Isle of Wight, respectively (Figure 2.7). In contrast, locations in S-West England showed a narrower range of SST between summer and winter when compared to both these regions (Figure 2.7). The AT range between summer and winter tends to have similar patterns across locations at N-Wales and S-West England (Figure 2.7).



**Figure 2.5. (A)** Box-plot of proportion of *P. depressa* to total limpets and **(B)** of *P. depressa* sizes (mm) at each location (summer 2015). In **(A)** dotted-grey horizontal line indicates 50% of proportion to total limpet population, and in **(B)** indicates a size reference of 15mm in length. A solid-grey vertical line on each plot separates each region: **N-Wales (left side)**: Trefor: A-TREFO, Nefyn: B-NEFYN, Porth Ysgaden: C-PYSGI, Porth Oer: D-POER, Aberdaron: E-ABERD, Abersoch: F-ABERS, Hafan y Môr: G-HYMOR, Crickieth: H-CRICC, Shell Island North: I-SHIN and Shell Island South: J-SHIS. **S-West England (middle)**: Duckpool: K-DPOO, Bude: L-BUDE, Polzeath: M-POLZ, Newquay: N-NEWQ, Porthleven: O-PELE, Looe: P-LOOE, Wembury: Q-WEMB, Prawle: R-PRAW and Brixham: S-BRIXH. **S-East England (right side)**: Lyme Regis: T-LREGI, Portland Bill: U-PBILL, Swanage: V-SWAN, Totland (Isle of Wight): W-TO (IW), Freshwater: X-FW (Isle of Wight), Bembridge: Y-BB (Isle of Wight), Southsea: Z-SSEA, Elmer: ZW-ELME, Brighton: ZX-BRIGH, Newhaven: ZY-NEWH and Eastbourne: ZZ-EBOU.

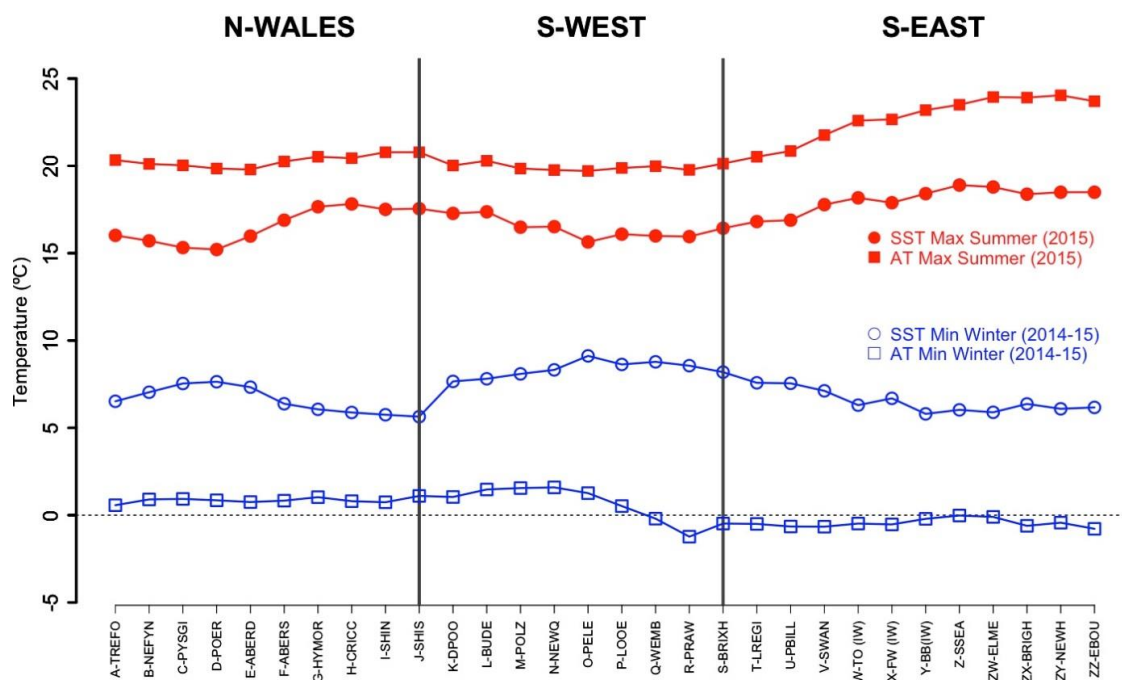


**Figure 2.6.** Cumulative size frequency curves for *P. depressa* (left hand) and *P. vulgata* (right hand) at locations (each black lines) separated by region, N-Wales (**top**), S-West (**middle**) and S-East England (**bottom**). Grey quadrats indicate the range of the median sizes (50% of total population) per location at each region.

#### 2.4.5. General Additive Models (GAMs)

GAMs were useful to fit extreme temperature values (2014/2015) with abundance as well as size of *P. depressa* across the sampled area in summer 2015. GAMs with Gaussian family errors and an identity link function represented the most appropriate and reliable fit for all models built. In the *P. depressa* proportion model, VIF values and Pearson correlations and scatterplots showed that both SST and AT MAX summer have a high correlation between them. Consequently, AT MAX summer was excluded since its VIF value was over three (VIF value = 5.34; Zuur *et al.*, 2010). The best fitted GAM to explain the mean *P. depressa* proportion at each location across regions comprised all temperatures in the base model built: 1) SST min winter 2) SST MAX

summer and 3) AT min winter (Table 2.1 and Figure 2.8). The model selection and results of the GAM fitting for the mean *P. depressa* proportion are shown in Table 2.1. Estimated smoothing curves obtained by the best GAMs showed that both SST MAX summer and SST min winter have a positive relation against the mean *P. depressa* proportion (P-value < 0.001; Table 2.1; Figures 2.8. A, B). However, for SST MAX summer, the mean *P. depressa* proportion decreased at locations with values over 17.5 °C (Figure 2.8. B). For AT min winter, locations with the highest values (> 1 °C) contained the greatest values of *P. depressa* proportion (P-value < 0.001; Table 2.1; Figure 2.8. C).

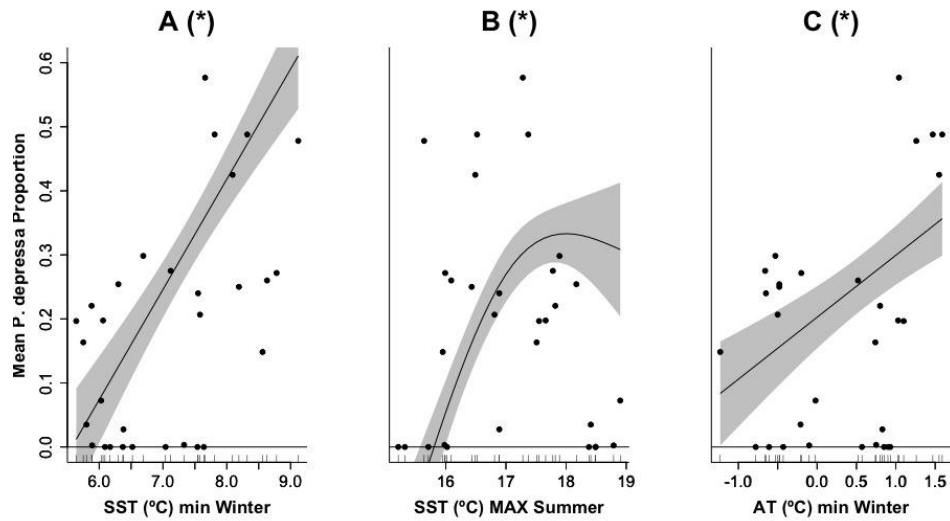


**Figure 2.7.** Daily maximum (red filled; summer 2015) and minimum (blue unfilled; winter 2014/2015) temperature values of SST (circle) and AT (square) at each location (n=30). Dotted-grey horizontal line indicates a temperature reference of 0 °C. Temperatures are expressed in Celsius degrees (°C). Solid-grey vertical lines separates regions: **N-Wales (left side):** Trefor: A-TREFO, Nefyn: B-NEFYN, Porth Ysgaden: C-PYSGL, Porth Oer: D-POER, Aberdaron: E-ABERD, Abersoch: F-ABERS, Hafan y Môr: G-HYMOR, Crickieth: H-CRICC, Shell Island North: I-SHIN and Shell Island South: J-SHIS. **S-West England (middle):** Duckpool: K-DPOO, Bude: L-BUDE, Polzeath: M-POLZ, Newquay: N-NEWQ, Porthleven: O-PELE, Looe: P-LOOE, Wembury: Q-WEMB, Prawle: R-PRAW and Brixham: S-BRIXH. **S-East England (right side):** Lyme Regis: T-LREGI, Portland Bill: U-PBILL, Swanage: V-SWAN, Totland (Isle of Wight): W-TO (IW), Freshwater: X-FW (Isle of Wight), Bembridge: Y-BB (Isle of Wight), Southsea: Z-SSEA, Elmer: ZW-ELME, Brighton: ZX-BRIGH, Newhaven: ZY-NEWH and Eastbourne: ZZ-EBOU.

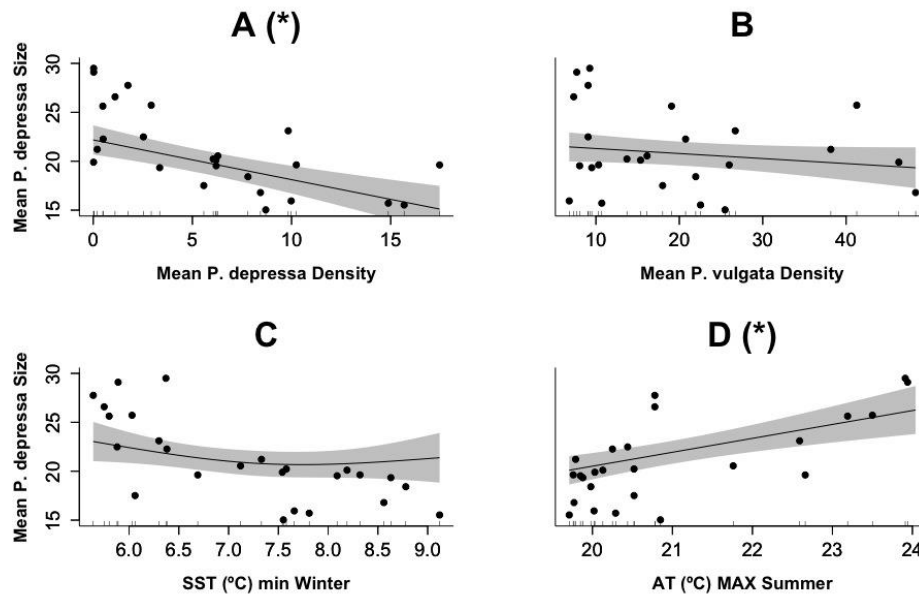
In the *Patella depressa* size model, in addition to extreme temperature values, biological variables such as *P. depressa* and *P. vulgata* densities were also included to explain the sizes of *P. depressa* throughout locations. Based on both data-sets, VIF values, Pearson correlations and scatterplots showed that both SST and AT MAX summer have a high correlation between them. Therefore, SST MAX summer was excluded in this model because of its high VIF value (VIF value = 12.59; Zuur *et al.*, 2010). The best fitted GAM to explain the mean size of *P. depressa* comprised just four explanatory variables from the base size model built: 1) mean *P. depressa* density, 2) mean *P. vulgata* density, 3) SST min winter and 4) AT MAX summer (Table 2.2; Figure 2.9). From this set of variables, the mean *P. depressa* density and the AT MAX summer were significant (P-value < 0.001; Table 2.2; Figures 2.9. A, D). The mean *P. depressa* density showed a negative relationship against mean *P. depressa* sizes, where locations with lowest mean density have the largest mean size values of *P. depressa* (P-value < 0.001; Figure 2.9. A). By contrast, AT MAX summer showed a positive association against the mean *P. depressa* size (P-value < 0.001; Figure 2.9. D). Locations having the highest maximum AT summer values contained the largest mean *P. depressa* sizes (Figure 2.9 D). In contrast, both mean density of *P. vulgata* and SST min winter values did not show a clear relationship against the mean size of *P. depressa* (P-value > 0.05; Figure 2.9. B, C).

**Table 2.1.** Summary of the best-fitted GAMs to examine the relationship between the mean proportion of *P. depressa* against a set of temperature values: **(1)** SST min Winter (SSTmW), **(2)** SST MAX summer (SSTMS) and **(3)** AT min Winter (ATmW). Variance Inflation Factor values (VIF-values) were used to select the predictor variables in the base model. GAMs selection were based on Adjusted R-squared (R-sq. (adj.)), deviance explained (%), Un-biased Risk Estimator (UBRE) and Akaike's Information Criterion (AIC). The best model considered is indicated by **bold** and *italic type*. P-value < 0.001 = significant.

GAMs	Predictors	VIF-Value	R-sq.(adj)	Deviance explained (%)	UBRE	P-Value	AIC
<b>Base model</b>	SSTmW	2.3	<b>0.82</b>	<b>84.1%</b>	<b>0.008</b>	< 0.001	<b>-63.5</b>
	SSTMS	2.6				< 0.001	
	ATmW	1.2				< 0.001	
<b>Without:</b> ATmW	SSTmW	-	0.65	68.7%	0.014	< 0.001	-45.2
	SSTMS	-				< 0.001	
<b>Without:</b> SSTMS	SSTmW	-	0.41	46.1%	0.024	< 0.001	-29.3
	ATmW	-				0.05	
<b>Without:</b> SSTmW	SSTMS	-	0.46	52.3%	0.023	0.04	-31.3
	ATmW	-				0.03	



**Figure 2.8.** Estimated smoothing curves obtained by the GAMs applied to the mean *P. depressa* proportion (summer 2015) against: **(A)** SST min winter (2014/2015), **(B)** SST MAX summer (2015); **(C)** AT min winter (2014/2015). Solid line shows the fitted GAMs function and the grey shading indicates 95% confidence intervals. Black dots indicates each location across regions (n=30). (\*) Indicates significant P-value ( $P < 0.001$ ).



**Figure 2.9.** Estimated smoothing curves obtained by the GAMs applied to the mean of *P. depressa* sizes against: **(A)** Mean of *P. depressa* density (late summer 2015), **(B)** Mean of *P. vulgata* density (late summer 2015), **(C)** SST minimum winter (2014/2015), and **(D)** AT maximum summer (2015). Solid line shows the fitted GAMs function and the grey shading indicates 95% confidence intervals. Black dots indicates each location (n=30). (\*) Indicates significant P-value ( $P < 0.001$ ).

**Table 2.2.** Summary of the best-fitted GAMs to determine the relationship between the mean of *P. depressa* sizes against a set of temperature values and also biological variables: **(1)** Mean of *P. depressa* density (Mean *Pd* Dens), **(2)** Mean of *P. vulgata* density (Mean *Pv* Dens), **(3)** SST min Winter (SSTmW), **(4)** AT min Winter (ATmW) and **(5)** AT MAX winter (ATMW). Variance Inflation Factor values (VIF-value) were used to select the predictor variables in the base model. GAMs selection was based on Adjusted R-squared (R-sq. adj), deviance explained, Un-biased Risk Estimator (UBRE) and Akaike's Criteria (AIC). The final model considered is indicated by **bold** and *italic type* P-value < 0.001 = significant.

GAMs	Predictors	VIF-Value	R-sq.(adj)	Deviance explained (%)	UBRE	P-Value	AIC
<b>Base model</b>	Mean <i>Pd</i> Dens	1.4	0.80	84.7%	6.606	< 0.001	110.4
	Mean <i>Pv</i> Dens	1.2				0.19	
	SSTmW	2.6				0.21	
	ATmW	1.8				0.59	
	ATMS	2.9				< 0.001	
<b>Without:</b> Mean <i>Pd</i> Dens	Mean <i>Pv</i> Dens	-	0.70	75.9%	9.236	0.11	120.4
	SSTmW	-				< 0.001	
	ATmW	-				0.28	
	ATMS	-				< 0.001	
<b>Without:</b> Mean <i>Pv</i> Dens	Mean <i>Pd</i> Dens	-	0.80	83.5%	6.082	< 0.001	110.4
	SSTmW	-				0.16	
	ATmW	-				0.31	
	ATMS	-				< 0.001	
<b>Without:</b> SSTmW	Mean <i>Pd</i> Dens	-	0.78	81.8%	6.087	< 0.001	111.7
	Mean <i>Pv</i> Dens	-				0.16	
	ATmW	-				0.35	
	ATMS	-				< 0.001	
<b>Without:</b> ATmW	Mean <i>Pd</i> Dens	-	<b>0.81</b>	<b>84.7%</b>	<b>5.644</b>	< 0.001	<b>108.6</b>
	Mean <i>Pv</i> Dens	-				0.11	
	SSTmW	-				0.12	
	ATMS	-				< 0.001	
<b>Without:</b> ATMS	Mean <i>Pd</i> Dens	-	0.73	79.1%	8.374	< 0.001	117.4
	Mean <i>Pv</i> Dens	-				0.07	
	SSTmW	-				< 0.001	
	ATmW	-				0.06	
<b>Without:</b> Mean <i>Pv</i> Dens ATmW ATMS	Mean <i>Pd</i> Dens	-	0.67	70.9%	7.879	< 0.001	120.5
	SSTminW	-				< 0.001	
<b>Without:</b> Mean <i>Pv</i> Dens SSTmW ATmW	Mean <i>Pd</i> Dens	-	0.76	77.6%	5.638	< 0.001	112.9
	ATMS	-				< 0.001	
<b>Without:</b> Mean <i>Pd</i> Dens Mean <i>Pv</i> Dens ATmW	SSTmW	-	0.68	71.70%	8.004	< 0.001	120.4
	ATMS	-				< 0.001	

## 2.5. DISCUSSION

### 2.5.1. Leading Range Edges of *Patella depressa* in Britain

My findings confirm that N-Wales as well as S-East England are poleward limits of *P. depressa* in the North west of Europe (Crisp & Knight-Jones, 1954; Crisp & Southward, 1958; Kendall *et al.*, 2004). However, different mechanisms determine the abundance and distribution of *P. depressa* at both of these regions in Britain. Additionally, long- and short- term comparisons have indicated that *P. depressa* abundance has been much lower in N-Wales compared with its eastern limit, S-East England (Figure 2.3, Figure 2.4 and Figure 2.5). It is known that *P. depressa* has recently expanded eastwards beyond the Isle of Wight in the English Channel, its eastern limit in the 1950s and 1980s (Mieszkowska *et al.*, 2005; Hawkins *et al.*, 2008, 2009; Keith *et al.*, 2011). Much less attention has been given to the leading edge in N-Wales; this range edge had contracted by ~70km from the 1950s, with residual and rare populations still present in the 1980s (Crisp & Knight-Jones, 1954; Kendall *et al.*, 2004; Hawkins, pers. comm.). During a warm climatic period in the 1950s in Britain (Mieszkowska *et al.*, 2006; Hawkins *et al.*, 2008, 2009), *P. depressa* was categorised as a “Common” species on the west coast of the Isle of Anglesey (Crisp & Knight-Jones, 1954). Ten years later, Crisp (1964) found few changes in abundance of *P. depressa* and its northern limit on Anglesey was unaffected during the cold winter in the 1960s (Crisp, 1964; the coldest winter since 1740). In 1980/1984, following the very cold winter of 1978/1979, which was almost as harsh a winter as during the 1960s (Firth *et al.*, 2015) it was categorized as an “Occasional” or “Rare” species on Anglesey (Kendall *et al.*, 2004). Currently, *P. depressa* is not present on the Isle of Anglesey, or even on the north coast of the Llyn peninsula (Figure 2.4). However, its abundance has increased at northern locations in Cardigan Bay (Aberdaron, Abersoch, Criccieth and Shell Island; Figure 2.4), which coincide with the increase in sea surface temperatures from the 1980s to the present (Lima & Wetthey, 2012; Mieszkowska *et al.*, 2006; Hawkins *et al.*, 2008, 2009; Luterbacher *et al.*, 2014; Varela *et al.*, 2018).

Crisp (1964) reported high mortalities for the honeycomb worm *Sabellaria alveolata* (a warm-water species) at many localities in N-Wales following a cold winter in the 1960s. After that, *S. alveolata* was badly affected further by the cold winter of 1980/1984 and it was assumed that mortality along the N-Wales coastline was complete (Firth *et al.*, 2015). This suggests that effects during winters in the late 1970s and early 1980s were just as high for *P. depressa* as the cold conditions experienced during winters of the 1960s. These cold conditions at the northern



limit of *P. depressa* clearly resulted in a range contraction on the Isle of Anglesey (Crisp & Knight-Jones, 1954; Crisp, 1964; Kendall *et al.*, 2004). However, in contrast to most other warm-water species, which have recovered their northern borders following both cold winter periods in Britain (*i.e.*, 1960s and 1980/1984; see Mieszkowska *et al.*, 2005, 2006, 2007 for details), *P. depressa* has not by any means fully recolonised, particularly around the Isle of Anglesey (Crisp & Knight-Jones 1954; Crisp, 1964; Kendall *et al.*, 2004). In addition, it seems that *P. depressa* does not disperse well, having not colonised Ireland when expanding northwards at the end of the ice age (Crisp & Southward, 1953).

Poleward and equatorward species' borders are likely to be affected by opposite processes due to climate change (Bates *et al.*, 2014) leading to species range contractions at their equatorial limits and by contrast, driving species range expansion at their poleward margins (Bennet *et al.*, 2015; Chuang & Peterson, 2016). An example of poleward expansion has been observed in the southern intertidal species *Patella rustica*, which has re-colonized a historical gap at the northern end of its distribution on the Portuguese coast during the late 1990s, where it was historically absent since at least the 1920s (Lima *et al.*, 2006, 2007). The change in its distribution has been attributed to several unusual oceanographic events characterized principally by negative values of upwelling index on the northern Portugal coast during the late 1990s (Lima *et al.*, 2006, 2007; Lima & Wetthey, 2012). A negative upwelling period is characterized by changes in offshore currents from south to north as well as by the strengthening of inshore poleward circulation and by an unusual increase in SST, which has facilitated the colonization of *P. rustica* from south to north on Portuguese rocky shores (Lima *et al.*, 2006, 2007; Lima & Wetthey, 2012). Undoubtedly, anthropogenic climatic change has produced changes in the North Atlantic sea currents over decades (Edwards *et al.*, 1999; Reid *et al.*, 2001ab; Philippart *et al.*, 2011; Lima & Wetthey, 2012). For instance, since the late 1980s sea warming temperatures have been typified by westerly winds and milder winters due to the prevalence of positive values of the North Atlantic Oscillation (hereafter NAO) across northern Europe (Reid *et al.*, 2001ab; Luterbacher *et al.*, 2004; Mieszkowska *et al.*, 2006; Broitman *et al.*, 2008; Philippart *et al.*, 2011; Mieszkowska *et al.*, 2014). NAO positive values have created a higher rate of Atlantic oceanic water inflows towards the Irish Sea, Nordic Sea and North Sea (Reid *et al.*, 2001a).

*Patella depressa*, unlike *Patella rustica* in Portugal, has failed to recolonise areas it once occupied at its poleward edge before 1980s in the Isle of Anglesey. This lack of recolonization

may be related to a hydrographic barrier to larval dispersal (Robins *et al.*, 2013; Adam *et al.*, 2014). Wethey *et al.* (2011) has proposed that when local extinctions are caused by extreme events or by decadal cycles, the rate of return of biogeographic distribution limits to their prior state is constrained by dispersal. Hence, I hypothesize that after *P. depressa* disappeared from north of the Llyn and Anglesey by the mid-1980s (Hawkins, pers. comm.), local and circular currents at the northern edge of Cardigan Bay (*i.e.*, eddies; Robins *et al.*, 2013) could be acting as a larval retention zone together with the physical barrier of Llyn Peninsula in N-Wales. In fact, northern locations are exposed to westerly winds in this area, but the shallow water of Cardigan Bay reduces the effect of wave action facilitating a larval accumulation area (Hiscock, 1998). Consequently, these physical oceanographic processes could be limiting the dispersal potential of *P. depressa* towards the Llyn Peninsula due to its short larval duration ( $\leq 14$  days; Crisp & Southward, 1953; Wright, 1977; Keith *et al.*, 2011).

### **2.5.2. Summer and Winter Temperature Effects on *Patella depressa***

Extreme temperatures offer opportunities to test the mechanism controlling the biogeographic limits of intertidal species (Crisp & Knight-Jones, 1954; Crisp & Southward, 1958; Crisp, 1964; Wethey *et al.*, 2011; Firth *et al.*, 2011, 2015). In my study, both SST of summer and winter (2014/2015) were significant factors in explaining the proportion of *P. depressa* across all locations (2015). In this context, seawater temperature is probably the ultimate factor driving geographic distributions of marine organisms including intertidal species (Hutchins, 1947), through its regulation of metabolism (Barry & Munday, 1959; Blackmore, 1969; Wright, 1977; Ling *et al.*, 2008). For *P. depressa*, as is the nature of a warm-water species (Hawkins *et al.*, 2008, 2009), favourable seawater temperatures close to its optimum will lead to more activity (Barry & Munday, 1959), greater growth as well as reproductive output and ultimately greater recruitment (Moore *et al.*, 2011). In addition, milder winters mean earlier onset of foraging and growth in spring (Orton *et al.*, 1956; Orton & Southward, 1961), earlier and longer gonad development (Moore *et al.*, 2011) and probably more than one spawning event in *P. depressa* (Orton & Southward, 1961; Moore *et al.*, 2011; Borges *et al.*, 2015). Milder winter conditions have persisted over the last three decades in the south of Britain (Mieszkowska *et al.*, 2006, 2007; Moore *et al.*, 2011). This temperature pattern could explaining its increase in proportion from the 1980s in certain locations (*i.e.*, north coasts of Devon and Cornwall; Hawkins *et al.*, 2008, 2009). Milder

winters, followed by warmer summers have most likely resulted in higher reproductive output of *P. depressa* populations located in S-West England (Moore *et al.*, 2011).

### 2.5.3. Sizes of *Patella depressa* at Leading Edges in Britain

Marginal populations showed larger sizes of *P. depressa* when compared with more central populations (*i.e.*, S-West England), indicating dominance of larger individuals at both poleward borders (Figure 2.5B and Figure 2.6). This suggests low recruitment of *P. depressa* towards N-Wales and S-East England, which leads to low densities in both regions, particularly in N-Wales populations (Lewis & Bowman, 1977; Kendall & Lewis, 1986). Size patterns of *P. depressa* also suggest a strong density dependent effect in populations in S-West England (Figure 2.5.B and Figure 2.9.A), which has been recognized in well-established central populations in Portugal (Boaventura *et al.*, 2002, 2003) and in core populations of *P. vulgata* in Britain (Thompson *et al.*, 2000; First *et al.*, 2009; Firth & Crowe, 2010). Similar patterns have been described in northern populations of *P. rustica* in Portugal, characterized by low densities and the predominance of large individuals, which is typical of populations that fail to reproduce successfully at their limits (Lima *et al.*, 2006, 2007). In N-Wales, *P. depressa* populations were sparse and dominated by large individuals, specifically at locations such as Shell Island, Abersoch and Aberdaron (Figures 2.5A and Figure 2.5B). However, the most northern locations in Cardigan Bay (Criccieth and Hafan y Môr; Figure 2.5B) showed a greater number of small individuals (< 15mm in length) as well as highest abundance of *P. depressa* in this area, which suggest the presence of *P. depressa* breeding populations. These patterns reinforce the hypothesis of a larval accumulation zone in Cardigan Bay in N-Wales, facilitated by local currents and influenced by the barrier of the Lleyn Peninsula (Crisp & Southward, 1953; Hiscock, 1998; Robins *et al.*, 2013; Adams *et al.*, 2014).

Comparing both poleward limits of *P. depressa* in Britain, populations towards S-East England tend to have smaller individuals than N-Wales (Figures 2.5. B and Figure 2.6). In the S-East England, air temperatures are warmer than N-Wales, especially in summer months (Figure 2.7). Bowman & Lewis (1977) suggests that warmer air conditions can facilitate rapid growth rates during limpet early stages, determining the ability to survive harsh and colder conditions after settlement (Lewis & Bowman 1975; Bowman & Lewis 1977, 1986). In my study, summer air temperatures (2015) did show significant correlation with the mean size of *P. depressa* (Table 2.2). Although size-structure of species populations come from sampling of several years (Lewis &

Bowman 1975; Bowman & Lewis 1977, 1986), size frequencies indicated that in certain locations in S-East England (*i.e.*, Portland Bill, Swanage and Freshwater) individuals of *P. depressa* successfully recruited before winter arrives (2014/2015). This pattern is indicated by the large proportion of small size classes (< 15mm in length) when compared with northern locations in N-Wales (except Criccieth and Hafan y Môr; Figure 2.5B). Thus, in S-East England juveniles may avoid high mortality in cold periods by gaining a size refuge during summer months.

Although S-East England populations are generally characterised by higher proportions of juveniles than N-Wales, at the extreme limit in S-East England towards the eastern side of the Isle of Wight (*i.e.*, Brembridge) as well as Southsea and Elmer, sparse populations are dominated by large individuals (Figures 2.5 B and Figure 2.6). These last two locations are characterized by artificial structures, which has facilitated the expansion of *P. depressa* towards the east of the Isle of Wight, but not in sufficient numbers to form a breeding population, particularly at Elmer (Mieszkowska *et al.*, 2005, 2006; Hawkins *et al.*, 2008). These findings coincide with the large number of hydrodynamic barriers found in the English Channel (Herbert *et al.*, 2009; Keith *et al.*, 2011), reflected by a gradient in abundance and sizes of *P. depressa* populations from western to eastern sites. Thus, the Isle of Wight is the most prominent barrier in the English Channel for benthic larval transport (Herbert *et al.*, 2009; Keith *et al.*, 2011) and coincides with a lack of suitable habitat; dominated by intertidal chalk platforms, sandy or shingle beaches towards S-East England (Crisp & Southward, 1958; Hiscock, 1998; Herbert & Hawkins, 2006; Herbert *et al.*, 2009; Keith *et al.*, 2011). Thus, weather conditions dictate that recruitment at the poleward limit in S-East England is generally high, but at the extreme distributional limit where populations are sparse, availability of larvae, dispersal and consequently recruitment is clearly limiting (N-Wales).

#### 2.5.4. Concluding Comments

In summary, both poleward limits of *Patella depressa* at northern latitudes have different shifts in pattern, evidenced by historical and current abundances in Britain - range contraction at N-Wales; and range expansion in S-East England. Further, both regions recorded the widest temperature differences between summer and winter 2014/2015 in SST. This suggests that seawater temperatures could be considered as an ultimate factor at both poleward edges of *P. depressa* (Hutchins, 1947; see also Box 1.3, Chapter 1), determining its distribution and abundance at northern latitudes and being mainly driven by winter conditions (Keith *et al.*, 2011). Air temperatures seem to be a proximate factor that plays a secondary role in the structuring of *P. depressa* populations in Britain (Helmuth *et al.*, 2006; see also Box 1.3, Chapter 1). Warmer summer and milder winter sea temperatures could be facilitating the increase in the proportion of *P. depressa* at northern locations in S-West England (more central populations). Finally, climate change is expected to increase the frequency and intensity of extreme weather events (Stachowicz *et al.*, 2002; Wethey *et al.*, 2011; Francis & Vavrus, 2012; Vasseur *et al.*, 2014). Therefore, a comprehensive understanding of the effects of extremes temperatures on *Patella* species is needed to disentangle their potential impacts on intertidal communities due to its role as a keystone species on temperate rocky shore systems.

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## **CHAPTER 3:**

### **Growth and mortality rates in northern co-occurrence zones between the cold-water *Patella vulgata* L. and warm water *Patella depressa* Pennant**

### 3.1. INTRODUCTION

Marine benthic molluscs have been the focus of many studies to elucidate how distribution of species and their performance varies in the context of responses to global warming (e.g., Hellberg *et al.*, 2001; Clarke *et al.*, 2004; Gilman, 2005, 2006; Ling *et al.*, 2008, 2009; Hidas *et al.*, 2010; Fenberg & Rivadeneira, 2011; Moore *et al.*, 2011; Shanks *et al.*, 2014; Borges *et al.*, 2015). According to the Abundant-Centre Hypothesis (hereafter ACH; Brown, 1984), individuals at the range edges of species would be expected to be less numerous and perform less well than more central populations (Caughley *et al.*, 1988). With climate warming, species have been showing poleward advances, with individuals performing better than expected at their poleward range edge, achieving faster growth, greater reproductive output and recruitment leading to population expansion and advance (Mieszkowska *et al.*, 2006, 2007; Ling *et al.*, 2008; Herbert *et al.*, 2009; Ling *et al.*, 2009; Moore *et al.*, 2011; Brown *et al.*, 2016). In contrast, at their trailing edge (*i.e.*, at the equatorward range edge), populations are vulnerable to climate warming and range contraction has been occurring (Wethey & Woodin, 2008; Wethey *et al.*, 2011; Bates *et al.*, 2014; Lima *et al.*, 2016). Impacts on phenological cycles leading to lower reproductive output and consequently lower recruitment may lead to local extinction of some species (Moore *et al.*, 2011; Brown *et al.*, 2016, Lima *et al.*, 2016). Thus, at the poleward and equatorward borders of a species, individuals are being affected by opposite mechanisms due to climate fluctuation and change (Bates *et al.*, 2014); this leads to species contraction and species expansion at their range edges that could also displace central populations polewards (Bates *et al.*, 2014; Bennet *et al.*, 2015; Chuang & Peterson, 2016).

Demographic attributes of populations play a major role in establishing species boundaries (Brown, 1984; Caughley *et al.*, 1988; Brown *et al.*, 1996; Guo *et al.*, 2005; Fordham *et al.*, 2013; Chuang & Peterson, 2016). Growth and mortality rates may serve as important indicators of individual performance influencing population dynamics at the species range limits (Clarke *et al.*, 2004; Herbert *et al.*, 2009; Herbert, 2011; Fordham *et al.*, 2013; Bates *et al.*, 2014; Chuang & Peterson, 2016). However, there are surprisingly few examples of greater species performance in central populations than marginal ones (Sagarin & Gaines, 2002ab; Sagarin *et al.*, 2006). At species range edges, populations tend to have limited or variable recruitment and therefore intraspecific competition is likely to be less intense (Guo *et al.*, 2005), leading to faster growth of individuals than in core populations (Lewis *et al.*, 1982). For instance, studies made on warm-

species such as *Gibbula umbilicalis* and *Monodonta lineata* (both re-named as *Steromphala umbilicalis* and *Phorcus lineatus*, respectively; Affenzeller *et al.*, 2017), both intertidal molluscs with poleward limits in Britain, indicated that growth was not reduced in northern populations when compared with southern populations (Williamson & Kendall, 1981; Lewis *et al.*, 1982; Kendall & Lewis, 1986; Kendall, 1987). Likewise, similar patterns have been found for the warm-water barnacle *Chthamalus montagui* in the central English Channel, one of its poleward limits around the British Isles (Herbert *et al.*, 2009). Despite a reduction in density from west to east, growth and mortality of *C. montagui* showed no differences between central and peripheral populations (Herbert *et al.*, 2009). Therefore, a better understanding of demographic attributes of species at their limits, such as growth and mortality rates, may contribute to ongoing debate regarding species responses under climate warming (Sagarin & Gaines, 2002ab; Clarke *et al.*, 2004; Gilman, 2005; Rivadeneira & Fernandez, 2005; Helmuth *et al.*, 2006; Ling *et al.*, 2008; Herbert *et al.*, 2009; Ling *et al.*, 2009; Fenberg & Rivadeneira, 2011; Moore *et al.*, 2011; Bates *et al.*, 2014).

On intertidal rocky shores of northwest Europe, patellid limpets have a clear role in controlling algal communities by grazing (Jones, 1948; Southward & Southward, 1978; Hawkins, 1981; Hawkins & Hartnoll, 1983; Hartnoll & Hawkins, 1985; Jenkins & Hartnoll, 2001; Jenkins *et al.*, 2005; Coleman *et al.*, 2006). *Patella depressa*, a warm-water southern species, and *Patella vulgata* a cold-water northern species, are sibling species but they differ in their geographical ranges (Figure 3.1. A). *P. depressa* is distributed from Senegal (Fischer-Piette, 1936, 1948; Orton & Southward, 1961; Guerra & Gaudencio, 1986) to North Wales (Crisp & Knight-Jones, 1954; Kendal *et al.*, 2004), being absent from Ireland (Crisp & Southward, 1953; Southward *et al.*, 1995). Its congener, *P. vulgata*, is distributed from Portugal (Guerra & Gaudencio, 1986; Ribeiro *et al.*, 2009; Lima *et al.*, 2016) to Norway (Fischer-Piette, 1936, 1948, Southward *et al.*, 1995). They coexist over a large area from Portugal to North Wales (Figure 3.1A; Guerra & Gaudencio, 1986; Southward *et al.*, 1995; Kendall *et al.*, 2004). In the southern half of Britain, *P. vulgata* may be considered to be at the centre of its range (Lima *et al.*, 2016); here it coincides with both poleward borders of *P. depressa*, occurring in North-west Wales and South-east England (Figure 3.1A; Crisp & Knight-Jones, 1954; Southward *et al.*, 1995; Kendal *et al.*, 2004). In South-west England, there are well-established populations of *P. depressa* (Orton & Southward, 1961, Southward *et al.*, 1995, Moore *et al.*, 2007ab, Borges *et al.*, 2015), and in many places, it is the most numerous mid-shore

limpet species (Kendall *et al.*, 2004; Hawkins *et al.*, 2008). Here, conditions may be considered analogous to those towards the centre of its range in Portugal (Orton & Southward, 1961, Guerra & Gaudencio, 1986; Boaventura *et al.*, 2002, 2003; Ribeiro *et al.*, 2009; Borges *et al.*, 2015).

Poleward limits of *Patella depressa* have recently shown differing patterns in terms of abundance and distribution (Chapter 2). At its leading edge in North Wales, abundance decreased markedly from the warmer 1950s to the cooler early 1980s (Crisp & Knight-Jones, 1954; Kendall *et al.*, 2004; Southward *et al.*, 2005) with populations to the north of the Llyn peninsula disappearing since then, probably in the 1980s (Hawkins, pers. comm.). Although populations to the south of the Llyn peninsula are doing much better than previously in response to recent warming, re-expansion to the north of Llyn has not occurred to any extent (Chapter 2). Thus, a range contraction of approximately 70km has occurred without subsequent recovery during recent warming (Chapter 2). An anomalous single individual was found on the Isle of Man by Prof S.J. Hawkins in 2010 (Hawkins, pers. comm.). In contrast, its other border has extended eastwards beyond the Isle of Wight in the English Channel (Mieszkowska *et al.*, 2005; Keith *et al.*, 2011), but only with breeding populations as far east as Southsea (Hawkins, pers. comm.). Further, as sea temperatures have risen over the last decades (Southward *et al.*, 1995; Mieszkowska *et al.*, 2006, 2007; Moore *et al.*, 2011) phenological comparisons suggest that increases in abundance of *P. depressa* in South-west England (Hawkins *et al.*, 2008, 2009) may be driven by an advance in gonadal development leading to a longer reproductive season with multiple broods compared to populations in the 1940s (Orton & Southward, 1961; Moore *et al.*, 2011). Conversely, *Patella vulgata* has shown a reduction in the proportion of advanced gonad stages and has failed to brood in some years (Orton *et al.*, 1956; Moore *et al.*, 2011), possibly leading to reduced abundance on certain shores in Britain (Moore *et al.*, 2011). Therefore, shifts in abundance of both *Patella* species could be explained by different phenological responses to climate change (Southward *et al.*, 1995, 2005; Hawkins *et al.*, 2008, 2009; Moore *et al.*, 2011). This might affect growth patterns, as more energy will be expended during reproduction, thereby simultaneously reducing the budget for growth (Wright, 1977; Wright & Hartnoll, 1981).

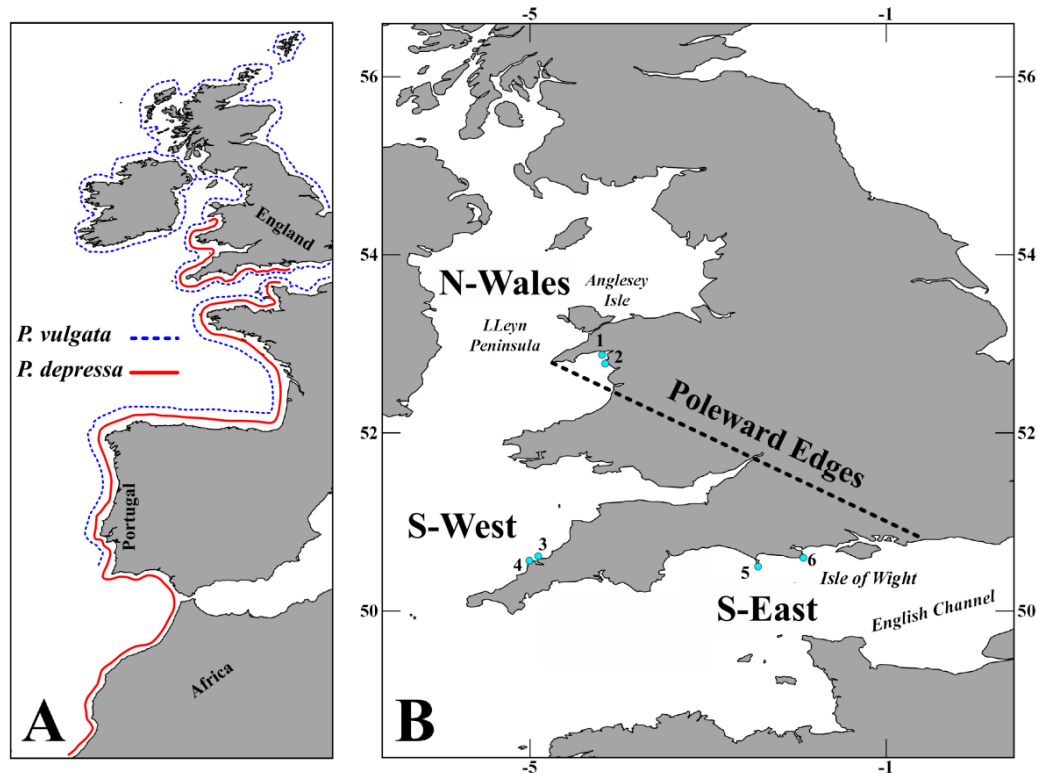
Winter temperatures have classically been considered primary drivers in the success of intertidal species at poleward limits (Hutchins, 1947; Crisp & Knight-Jones, 1954; Lewis, 1964, 1986). In northern co-occurrence zones between *P. vulgata* and *P. depressa*, sea surface temperatures have increased in recent decades (Southward *et al.*, 1995; Mieszkowska *et al.*, 2006,

2007; Hawkins *et al.*, 2008, 2009; Moore *et al.*, 2011), particularly in relation to winter temperatures when compared to summer temperatures (Figure 3.2). In this context, milder winter conditions can facilitate rapid growth rates during limpet early stages, determining the ability to survive harsh and colder conditions after settlement (Lewis & Bowman, 1975; Bowman, 1985; Bowman & Lewis, 1986; Lewis, 1986; Helmuth *et al.*, 2006). By contrast, cold winters stunt normal growth and produce irreversible shell damage, which can lead ultimately to death (Bowman, 1981; Bowman & Lewis, 1986). Mortality of limpets can be very high in northern populations when settlement occurs very late and new recruits are exposed to cold temperatures (Bowman, 1981, 1985). Mortality appears to be high towards species boundaries (Hutchins, 1947; Brown, 1984; Caughley *et al.*, 1988), but warm winter conditions could reduce this pattern at the northern boundaries of species (Hutchins, 1947). Therefore, it would be expected that demographic attributes such as growth and mortality rates of limpet populations could differ between both leading edges of *P. depressa* due to regional variations in winter conditions around the British Isles (Hutchins, 1947; Crisp & Knight-Jones, 1954; Lewis, 1964; Lewis, 1986).

Consideration of regional variation in limpet growth rates must take account of the factors modifying growth at local spatial scales (Clarke *et al.*, 2004). Growth patterns in *Patella* species show an asymptotic shape represented by the von Bertalanffy growth curve (Branch, 1974, 1975; Ekaratne & Crisp, 1984) with fast growth in early-stages and then declining gradually to an asymptote (Orton, 1928; Blackmore, 1969; Branch, 1974, 1975; Lewis & Bowman, 1975; Wright, 1977). In northern latitudes, *P. vulgata* has been the model species to investigate growth patterns in *Patella* species (see Table 3.1 for details). For instance, *P. vulgata* show two peaks over a year: growth rate progressively increases from early-spring to early-summer; and then declines or ceases over the summer, before increasing again between late-autumn to mid-winter (Orton, 1928; Wright, 1977; Hawkins & Hartnoll, 1982; Ekaratne & Crisp, 1984;). At small scales, limpets living among barnacles on high intertidal levels have a slower growth rate than those limpets living at mid- and low-levels (Bowman & Lewis, 1977). Lower on the shore conditions are always moist facilitating suitable growing areas for *Patella* species (Lewis & Bowman, 1975; Bowman & Lewis, 1977; Hawkins & Hartnoll, 1982). Furthermore, at a wider spatial scale, individuals over 35 mm in length grow up to 2 mm/year on sheltered shores compared to 4.4 mm/year on exposed shores (Jenkins & Hartnoll, 2001). Hence, although limpet growth curves would be expected to



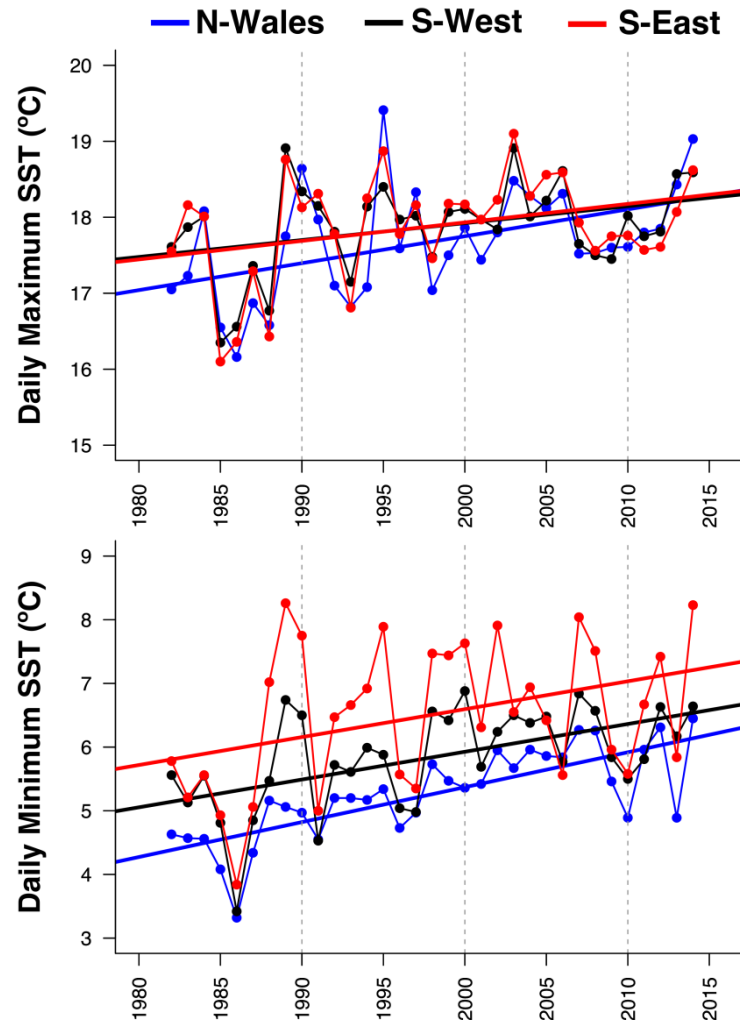
generally follow an asymptotic shape, inter-individual differences due to type of habitat or different exposure level are highly likely.



**Figure 3.1.** (A) Distributional range of *P. depressa* (red) and *P. vulgata* (blue) in the North-west of Europe. (B) Locations ( $n=6$ ; light blue circles) selected to measure growth and mortality rates (2015/2016) of both limpets species in N-Wales (1= Criccieth and 2= Shell Island), S-West England (3= Polzeath and 4= Trevone) and S-East England (5=Portland Bill and 6= Swanage), Britain.

Intraspecific competition of species will depend on density-dependent effects within populations (Begon *et al.*, 1996). Intraspecific competition occurs when a common resource is limited (*e.g.*, space or food). Its effects on species can be measured in terms of growth and mortality (Jenkins *et al.*, 2008). Manipulative experiments have demonstrated the effects of intraspecific competition in *Patella* species (Branch, 1974, 1975; Thompson *et al.*, 2000; Boaventura *et al.* 2002, 2003). For example, Thompson *et al.* (2000) showed higher growth rates at reduced densities of *Patella depressa* and *Patella vulgata* near to the range edge of *P. depressa* in the English Channel. However, mortality rates of *P. vulgata* increased at higher densities and *P. depressa* was unaffected in the same intra-specific conditions (Thompson *et al.*, 2000). These

mortality patterns of limpet species in northern co-occurrence zones suggest that intraspecific competition of *P. depressa* could be regulated by the input of recruits (Boaventura *et al.*, 2002, 2003), which is reduced at the range edges in the eastern half of the English Channel (Keith *et al.*, 2011) and in North Wales (Chapter 2).



**Figure 3.2.** Minimum (December-February) and maximum (June-August) Sea Surface Temperatures (SST) from 1982 to 2014 in N-Wales, S-West England and S-East England. Both SST were selected from the coastline to the sea on a distance of 20km at each region. For N-Wales, temperatures correspond to the north of Cardigan Bay, from Shell Island to Criccieth. For the S-West England, from Trevone to Polzeath in Cornwall peninsula; and for S-East England, from Portland Bill to Swanage in the English Channel. SST was obtained from the Atlantic European North West Shelf Ocean - High Resolution Sea Surface Temperature Reprocessed (from 1982 to 2014) - provided by the Monitoring Service Marina Copernicus (<http://marine.copernicus.eu/>).

*Patella* species are a good model to test hypotheses about how individual and population traits vary across distributional ranges. They are an accessible and tractable marine species; their sessile nature and homing behaviour mean that observations of growth and mortality rates in the field are relatively straightforward (Orton, 1928; Blackmoore, 1969, Lewis & Bowman, 1975; Wright, 1977; Hawkins & Hartnoll, 1982; Jenkins & Hartnoll, 2001). Based on the ACH (Abundant-Centre Hypothesis), populations of *Patella depressa* towards both poleward limits are expected to have reduced growth rates as well as higher mortality rates (Brown, 1984), when compared with more central populations in South-west England in Britain (Orton & Southward, 1961; Moore *et al.*, 2007ab; Borges *et al.*, 2015). In contrast, *Patella vulgata* is expected to have equivalent growth and mortality rates between these regions, as it may be considered to be at the centre of its range (Lima *et al.*, 2016). However, different abundance patterns of *P. depressa* between both leading edges in Britain (*i.e.*, North Wales and South-east England; Chapter 2) could modify any abundant-centre effects (Brown, 1984) on performance traits of limpet species in northern co-occurrence zones. Therefore, my main aim was to test the ACH by determining growth and mortality rates using tagged limpets at central populations of both *Patella* species (South-west England) and towards both leading edges of *P. depressa* in Britain. Specifically, growth performance of both *P. vulgata* and *P. depressa* were compared using von Bertalanffy growth parameters, such as the theoretical maximum length that the species would reach ( $L_{\infty}$ ) and the growth coefficient (K). These comparisons were made following the regional comparison done by Clarke *et al.* (2004) for patellacean species. For mortality, the instantaneous rate of total mortality was also estimated (King *et al.*, 2007). In addition, growth and mortality rates were also assessed to identify whether *P. depressa* and *P. vulgata* differ in their northerly co-occurrence regions. As an alternative hypothesis, the proposition that local conditions including density-dependent processes over-ride the ACH was explored.

**Table 3.1.** Growth rates recorded for *Patella vulgata* in the British Isles from 1909 to 2001. Growth rates are indicated according to the temporal scale used at each study. IL= Initial Length (mm).

Paper	Region	Period	IL Range (mm)	Growth Rate	Habitat
Russell (1909)	Scotland / N-West	1906	15 - 20	18.1 mm / 40 days	Not specified
			20 - 25	15.7 mm / 40 days	
			25 - 30	7.9 mm / 40 days	
			35 - 40	9.0 mm / 40 days	
			40 - 45	2.8 mm / 40 days	
Orton (1928)	England / S-West	1912 - 1913	26 - 35	13 mm / year	Railway Docks
		1913 - 1914	11 - 27	23 - 36 mm / year	
		Jul - Aug 1919	~ 25	0.6 - 3.4 mm / 2 months	
Blackmore (1969)	England / N-East	Jan - Jun 1965	< 5	0.4 mm / 6 month	Between high- and low-shore levels
		Jun - Dec 1965	> 5	2 mm / 6 month	
		Jul - Dec 1966	>10	0.53 mm / 6 month	
Lewis & Bowman (1977)	England / N-East	1966 - 1969	9.5 - 10.5	8.5 mm / year	Barnacles high-shore
			19.5 - 20.5	2.5 mm / year	Barnacles mid-shore
			9.5 - 10.5	10 mm / year	
			19.5 - 20.5	7.5 mm / year	Mussels/Barnacles mid-shore
			9.5 - 10.5	15 mm / year	
			19.5 - 20.5	13 mm / year	Bare rock low-shore
Hawkins & Hartnoll (1982)	Isle of Man / N-West	Mar - Jul 1978	15 - 35	0.07 / 4 months	100% Barnacles cover
				0.10 / 4 months	50% Barnacles cover
				0.18 / 4 months	< 2% Barnacles cover
		Mar - Jul 1979	15 - 35	0.12 / 4 months	100% Barnacles cover
				0.10 / 4 months	50% Barnacles cover
				0.16 / 4 months	< 2% Barnacles cover
Jenkins & Hartnoll (2001)	Isle of Man / N-West	1997 - 1998	~ 35	2.0 mm / year	Sheltered mid-shore
				4.4 mm / year	Exposed mid-shore

### 3.2. MATERIALS AND METHODS

The general approach adopted was to use mark and recapture methodology with individual tagging in the field. In this way, individual length increments were measured to assess growth and the loss of marked individuals used to determine mortality. Measures were taken over one year, a period based on previous works (*e.g.*, Bowman, 1981; Jenkins & Hartnoll, 2001) that is sufficient for measurable limpet growth to take place.

#### 3.2.1. Locations and pre-Labeling of Limpets Species

In order to have a sufficient number of individuals to allow growth and mortality rate estimates in both *Patella depressa* and *Patella vulgata*, locations were selected reflecting current limpet abundances (Chapter 2), with at least 20% of *P. depressa* in relation to the total number of individuals of *Patella* species (see Figure 2.5. A, Chapter 2). In South-west England, *P. depressa* form approximately 50% of the limpet population over recent decades (Orton & Southward, 1961; Kendall *et al.*, 2004; Hawkins *et al.*, 2008, 2009; Moore *et al.*, 2011), analogous to the centre range conditions in Portugal (Guerra & Gaudencio, 1986; Boaventura *et al.*, 2002, 2003; Ribeiro *et al.*, 2009). Thus, six locations were chosen during mid-2015, which were grouped by region: North Wales (hereafter N-Wales) - Criccieth and Shell Island, South-west England (hereafter S-West) - Polzeath and Trevone and South-east England (hereafter S-East) - Portland Bill and Swanage (Figure 3.1B).

At each location, surveys of abundance between September and late-October 2015 were made, except for Trevone - where data from Marclim archives were used. The area of survey extended from approximately Mean High Water Neap (MHWN) to Mean Tide Level (MTL) where both limpet species reach their maximum abundances on both semi-exposed and exposed shores (Orton & Southward, 1961; Hawkins & Hartnoll, 1983). Ten 0.5 x 0.5 m quadrats were sampled along a transect parallel to the coastline, ~ 1 m apart, where the total number of both limpet species were counted. Barnacle cover in each quadrat was also recorded.

#### 3.2.2. Tagged Limpets

In order to estimate growth and mortality rates of both *Patella* species, locations were divided into two patches. All patches were made up of gently sloping and/or horizontal rock, avoiding vertical faces and were separated by ~50-100 meters. Between 40 and 90 individuals of

each limpet species of different sizes over a horizontal distance of ~5 m in the middle of the intertidal zone were selected.

Individual-marking methods have been widely used in limpet species to examine growth and mortality rates (Branch, 1974, 1975; Jenkins & Hartnoll, 2001; Kido & Murray, 2003; Clarke *et al.*, 2004; Espinosa *et al.*, 2008). Following the general approach of most studies, shells were initially gently scraped, cleaned and dried close to the apex. After that, glue was placed to fix a small waterproof numerical label of 5 x 5 mm (Brady®, TMM-0-49-PK model, USA, <https://www.bradyid.com>). Double labels were used to account for tag loss. Additionally, two different colours of nail varnish were applied to identify each *Patella* species.

The maximum initial shell length (hereafter  $L_0$ ) of each individual was recorded at a single point in time (hereafter  $t_0$ ) during June/July 2015 at all locations. Change in limpet shell length was evaluated by measuring at three different times over the period until late-May 2016 (~12 months). Thus, each measuring time corresponded to the limpet growth in length over the periods: 1) from  $t_0$  to September 2015 ( $t_1$ ), which corresponds to the summer months; 2) from  $t_1$  to December 2015 ( $t_2$ ), which reflects autumn months; and 3) from  $t_2$  to late-May 2016 ( $t_3$ ), over the winter/early-spring months.

In order to track each tagged limpet in the field, a small-scale map for each of the six locations was drawn. When a previously labelled limpet was not found, a thorough search around the rocks was performed over a period of ~20-30 minutes. After that, if a tagged limpet was not found, that limpet was considered dead and replaced by another one with the same length. Nail varnish on the shell lasts between 3 to 4 months (pers. obs. in the field). Therefore, individuals that had missing labels were easily identified due to the colour on their shells and their mapped position at a small scale.

### 3.2.3. Von Bertalanffy Growth Parameters: Gulland-Holt Plot Approach

In order to compare growth performance between both *Patella* species from populations in different regions, von Bertalanffy growth parameters such as  $L_\infty$  (theoretical maximum length) and  $K$  (growth coefficient) were estimated (King *et al.*, 2007). The Von Bertalanffy growth function is defined by the equation:

$$L_t = L_\infty (1 - e^{-K(t - t_0)})$$

where  $L_t$  is the length at time  $t$ ;  $L_\infty$  is the theoretical maximum length that species would reach;  $K$  parameter is a growth coefficient which determines how fast the individual approaches its  $L_\infty$ ; and  $t_0$  is the theoretical age at zero length which often has a small negative value (King *et al.*, 2007). “Forced” Gulland-Holt plots were useful to estimate both  $L_\infty$  and  $K$  because this approach allows length data collected over a specific time through a mark-recapture method to be used (see King *et al.*, 2007 for details). Nevertheless, it is not possible to calculate  $t_0$  using this method (Sparre & Venema, 1998; King *et al.*, 2007). Basically, “Forced” Gulland-Holt plots show the linear relationship between individual growth rates (y-axis) against individual mean length (x-axis), which is the average between two individual lengths measured at two different times, *e.g.*, Length<sub>initial</sub> (here after  $L_{initial}$ ) and Length<sub>final</sub> (hereafter  $L_{final}$ ). Growth rates corresponds to the difference between  $L_{final}$  and  $L_{initial}$ , divided by change in time, *i.e.*,  $L_{final} - L_{initial} / t_{final} - t_{initial}$  (King *et al.*, 2007). In this relationship, the intercept on the x-axis (where the growth rates is zero) is an estimate of  $L_\infty$  and can be calculated as the negative of the y-axis intercept, divided by the slope, *i.e.*,  $L_\infty = a/-b$  (King *et al.*, 2007). In order to calculate the  $K$  value, “Forced” Gulland–Holt plots fix a value of  $L_\infty$  on the x-axis, which is defined by the formula:  $K = \text{mean Growth Rates} / L_\infty - \text{mean length}$  (King *et al.*, 2007).

Estimations of both  $L_\infty$  and  $K$  were based on individuals that survived from June/July 2015 ( $t_0$ ) to the last sampling period (~ late-May 2016;  $t_3$ ). Nevertheless, the number of individuals of each *Patella* spp. was not similar throughout locations (see next section 3.3. in Results) and estimations of  $L_\infty$  and  $K$  were grouped by region and species (Clarke *et al.*, 2004). Thus, comparisons of  $L_\infty$  and  $K$  were made following the previous regional growth comparison made by Clarke *et al.* (2004) for patellacean species. Furthermore, as in fishes and invertebrates, whose growth process can be described by the von Bertalanffy growth curve, comparisons were also made through the overall growth performance index, *i.e.*,  $\Phi' = \log K + 2\log L_\infty$  (see Clarke *et al.*, 2004; Pörtner *et al.*, 2005 for details). According to Pauly (1979), the overall growth performance index describes the growth rate at the point of inflection of the Von Bertalanffy growth curve (*i.e.*, maximum growth rate; Heilmayer *et al.*, 2004).

Additionally, the “Forced” Gulland-Holt approach was used for each measuring period (King *et al.*, 2007) to explore seasonal differences. Here, individual limpet replacement because of mortality was included. The coefficient of determination ( $R^2$ ) was calculated for each relationship to estimate how much individual growth rates can be explained by individual mean

size in limpets (*i.e.*, “Forced” Gulland-Holt approach; King *et al.*, 2007) for each region and species (Gotelli & Ellison, 2013). The “TropFishR” package was used to build “forced” Gulland–Holt plots and to estimate growth parameters from tagging data in the CRAN R project (R Development Core Team 2014; Mildenerberger *et al.*, 2017).

The loss of limpets in a target population through death can be estimated as the instantaneous rate of total mortality (mortality rate) over a particular time interval (King *et al.*, 2007). This parameter takes values greater than 1 and is defined by equation:  $Z = \ln [N_{t+1}] - \ln [N_t]$ ; where  $N_{t+1}$  is the number of individuals at  $t_{\text{final}}$ , and  $N_t$  is the number of individuals at  $t_{\text{initial}}$ . Thus, mortality rate was calculated for each *Patella* species, location and sampling period.

#### 3.2.4. Growth and Mortality Rates of *Patella* Species in Britain

In order to determine whether growth and mortality rates differ between both *Patella* species and regions, a Generalized Linear Mixed model (GLMM) for each response variable was applied. Variables were analysed using family errors such as Gaussian identity for growth rates, and Binomial for mortality rates, respectively (Bolker *et al.*, 2009).

In terms of growth rates, temporal non-independence was included in the analysis (*i.e.*, repeated measures; Bolker *et al.*, 2009; Zuur *et al.*, 2009). The repeated measures analysis refers to multiple measurements made on the same experimental unit (*i.e.*, each tagged limpet) observed either over time or space. This was added as a random factor to the analysis to account for the lack of independence between growth measurements of the same individual (Bolker *et al.*, 2009; Zuur *et al.*, 2009). Unlike “Forced” Gulland-Holt plots, which use the mean size as an independent variable, the initial length ( $L_0$ ) of each individual at each sampling period ( $t_1$ ,  $t_2$  and  $t_3$ ) was considered as a co-variable as well as a random factor in this analysis. Further, there were also three fixed factors: 1) Region, with three levels: N-Wales, S-West and S-East England; 2) Sampling Period, with three levels: summer (from  $t_0$  to  $t_1$ ), autumn (from  $t_1$  to  $t_2$ ) and winter/early-spring (from  $t_2$  to  $t_3$ ); and 3) Species, with two levels: *P. depressa* and *P. vulgata*. Additionally, location was a nested random factor within Region.

Since *Patella* growth curves show an asymptotic shape during their life span (Branch, 1974; Ekaratne & Crisp, 1974; Branch, 1975), the analysis was made only on individuals below 30 mm in length, where individual replacement because of mortality was included. Thus, this approach will capture those variables that are influencing actively growing individuals. For



mortality rates, the analysis performed considered the following fixed factors: 1) Region (three levels: N-Wales, S-West and S-East) and 2) Species (two levels: *P. depressa* and *P. vulgata*). Further, Location was a nested random factor into Region.

Diagnostic plots (*i.e.*, histogram of residuals and residuals vs linear predictor) to evaluate both model fitness and statistical assumptions of residuals were used (Zuur *et al.*, 2009, 2010). For each variable response (growth and mortality rates), when interaction terms were significant ( $\alpha = 0.05$ ), Tukey post-hoc tests were carried out for multiple pairwise comparison (Bolker *et al.*, 2009; Zuur *et al.*, 2009).

All statistical analyses were made in the CRAN R project (R Development Core Team 2014). The “glmmTMB” package (Generalized Linear Mixed Models using Template Model Builder) to fit each GLMM was useful. Tukey post hoc tests were carried out using the “emmeans” package (Estimated Marginal Means, Least-Squares Means).

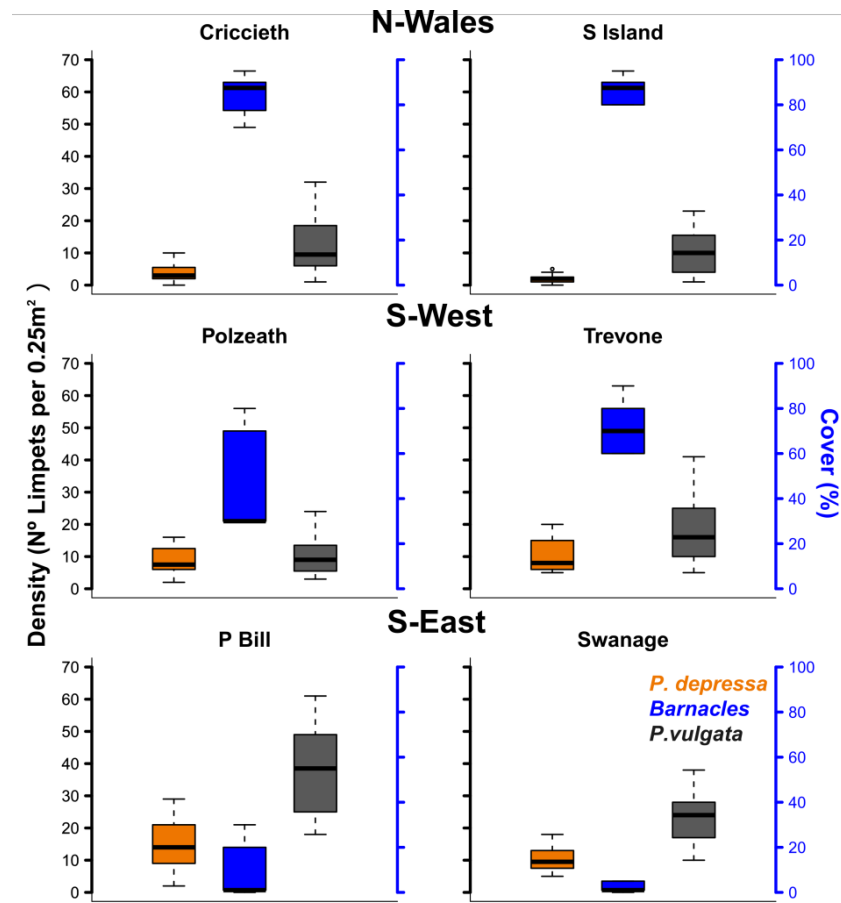
### **3.2.5. Density-Dependent Effects on Performance Traits of *Patella* Species**

The effect of local density on growth and mortality rates of *Patella* species was determined. Mean total limpet density was calculated for each location (*i.e.*, quadrat number= 10) and the relationship with mean growth and mortality rates of both *Patella* species was explored. In order to determine how much the total density of limpets can explain growth and mortality patterns in *Patella* species, linear regressions were estimated and the coefficient of determination ( $R^2$ ) for each relationship was calculated (Gotelli & Ellison, 2013).

### 3.3. RESULTS

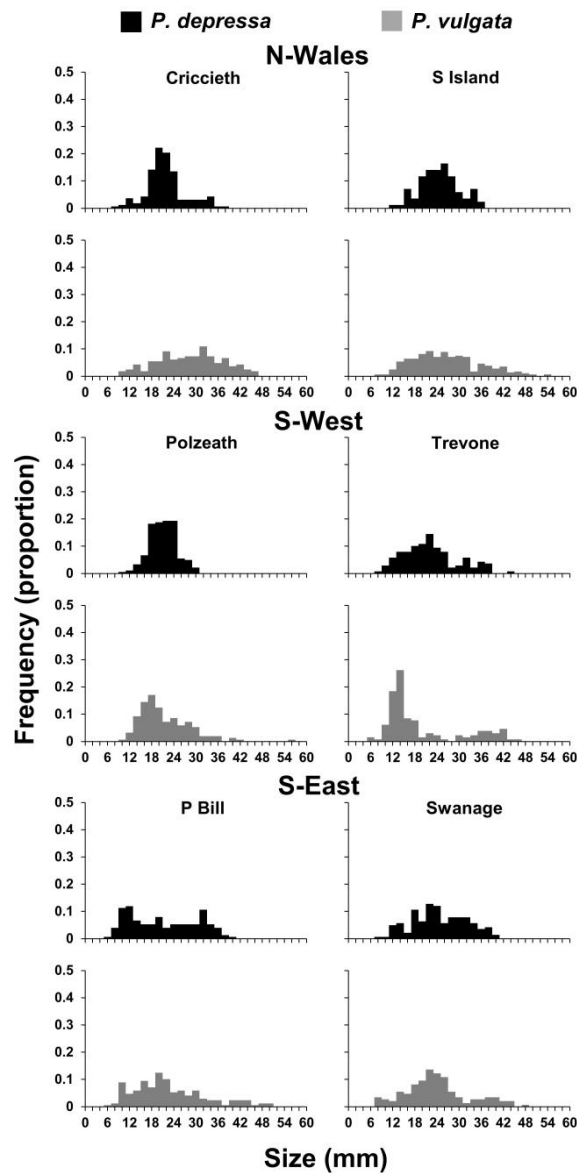
#### 3.3.1. Locations and pre-Labeling of Limpet Species

Barnacle cover was lower in S-East England when compared with both N-Wales and S-West England (Figure 3.3). *Patella depressa* was much less dense than *Patella vulgata* at both its poleward limits (*i.e.*, N-Wales and S-East England; Figure 3.3). In contrast, in S-West England, densities of both *Patella* species tended to be similar (Figure 3.3). However, locations in S-East England (*i.e.*, Portland Bill and Swanage) had higher limpet abundances compared with both N-Wales and S-West England (Figure 3.3).



**Figure 3.3.** Box-plot of *P. depressa* (orange), *P. vulgata* (grey) and barnacles (blue) densities evaluated at the beginning of the experimental manipulation (September/October 2015) at each location (n=10 quadrats). Black left axis indicates both *Patella* species densities. Blue right axis shows barnacle cover in percentage (%). Locations are separated by region, *i.e.*, N-Wales: Criccieth and Shell Island; S-West: Polzeath and Trevone; S-East: Portland Bill and Swanage.

The size range of limpets selected to measure growth and mortality rates across all regions was between 5.8 and 43.1 mm in length for *P. depressa* (n=858), and between 5.0 and 55.9 mm for *P. vulgata* (n=1042; Figure 3.4). Frequency histograms showed that most of the individuals tagged were between 10 and 30 mm in length at all locations (Figure 3.4). However, larger sizes were more common in both N-Wales and S-East England for both species when compared with S-West England, except for *P. depressa* at Trevone (Figure 3.4).



**Figure 3.4.** Frequency (proportion) of individual initial sizes (maximum length, separated by 2mm) selected to measure growth and mortality rates of both limpets species at each location separated by region (June/July 2015). Black colour indicates *Patella depressa* and grey colour shows *P. vulgata* sizes.

**Table 3.2.** Initial Number (IN) and Individuals Recaptured (IR) of both *Patella* species at three different sampling ( $t_1$ ,  $t_2$  and  $t_3$ ) over a time of ~12 months. Values are separated by location and region. Labels lost (%) is also indicated.

Region	Location	Months	Time	<i>P. depressa</i>			<i>P. vulgata</i>		
				IN	IR	Labels Lost	IN	IR	Labels Lost
N-WALES	Shell Island	Jun / Jul '15	$t_0$	85	-	-	280	-	-
		Sep / Oct '15	$t_1$	85	77	5%	280	262	8%
		Dec '15 / Feb '16	$t_2$	85	75	12%	280	206	13%
		Apr / May '16	$t_3$	85	67	9%	280	238	14%
	Criccieth	Jun / Jul '15	$t_0$	162	-	-	164	-	-
		Sep / Oct '15	$t_1$	162	134	10%	164	130	13%
		Dec '15 / Feb '16	$t_2$	162	124	17%	164	123	8%
		Apr / May '16	$t_3$	162	118	10%	164	128	14%
S-WEST	Polzeath	Jun / Jul '15	$t_0$	181	-	-	152	-	-
		Sep / Oct '15	$t_1$	181	160	9%	152	114	11%
		Dec '15 / Feb '16	$t_2$	181	156	10%	152	125	16%
		Apr / May '16	$t_3$	181	147	9%	152	107	14%
	Trevone	Jun / Jul '15	$t_0$	138	-	-	130	-	-
		Sep / Oct '15	$t_1$	138	97	12%	130	76	16%
		Dec '15 / Feb '16	$t_2$	138	107	11%	130	89	11%
		Apr / May '16	$t_3$	138	111	16%	130	95	8%
S-EAST	Swanage	Jun / Jul '15	$t_0$	141	-	-	147	-	-
		Sep / Oct '15	$t_1$	141	74	16%	147	71	16%
		Dec '15 / Feb '16	$t_2$	141	90	17%	147	84	17%
		Apr / May '16	$t_3$	141	79	15%	147	92	15%
	Portland Bill	Jun / Jul '15	$t_0$	151	-	-	169	-	-
		Sep / Oct '15	$t_1$	151	98	9%	169	109	15%
		Dec '15 / Feb '16	$t_2$	151	76	11%	169	76	13%
		Apr / May '16	$t_3$	151	75	13%	169	84	11%

### 3.3.2. Tagged Limpets

Table 3.2 shows numbers of individuals tagged and recaptured during each sampling period as well as the percentage of labels lost between June 2015 and late-May 2016. Limpet numbers tagged at each location varied from 85 to 181 individuals for *Patella depressa* and from 130 to 280 for *P. vulgata*, reflecting differences in relative abundance of both *Patella* species across the study area (Table 3.2; Figure 3.3 and Figure 3.4).

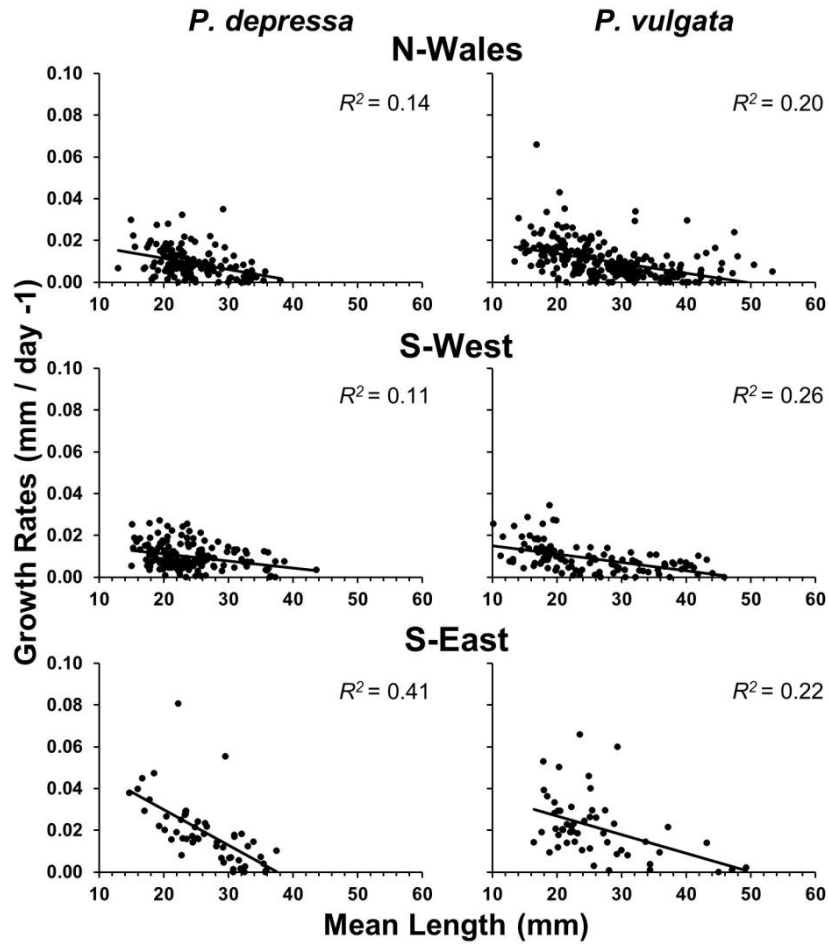
### 3.3.3. Von Bertalanffy Growth Parameters: Gulland-Holt Plot Approach

Individuals that survived from June/July 2015 ( $t_0$ ) to the last sampling period (~ late-May 2016;  $t_3$ ) exhibited a negative relationship between growth rate and mean length (“Forced” Gulland-Holt plots; Figure 3.5). Higher coefficient of determination ( $R^2$ ) was found in populations of *Patella depressa* in S-East England than N-Wales and S-West England, particularly in Portland Bill (Figure 3.5). For *Patella vulgata* populations, these values were almost the same across the three regions (Figure 3.5). Additionally, based on the regional limpet comparison made by Clarke *et al.* (2004) for patellacean species, von Bertalanffy parameters ( $K$  and  $L_\infty$ ) as well as growth performance index ( $\Phi'$ ) of both *Patella* species are shown in Table 3.3. *P. vulgata* reached larger sizes of  $L_\infty$  (theoretical maximum length) than *P. depressa*, except for populations in S-West England (Table 3.3). These length values were not surprising because individuals of *P. depressa* never grow as large as *P. vulgata* (Evans, 1947; Bowman, 1981; Borges *et al.*, 2015). However, in S-West England, higher values of  $L_\infty$  for *P. depressa* when compared with *P. vulgata* values suggest that density-dependent mechanisms could be affecting the maximum length of both *Patella* species in this region (Table 3.3).

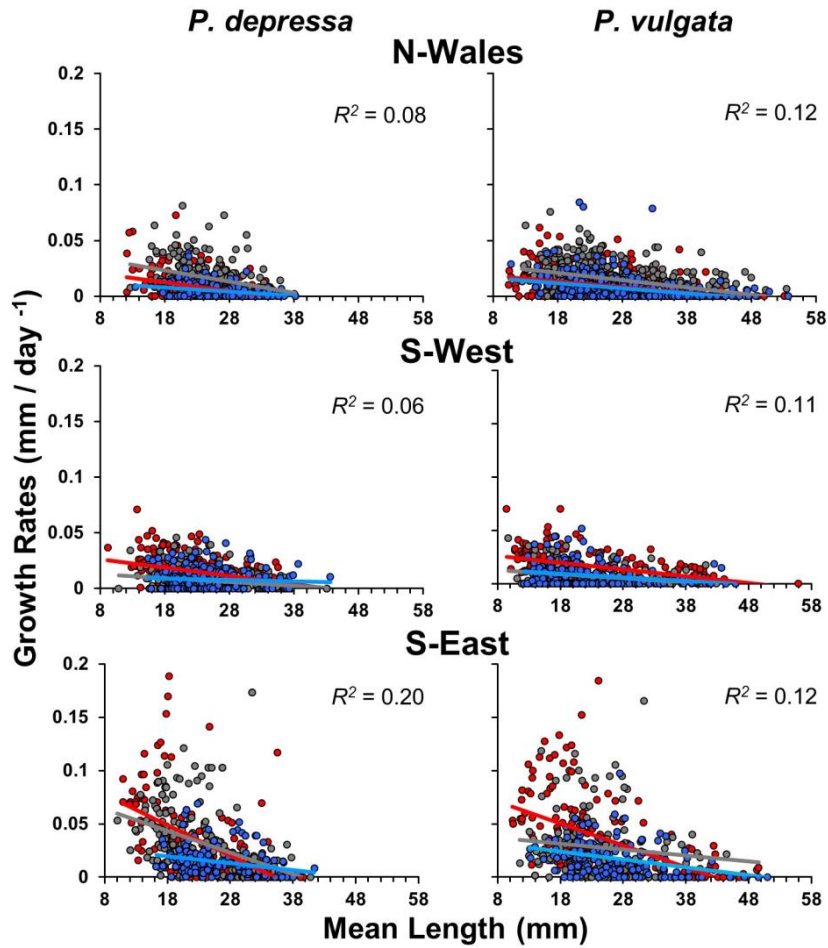
On the other hand, highest  $K$  values (growth coefficient) and  $\Phi'$  (growth performance index) were found in S-East England for both limpet species (Table 3.3). Thus, limpet growth measured as  $K$  and  $\Phi'$  differ between the two separate poleward boundaries of *P. depressa* in Britain. In addition,  $K$  and  $\Phi'$  values of *P. vulgata* indicated that our results do not agree with the ACH (Brown, 1984; Table 3.3), as *P. vulgata* may be considered to be at the centre of its range throughout regions (Lima *et al.*, 2016).

The “Forced” Gulland-Holt approach was also useful to explore seasonal differences in growth rates of limpets species between regions (Figure 3.6). In general, limpet populations in S-East England reached higher growth rates when compared with both S-West England and N-Wales populations (Figure 3.6). In particular, regional variation in relation to the maximum growth period was identified (Figure 3.6). For instance, in S-West and S-East England, limpet growth rates over summer months (from  $t_0$  until  $t_1$ ) were higher when compared with both growth rates recorded over autumn (from  $t_1$  to  $t_2$ ) and winter months (from  $t_2$  to  $t_3$ ; Figure 3.6). Conversely, in N-Wales, limpet growth rates were higher over autumn months (from  $t_1$  to  $t_2$ ) than other measuring periods (Figure 3.6). Greater coefficient of determination ( $R^2$ ) was found in populations of *P. depressa* in

S-East England than N-Wales and S-West England, principally in Portland Bill (Figure 3.6). In *P. vulgata* populations, these values were almost the same throughout regions (Figure 3.6).



**Figure 3.5.** “Forced” Gulland-Holt plots for those individuals that survived from June/July 2015 ( $t_0$ ) to late-May 2016 ( $t_3$ ) of both *Patella* species at each region. Dots indicate individual growth rates (y-axis) against the individual mean length (x-axis) without replacement of limpet because of individual mortality. Coefficient of determination ( $R^2$ ) is also indicated for each region and each *Patella* species ( $P < 0.05$ ).



**Figure 3.6.** “Forced” Gulland-Holt plots separated by different sampling period from June/July 2015 to late-May 2016 for both *Patella* species at each region. Dots indicate individual growth rates (y-axis) against the individual mean length considering individual replacement of limpet because of mortality. In red: summer period (2015); in grey: autumn (2015/2016); in blue: winter period (2016). Coefficient of determination ( $R^2$ ) is also indicated for each region and each *Patella* species ( $P < 0.05$ ).

### 3.3.4. Growth and Mortality Rates of *Patella* species in Britain

Both analyses for limpet growth and mortality rates (2015/2016) do not agree with the ACH (Brown, 1984) for *P. depressa* populations in Britain. *P. vulgata* also showed much variation in growth and mortality, despite being in the centre of its geographic distribution in the British Isles (Figure 3.7 and Figure 3.8).

**Table 3.3.** Comparison of  $L_{\infty}$  and K parameters estimated by “Forced” Gulland-Holt plots for both *Patella* species at each region from June/July 2015 ( $t_0$ ) to late-May 2016 ( $t_3$ ). Both parameters were calculated without individual replacement because of limpet mortality (see Figure 3.5). N° Ind. = number of individuals.  $L_{\infty}$  (mm) is the theoretical maximum length that species can reach; K ( $\text{year}^{-1}$ ) is a measure of the rate at which maximum size can be reached. Growth performance index ( $\Phi'$ ) is also indicated, i.e.,  $\Phi' = \log K + 2\log L_{\infty}$  (Clarke *et al.*, 2004).

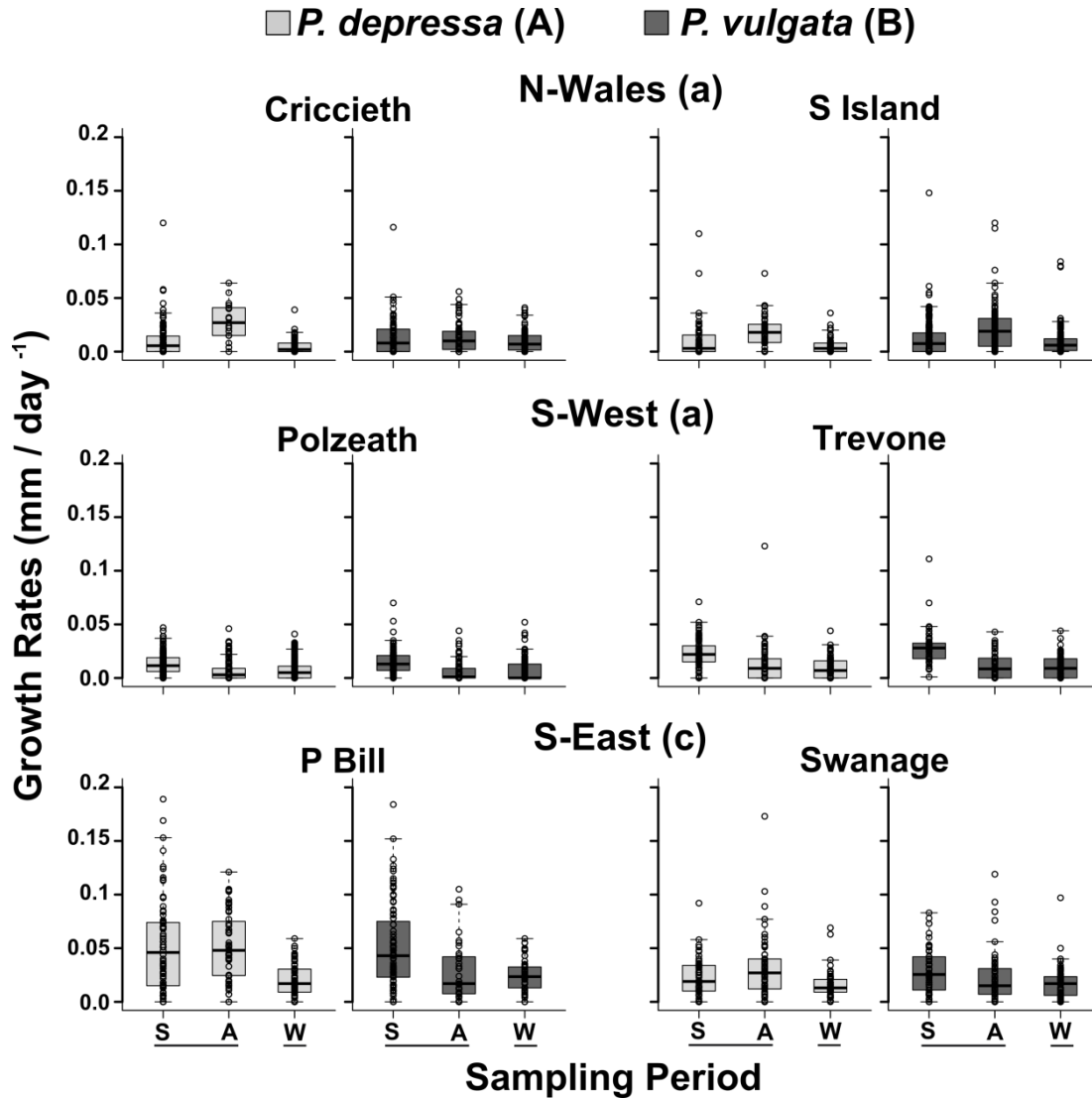
	<i>P. depressa</i>				<i>P. vulgata</i>			
Region	N° Ind.	$L_{\infty}$ (mm)	K ( $\text{year}^{-1}$ )	$\Phi'$	N° Ind.	$L_{\infty}$ (mm)	K ( $\text{year}^{-1}$ )	$\Phi'$
N-WALES	145	40.3	0.235	5.76	268	50.4	0.152	5.86
S-WEST	166	44.8	0.254	5.77	115	42.4	0.224	5.79
S-EAST	53	36.6	0.469	6.51	52	44.1	0.368	6.60

In terms of growth rates (Figure 3.7), the analysis did not show significant differences between *Patella* species and regions (Table 3.4; P-value > 0.05). However, the interaction between Species, Region and Period was significant, which means that growth patterns of *P. depressa* and *P. vulgata* differ depending on the region and sampling period (Figure 3.7, Table 3.4; P-value < 0.05). In this context, differences were found between S-East England when compared with both N-Wales and S-West England (Figure 3.7; Tukey post-hoc test,  $\alpha = 0.05$ ). Comparisons within limpet populations in S-East England indicated that growth rates of *P. depressa* were higher than *P. vulgata*, particularly over both summer and autumn months, when compared to winter months (Figure 3.7; Tukey post-hoc test,  $\alpha = 0.05$ ). For limpet populations in N-Wales, growth rates seems to be higher over the autumn than both summer and winter periods (Figure 3.7). There was no clear difference in growth rates between both *Patella* species populations in N-Wales and S-West England (Figure 3.7; Tukey post-hoc test,  $\alpha = 0.05$ ).

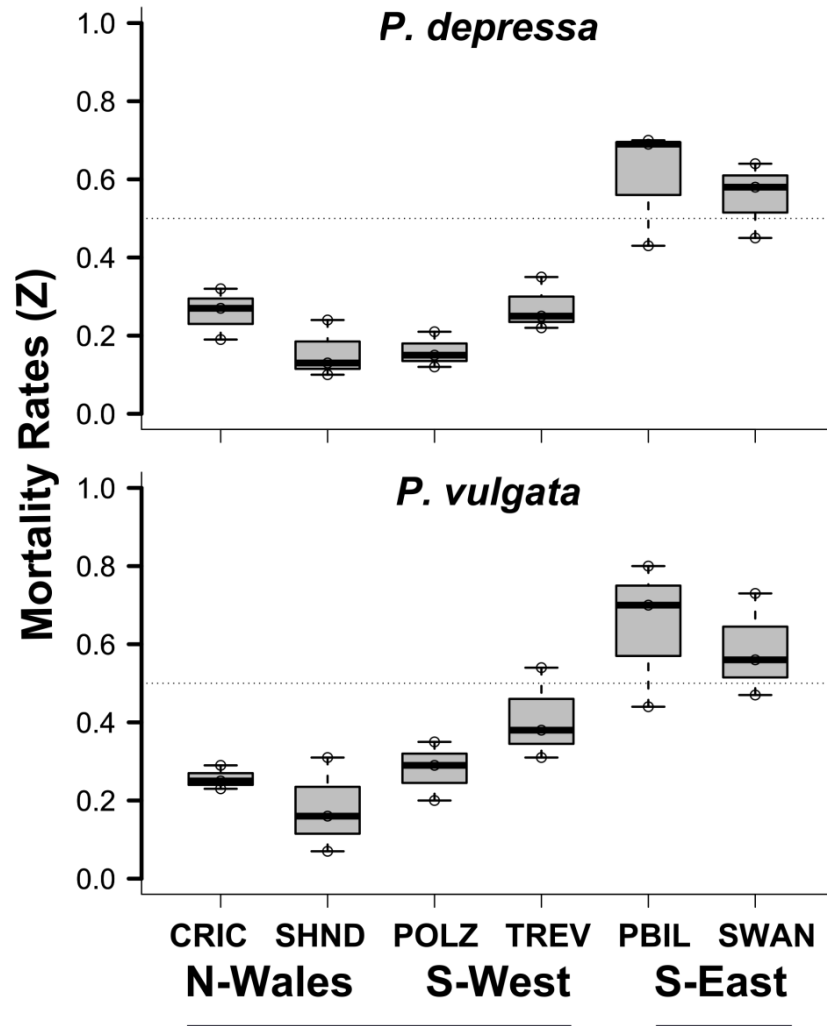
For mortality rates (Figure 3.8), the analysis did not show differences between *Patella* species (Table 3.5; P-value > 0.05). However, mortality rates of limpet species differed significantly between regions (Figure 3.8; Tukey post-hoc test,  $\alpha = 0.05$ ). Mortality rates for both *Patella* species were significantly higher in S-East England when compared with both N-Wales and S-West England populations (Figure 3.8, Table 3.5). In contrast, there were no differences in limpet mortality between N-Wales and S-West England populations (Figure 3.8; P-value < 0.05).



Thus, mortality rates of both limpet species were higher in the faster growing populations in S-East England (Figure 3.8).



**Figure 3.7.** Box-plot of growth rates (mm / days<sup>-1</sup>) for both *Patella* species measured from June/July 2015 to late-May 2016 and separated by location nested at each region. Sampling period indicates growth rates estimated during: Summer (S:  $t_0$  to  $t_1$ ), Autumn (A:  $t_1$  to  $t_2$ ) and Winter (W:  $t_2$  to  $t_3$ ). Dots indicate individual growth rates for limpets with less of 30 mm in length considering individual limpet replacement by mortality. Differences by levels are indicated for each fixed factor: Species = (A) and (B); Region (with each location nested) = (a) and (c). For Sampling Period, differences are shown by the straight black line in the bottom (Tukey post-hoc test,  $P < 0.005$ ).



**Figure 3.8.** Box-plot of instantaneous rate of total mortality ( $Z$ ) of both *Patella* species calculated for each measuring period ( $n=3$ ) from June/July 2015 to late-May 2016 at each location separated by region: N-Wales: CRIC= Criccieth and SHND= Shell Island; S-West England: POLZ= Polzeath and TREV= Trevone; and S-East England: PBIL= Portland Bill and SWAN= Swanage. Differences between regions (with each location nested) are showed with a straight black line in the bottom (Tukey post-hoc test for multiple pairwise comparison,  $\alpha = 0.05$ ). Dotted-grey horizontal line indicates a value of  $Z = 0.5$  on each plot.

**Table 3.4.** Summary of GLMM performed with fixed and random effects on both limpet growth rates (June/July 2015 to late-May 2016). Fixed effects: Region (N-Wales, S-West and S-East England), Sampling Period (Summer, Autumn and Winter), and Species (*P. depressa* and *P. vulgata*). As random effects: ID tagged (*i.e.*, individual tag), Initial length (*i.e.*,  $L_0 < 30$  mm in length) and Location nested in Region (N-Wales: Criccieth and Shell Island; S- West England: Polzeath and Trevone; S-East England: Portland Bill and Swanage). Significant terms for fixed factors are indicated (P-value < 0.005). SE= Standard Error.

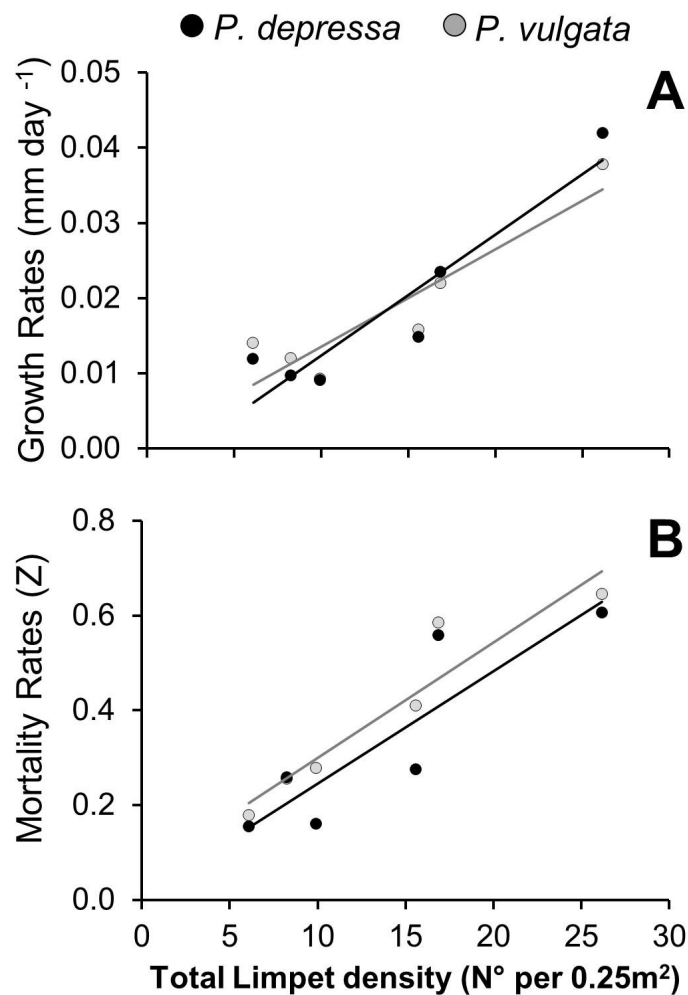
Fixed Effects	Estimate	SE	Z-value	P-value
Intercept	0.014	0.003	4.243	< 0.005
Species	0.001	0.002	0.316	0.752
Region	0.024	0.005	5.194	< 0.005
Species * Region	0.002	0.002	1.123	0.261
Species * Season	-0.007	0.002	-1.307	< 0.005
Species * Region * Period	-0.005	0.004	-3.350	< 0.005
Random effect	Variance	SE		
ID Tagged	4.4E-05	0.007		
Initial Length	1.5E-04	0.012		
Location (Region)	1.8E-05	0.004		
Residuals	2.2E-04	0.015		

**Table 3.5.** Summary of GLMM performed with fixed and random effects on both limpet mortality rates (2015/2016). Fixed effects: Region (N-Wales, S-West and S-East England) and Species (*P. depressa* and *P. vulgata*). As a random effect: Location nested in Region, *i.e.*, N-Wales: Criccieth and Shell Island; S-West England: Polzeath and Trevone; S-East England: Portland Bill and Swanage. Significant terms for fixed factors are indicated (P < 0.005). SE= Standard Error.

Fixed Effect	Estimate	SE	Z-value	P-value
Intercept	0.208	0.043	4.855	< 0.005
Species	0.010	0.055	0.181	0.856
Region	0.373	0.061	6.152	< 0.005
Species * Region	0.118	0.078	1.517	0.129
Random effect	Variance	SE		
Location (Region)	6.4E-04	0.025		
Residuals	9.1E-03	0.096		

### 3.3.5. Density-Dependent effects on Performance Traits of *Patella* Species

Biological local conditions such as density-dependent effects on growth and mortality rates of *Patella* species were also explored (Figure 3.9). Mean growth and mortality rates of both *Patella* species were positively related with the mean of total limpet density at each location (Figure 3.9;  $P < 0.05$ ). Higher growth and mortality rates occurs in locations with higher mean abundances of both *Patella* species across the three regions (Figure 3.9).



**Figure 3.9.** Relation between the mean total limpet density at each location (n=10 per quadrat) against (A) the average growth rates of *P. depressa* ( $R^2 = 0.84$ ) and *P. vulgata* ( $R^2 = 0.87$ ); and (B) the mean of instantaneous rate of total mortality (n=3 per location) of *P. depressa* ( $R^2 = 0.77$ ) and *P. vulgata* ( $R^2 = 0.89$ ) ( $P < 0.05$ ).

### 3.5. DISCUSSION

#### 3.5.1. Growth and Mortality Rates of *Patella* Species in Britain

My results showed that growth and mortality rates do not differ substantially between *Patella depressa* and *Patella vulgata*. However, both growth and mortality rates of both limpet species were higher in S-East England when compared with populations in N-Wales and S-West England (Figure 3.5, Figure 3.6, Figure 3.7 and Figure 3.8). Therefore, the present findings indicate that performance traits of *P. depressa* differ between the two separate poleward boundaries (see also Chapter 2) and there was not a clear consistent separation between more central population (S-West England) and range edge populations in Britain (N-Wales and S-East England). In addition, perhaps surprisingly *P. vulgata*, which may be considered in its centre range of distribution across all regions in the British Isles, showed patterns very similar to *P. depressa*. This shows the primacy of local contextual factors, which over-ride any abundant-centre effects on species geographic distribution (Brown, 1984).

#### 3.5.2. Regional and Seasonal Effects on Growth and Mortality of Limpets

Limpet growth patterns obtained suggest that regional differences between *Patella* species are related to seasons, perhaps due to slow-down during gonad development (Figure 3.7; Orton, 1928; Orton & Southward, 1956, 1961; Lewis & Bowman, 1975; Wright, 1977; Ekaratne & Crisp, 1984). Limpet populations in N-Wales had highest growth rates during autumn months (2015/2016; Figures 3.6 and Figure 3.7). In contrast, both limpet populations in S-West and S-East England showed the greatest growth in summer months (2015; Figure 3.6 and Figure 3.7). These contrasting geographical growth patterns between southern and northern populations can be associated with warmer temperatures over the summer, where high temperatures move progressively from south to north in Britain (Crisp & Southward, 1958; Lewis, 1964; Hiscock, 1998; Hiscock *et al.*, 2004). In this study, size monitoring of tagged individuals started between early and mid-summer across all regions (June/July 2015; Table 3.2), which possibly means that annual growth peak of both species may have already passed. Earlier studies have reported that *Patella vulgata* has maximum growth rate from early spring to early summer, with late summer growth limited by gonadal development (Orton, 1928; Orton & Southward, 1956; Blackmore, 1969; Wright, 1977). Additionally, owing to a resting gonadal phase during late autumn or early winter (Orton & Southward 1956), a second growth peak is highly likely (Orton, 1928; Orton &

Southward, 1956; Wright, 1977; Ekaratne & Crisp, 1984). By contrast, maximum growth of *Patella depressa* could simply be limited to the period between early spring and early summer, without a second growth period, since it has multiple spawning events over the year in Britain (Orton & Southward, 1961; Moore *et al.*, 2011). Hence, these growth patterns could suggest that I have captured the end of the first growth peak in *Patella* species, which was enough to identify regional differences in growth and mortality rates between species.

Seawater temperature is probably the ultimate factor driving geographic distributions of marine organisms including intertidal species (Hutchins, 1947) through its regulation of metabolism (Barry & Munday, 1959; Blackmore, 1969; Wright, 1977). Favourable temperatures close to the optimum for species will lead to more activity (Barry & Munday, 1959; Blackmore, 1969), greater growth and reproductive output and ultimately greater recruitment (Wright, 1977; Ling *et al.*, 2008, 2009; Moore *et al.*, 2011). In Britain, winter temperatures arrive earlier in northern latitudes than in southern ones and the opposite is true for summer temperatures (Crisp & Southward, 1958; Lewis, 1964; Bowman & Lewis, 1986; Lewis, 1986; Hiscock, 1998). The length of the interval between winter and summer conditions defines the frequency of cold periods after the main limpet-spawning event (Lewis & Bowman, 1975; Bowman, 1985; Bowman & Lewis, 1986; Lewis, 1986). In the south, this frequency is lower as the interval is shorter and therefore temperatures have been shown to stimulate growth and reduce mortality in juvenile limpets (Lewis & Bowman, 1975; Bowman, 1985; Bowman & Lewis, 1986). However, our results showed a complicated performance pattern across central and marginal limpet populations. Growth and mortality rates of both limpet species were higher in the range edge of *P. depressa* in S-East England, but lower in both S-West England (more central populations) and N-Wales populations of *P. depressa*. Thus, warmer weather temperatures in S-East England (Figure 3.2), might not only favour higher growth in *Patella* species but also increase mortality rates, suggesting that both leading borders of *P. depressa* are being influenced by opposite sea temperature patterns (see also Chapter 2).

### 3.5.3. Abundant-Centre Hypothesis (ACH) on *Patella* Species

Based on the ACH, individuals at the range edges would be expected to perform less well than more central populations (Brown, 1984; Caughley *et al.*, 1988). However, biological and physical factors could over-ride this normal-shaped distribution of species (Hellberg *et al.*, 2001; Sagarin & Gaines, 2002ab; Clarke *et al.*, 2004; Gilman, 2005, 2006; Sagarin *et al.*, 2006; Ling *et*

*al.*, 2008; Herbert *et al.*, 2009; Ling *et al.*, 2009; Hidas *et al.*, 2010; Fenberg & Rivadeneira, 2011; Herbert, 2011; Moore *et al.*, 2011). My results coincide with other studies made on warm-water species (Williamson & Kendall, 1981; Lewis *et al.*, 1982; Kendall & Lewis, 1986; Herbert *et al.*, 2009). Specifically, higher growth rate has been reported for southern intertidal species with northern geographical limits on the British coasts (Williamson & Kendall, 1981; Lewis *et al.*, 1982; Kendall & Lewis, 1986; Herbert *et al.*, 2009). For example, slower growth rates of *Phorcus lineatus* (ex *Monodonta lineata*, Affenzeller *et al.*, 2017) were recorded in populations in N-Wales, when compared with individuals from the English Channel, both poleward limits of its distribution in northern latitudes (Kendall, 1987). By contrast, higher growth rates in *S. umbilicalis* (ex *Gibbula umbilicalis*, Affenzeller *et al.*, 2017) can be found at the most northern location of its range distribution, possibly due to lower intra-specific competition (Williamson & Kendall, 1981; Lewis *et al.*, 1982; Kendall & Lewis, 1986). In my study, lowest values of  $L_{\infty}$  (theoretical maximum length) for both *Patella* species were reported in S-West England, which suggest that competitive interactions could be limiting their maximum length as well. These lower growth performances may be due to higher competition for food, particularly in summer periods where chlorophyll is scarce (Jenkins *et al.*, 2001). Thus, experiments on a large geographical scale between both *Patella* species could be useful to understand the effects of competitive interactions on species performances traits.

### 3.5.4. Growth Patterns in Patellacean Species

*Patella* growth rates did not show a gradient from southern to northern populations, as Clarke *et al.* (2004) has described for cold-water patellacean species. Growth rates of both *Patella* species were higher towards S-East England as well as K values (growth coefficient) and growth performance index ( $\Phi'$ ). However, values of K are still lower when compared with other patellacean species (Branch, 1974, 1975, 1981; Clarke *et al.*, 2004). In addition, Clarke *et al.* (2004) have reported that growth performance index ( $\Phi'$ ) generally declines with increasing latitude. However, this relationship does not match my results, as both limpet species reached almost the same growth performance in populations in S-West England ( $\sim 50^{\circ}$ ) and N-Wales ( $\sim 53^{\circ}$ ) (Table 3.3). Values of growth parameters (K and  $\Phi'$ ) reported for both limpet species compared with those reported by Clarke *et al.* (2004) must be related with the temporal scale used in this study, which normally takes over two-year using other methods (*e.g.*, length-frequency ; Branch, 1974, 1975, 1981; Brêthes *et al.*, 1994; Clarke *et al.*, 2004; Khow, 2007).

### 3.5.5. Concluding Comments

Changes in demographic attributes of limpets will have consequences on intertidal communities (Hawkins, 1981, Hawkins & Hartnoll, 1983; Hartnoll & Hawkins, 1985; Jenkins & Hartnoll, 2001; Jenkins *et al.*, 2005; Coleman *et al.*, 2006). In this context, *P. depressa* has extended its breeding season with greater reproductive output in adults in S-West England (Moore *et al.*, 2011). This phenological change seems to be accompanied with its recent range expansions into the English Channel - one of its range edges in Britain. In contrast, its other range edge in N-Wales has contracted when compared with its distribution recorded in 1950s around Anglesey, where low abundance and large individuals have been found (Chapter 2). This study has documented growth and mortality rates in northern co-occurrence zones between *P. vulgata* and *P. depressa*. The reported growth and mortality rates do not lend support to the ACH assumption (Brown, 1984) for both limpet species in Britain. Growth and mortality patterns did not vary between species at the centre range of one (*P. vulgata*) and towards both range edges of the other (*P. depressa*). A potential explanation comes from the spatiotemporal changes in sea surface temperature and density effects of both limpet species in Britain, which may alter their dynamics and structure at species geographical ranges (Gaston, 2009, 2003). Therefore, comparisons between key species across their range distribution can be useful to understand their potential impacts because of warming on intertidal assemblages.



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**CHAPTER 4:**  
**Annual growth lines of the southern species *Patella***  
***depressa* Pennant at poleward boundaries**  
**of its range distribution**

#### 4.1. INTRODUCTION

Invertebrate skeletons, particularly of molluscs, provide a continuous record of growth and an archive of environmental variation during their lifespan (Rhoads & Lutz, 1980). In molluscs, changes in growth may be visible as lines that can be observed on the surface and cross-section of their shells (Rhoads & Lutz, 1980), as layers are accreted during shell formation (MacClintock, 1967). These accretions are commonly referred to as increments, which are separated by growth lines (MacClintock, 1967). The temporal nature of these increments can be regulated by cyclical periods such as days (Bock *et al.*, 1994; Schöne *et al.*, 2005), tides (Ekaratne & Crisp, 1982; Bock *et al.*, 1994; Gutierrez-Zugasti *et al.*, 2017), and years (Ekaratne & Crisp, 1984; Clarke *et al.*, 2004; Buttler *et al.*, 2009; Surge *et al.*, 2013; Prusina *et al.*, 2015) or a combination of the all three (Surge & Schöne, 2014). In the case of the annual increments, the environmental and/or biological signal that leads to their formation differs among species, even among populations of the same species (Sato *et al.*, 1995; Surge *et al.*, 2013; Surge & Schöne, 2014). Thus, surprisingly, given the level of research activity in this area, in some mollusc species the underlying reason for annual growth lines remains obscure (Surge & Schöne, 2014).

Possible mechanisms proposed for growth line formation include a synergy between seasonal temperatures and species reproductive traits (Bachelet, 1980; Pörtner *et al.*, 2005; Surge & Schöne, 2014). Seasonal temperatures can have substantial impacts on growth in benthic molluscs (Bachelet, 1980; Picken, 1980; Branch, 1981; Williams & Kendall, 1981; Ekaratne & Crisp, 1984; Sato, 1995; Surge *et al.*, 2013). Severe winter conditions can inhibit normal growth and produce irreversible shell damage (Lewis & Bowman, 1975; Williams & Kendall, 1981; Bowman, 1985), which results in slower growth rates and therefore narrower increments (Ekaratne & Crisp, 1984; Williams & Kendall, 1981). In contrast, rapid shell growth, as illustrated by wider increments, driven by more favourable temperature are easily distinguishable when compared with finer increments accreted or deposited during colder conditions (Picken, 1980; Williams & Kendall, 1981; Ekaratne & Crisp, 1982, 1984; Sato, 1995).

In species that show increments stimulated by cyclical periods (*e.g.*, days and tides), the annual line formation depends on species reproductive traits (Sato, 1995). Species reproduction processes require an intense energy synthesis (Barry & Munday, 1959; Blackmore, 1969; Wright, 1977; Pörtner *et al.*, 2005), which in many species would be channelled exclusively into

reproduction, thereby simultaneously reducing the budget for shell growth (Wight, 1977; Wright & Hartnoll, 1981; Sato, 1995; Pörtner *et al.*, 2005). Thus, the annual line is commonly formed at the end of the gonadal development and spawning periods, when cessation of shell growth produces a break in the shell's microstructure, which may be recognized as a thick line in both cross-section and external features of shells (MacClintock, 1967; Williams & Kendall, 1981; Sato, 1995; Richardson, 2001). For example, in the northern hemisphere, the annual line in bivalve species has been documented over winter time towards high latitudes, and by contrast during summer time in southern latitudes (see Sato, 1995 for details). Hence, these seasonal influences and differences in reproductive strategies imprinted on shells can be recognizable as well as quantifiable as records of different species growth rates.

Patellids play a major role in controlling and structuring intertidal communities by the consumption of microbial biofilms, which are composed of cyanobacteria, microalgae, spores and other propagules of macroalgae, thereby regulating algal cover (Hawkins, 1981; Hawkins & Hartnoll, 1983; Hartnoll & Hawkins, 1985; Jenkins *et al.*, 2005; Coleman *et al.*, 2006). Due to their simple geometrical morphology (Ekaratne & Crisp, 1983) as well as their sessile nature and homing behaviour (Santini *et al.*, 2014), limpets have been a model species used to test hypotheses regarding growth. The main approaches used have been mark-recapture methods (Branch 1974, 1975; Bretos, 1980; Jenkins & Hartnoll, 2001; Kido & Murray, 2003; Espinosa *et al.*, 2008) and length-frequency analysis (Wright, 1977; Blackmore, 1969; Brêthes *et al.*, 1994; Khow, 2007). In addition, their growth increments are often well preserved and quantifiable under the naked eye (Bretos, 1980; Picken, 1980). However, in some species, these features are only clearly visible through shell-cross sections (Schackleton, 1973; Ekaratne & Crisp, 1982, 1983, 1984; Clarke *et al.*, 2004; Prusina *et al.*, 2015; Gutierrez-Zugasti *et al.*, 2017; Prendergast & Schöne, 2017). Studies of shell-cross sections have the advantage of enabling analysis of growth lines produced by periodic cycles, *e.g.*, annual (Ekaratne & Crisp, 1984; Clarke *et al.*, 2004; Prusina *et al.*, 2015) and fortnightly (Ekaratne & Crisp, 1982; Gutierrez-Zugasti *et al.*, 2017; Prendergast & Schöne, 2017) by measuring internal growth line patterns. Thus, growth lines separate the growth pattern into time slices referred to as growth increments (Richardson, 2001) and together could be useful to estimate the life span and growth rates of limpet species (Ekaratne & Crisp, 1982, 1983, 1984).

*Patella depressa* is a southern intertidal limpet species distributed from North Wales (Crisp & Knight-Jones, 1954; Crisp & Southward, 1958; Kendal *et al.*, 2004) to North Africa (Orton & Southward, 1961; Guerra & Gaudencio, 1986; Ribeiro *et al.*, 2009). In Britain, together with its congener, the northern limpet *Patella vulgata*, they are the most conspicuous grazers (Hawkins *et al.*, 2008, 2009) and both have been considered climate indicator species (Lewis, 1986; Mieszkowska *et al.*, 2005), being more abundant *P. depressa* in warmer period than cooler periods, and the opposite is true for *P. vulgata* (Kendal *et al.*, 2004; Hawkins *et al.*, 2008). Due to the physical outline of the British coastline (Lewis, 1964), *P. depressa* has poleward limits in both North Wales and South-east England (Crisp & Knight-Jones, 1954; Crisp & Southward, 1958; Kendal *et al.*, 2004; see also Chapter 2). In South-west England, there are well-established populations of *P. depressa* (Hawkins *et al.*, 2008, 2009) where conditions may be considered analogous to those in the centre of its range in Portugal (Guerra & Gaudencio, 1986; Boaventura *et al.*, 2002, 2003; Ribeiro *et al.*, 2009; Borges *et al.*, 2015). Results reported in Chapter 3 have shown that *P. depressa* has different growth patterns between its two separate poleward boundaries. In addition, there was no clear difference between populations from North Wales and populations in South-west England (see Chapter 3 for details). Increases in abundance of *P. depressa* have been attributed to an advance in its gonadal development, typified by longer reproductive seasons compared with populations from the 1940s around the British Isles (Hawkins *et al.*, 2008, 2009; Moore *et al.*, 2011). Individuals with faster gonadal development and shorter life span could be facilitating its increasing in abundance in South-west Britain (Moore *et al.*, 2011) and its current extension towards the east in the English Channel (Mieszkowska *et al.*, 2005; Keith *et al.*, 2011; see also Chapter 2). These patterns suggest that populations of *P. depressa* could be characterized by different growth performance between both poleward edges. Therefore, a deeper understanding of species traits close to their boundaries could be helpful to understand population dynamics (Fordham *et al.*, 2003; Brown *et al.*, 2016), particularly on species that are showing opposite shifts in distribution in their poleward frontiers, which is the case for *P. depressa* in Britain (see Chapter 2 for details).

In North-west Europe, little information on growth patterns of *Patella depressa* is available close to its poleward limits. In Britain, studies have mainly focused on its congener, *Patella vulgata* (see Table 3.1; Chapter 3 for details). In general, growth patterns in *P. vulgata* show an asymptotic shape represented by the von Bertalanffy growth curve (Ekaratne & Crisp,

1984), with fast growth in early-stages and then declining gradually to an asymptote (Orton, 1928; Blackmore, 1969; Lewis & Bowman, 1975; Wright, 1977). Earlier studies have reported that its maximum growth rate is from early spring to early summer (March-June), with later summer growth limited by gonadal development at this time (Orton, 1928; Blackmore, 1969; Lewis & Bowman, 1975; Wright, 1977). Additionally, owing to a resting gonadal phase during late autumn or early winter (Orton *et al.*, 1956), a second growth peak is highly likely (Orton, 1928; Lewis & Bowman, 1975; Wright, 1977; Ekaratne & Crisp, 1984). Such patterns were verified by Ekaratne & Crisp (1984) through analysis of tidal micro-growth increments from *P. vulgata* shells collected in North Wales. They identified seasonal growth with two maximum growth periods in late spring (May-June) and early autumn (September-October), whereas shell growth in January was suppressed.

The difference in life cycles between *Patella depressa* and its sibling species *Patella vulgata* is expected to have a strong effect on growth patterns (Orton *et al.*, 1956, Orton & Southward, 1961; Wright, 1977). As is the nature of a warm-water species (Hawkins *et al.*, 2008, 2009), *P. depressa* is considered a multiple spawner over the summer period (Orton & Southward, 1961), whereas *P. vulgata* is a single spawner over a year during winter months (Orton *et al.*, 1956; Wright, 1977). In South-west Britain in the cooler 1940s, gonad development in *P. depressa* generally started in April and May with ripening in June or July (Orton & Southward, 1961), with incomplete emptying of gonads as there is no resting period as seen in *P. vulgata* (Orton & Southward, 1961). There is evidence of earlier onset of maturation in early spring and a prolonged spawning season into the autumn in recent years as a response to warming (Moore *et al.*, 2011). Such a pattern is found further south in Europe (Ribeiro *et al.*, 2009). Thus, due to the high energetic cost involved in the limpet reproductive processes (Barry & Munday, 1959; Blackmore, 1969; Wright, 1977; Wright & Hartnoll, 1981), the main growth season for *P. depressa* may be restricted to one period and without a second growth period over a year as in *P. vulgata* (Orton, 1928; Lewis & Bowman, 1975; Wright, 1977; Ekaratne & Crisp, 1984). In fact, individuals of *P. depressa* never grow as large as *P. vulgata* (Evans, 1947; Borges *et al.*, 2015). These potential growth patterns may be revealed by shell records in *P. depressa*. If annual increments can be distinguished in shells of *P. depressa*, it will be possible to estimate the age and growth rates of populations in northern latitudes.

Density dependent effects can also alter *Patella* species growth patterns (Thompson *et al.*, 2000; Boaventura *et al.*, 2002, 2003). The intensity of intraspecific impacts between species can be measured for example, as species growth performance (Branch, 1974, 1975, 1981; Jenkins *et al.*, 2008). Non-manipulative studies have shown strong intraspecific competition in limpet species (Branch, 1974, 1975; Lewis & Bowman, 1975). For example, Lewis & Bowman (1975) suggested that intraspecific competition arises from areas with densities of *P. vulgata* between 300-450 limpets/m<sup>2</sup>, which potentially can reduce individual growth rates (Branch, 1974, 1975, 1981). Based on my previous inter-regional surveys of limpet abundance at small scales in Britain (see Chapter 2 for details), limpet density can be one or two orders of magnitude higher in South-east England when compared with the other leading edge of *P. depressa* in North Wales (Chapter 2). These density dependent effects could be evaluated on individuals of *P. depressa*, through analysis of shell increments.

Limpets with slow growth rates are generally associated with longer lifespans, whilst limpets with high growth rates have shorter ones (Branch, 1981; Hawkins & Hartnoll, 1983; Clarke *et al.*, 2004; Pörtner *et al.*, 2005). However, consideration of regional variation in species traits must also be taken into account across a large geographical range (Jenkins *et al.*, 2001; Jenkins & Hartnoll, 2001; Jenkins *et al.*, 2005). My analyses have shown a lack of small size classes of *Patella depressa* in populations in North Wales (see Chapter 2 and 3 for details), when compared with limpet populations in South-west and South-east England where breeding and recruitment are thought to be more regular and successful (Borges *et al.*, 2015). This suggests that populations of *P. depressa* in North Wales have resulted from sporadic settlement events due to recruitment failures, thereby being dominated by older age-classes when compared with its other leading edge in South-east England and more central populations in Britain. These population patterns suggest that both poleward edges of *P. depressa* could be characterized by different individual performance traits, which can be imprinted in shells as growth records. The main aim of my study was to investigate the age and growth patterns of individuals of *P. depressa* from populations at both of its range edges in the British Isles and in central areas of its range distribution with consistent recruitment (*i.e.*, South-west England). This was made by analysing the inner growth lines visible in shell sections and acetate peel replicas. Thus, I hypothesized that at central population of *P. depressa*, individuals occur with higher growth rates, which are characterized by younger individuals than both range edges. By contrast, in

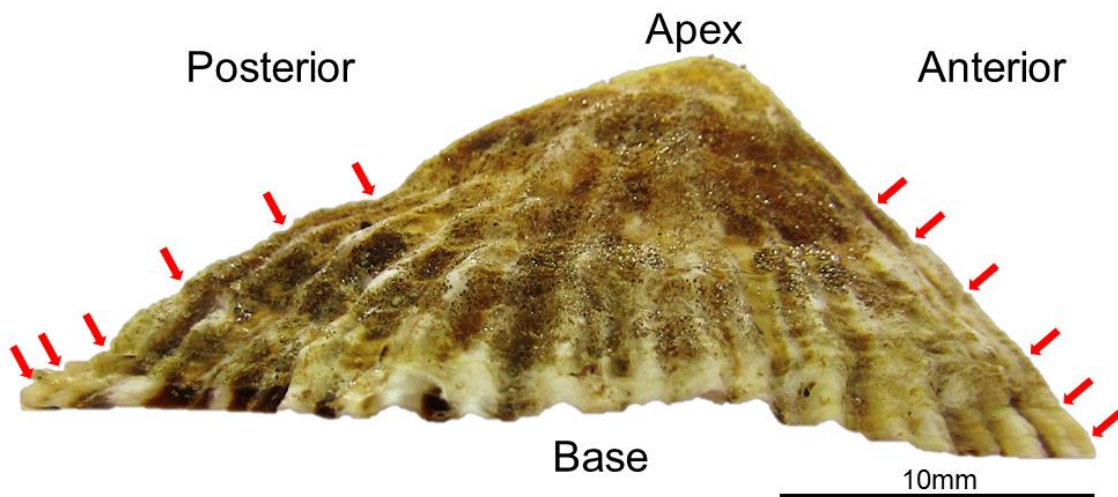


North Wales, populations are expected to have individuals with slower growth rates and typified by older individuals; whereas in South-east England, the other poleward edge of *P. depressa*, individuals would be expected to have higher growth and younger individuals than population at North Wales, being more similar to those in South-west England (see Chapter 3). In addition, the influence of local density on growth performance on individuals of *P. depressa* was tested at the scale of the habitat patch (*i.e.*, 0.5 x 0.5 m quadrat level).

## 4.2. MATERIALS AND METHODS

### 4.2.1. Morphology of *Patella depressa*

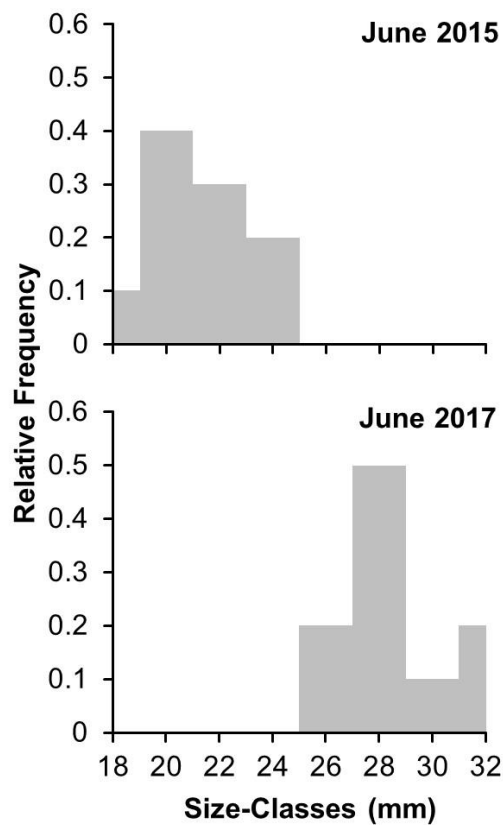
The shell of *P. depressa* is usually flatter compared to other *Patella* species (*e.g.*, *P. vulgata* and *P. ulysiponensis*) with distinctive orange-brown marginal rays on the inner surface (Evans, 1947; Bowman, 1981). The apex is located towards the anterior side from the central axis of the shell (Figure 4.1; Evans, 1947; Bowman, 1981). Shells have fine radiating ribs and a markedly oval or triangular shape on their posterior side (Bowman, 1981) and never grow as large as *P. vulgata* (Evans, 1947; Borges *et al.*, 2015). The maximum length is between 30 and 35 mm (Bowman, 1981). Although, bigger individuals than 35mm can also be found (this study, 43.1 mm).



**Figure 4.1.** Shell external morphological traits of *P. depressa*. Arrows indicates potential marks of annual growth lines, which were validated according to both field and laboratory measurements during 2015/2017.

#### 4.2.2. Field Validation of Growth Lines

A total of 80 individual *Patella depressa* were labelled in early June 2015 at Shell Island, North Wales (52° 49' N, 4° 08' W) (see Chapter 3 for details). Measurements of the maximum length of each tagged limpet were made at three different times: August 2015, November 2015 and March 2016. All field measurements were made with Vernier callipers to a resolution of 0.1mm. In June 2017, after a two-year period, 18 individuals of those limpets still labelled were collected. In the field, the maximum length of individuals was measured and then following removal of soft tissue, shells were rinsed clean with freshwater in the laboratory and air-dried at ambient temperature before being embedded in resin. A subgroup of ten shells was selected to validate annual growth increment measurements of *P. depressa* based on field length measurements (Figure 4.2). These individuals increased in length by approximately 6 mm over a period of two years (Figure 4.2).



**Figure 4.2.** Relative frequency of the maximum length (size) of *P. depressa* individuals selected for field validation of growth lines. Their sizes were recorded from June 2015 (tagging date) to June 2017 (data collection) at Shell Island, N-Wales.

#### 4.2.3. Shell Selection for Age and Growth Analysis

Shells of *Patella depressa* were collected between June and July 2016 from six locations located in three different regions: 1) Criccieth (52° 54' N; 4° 14' W) and 2) Shell Island in North Wales (hereafter N-Wales); 3) Polzeath (50° 34' N; 4° 55' W) and 4) Trevone (50° 32' N; 4° 58' W) in South-west England (hereafter S-West); and 5) Portland Bill (50° 30' N; 2° 31' W) and 6) Swanage (50° 36' N; 1° 56' W) from the South-east of England (hereafter S-East).

At each location, surveys of *Patella depressa* abundance were made. The area of survey extended from approximately Mean High Water Neap (MHWN) to Mean Tide Level (MTL) where *P. depressa* reach their maximum abundances on both semi-exposed and exposed shores (Orton *et al.*, 1956, Orton & Southward, 1961; Hawkins & Hartnoll, 1983). Ten 0.5 x 0.5 m quadrats were sampled along a transect parallel to the coastline, ~ 1 m apart, where the total number of limpets were counted. From each quadrat, the biggest specimen of *P. depressa* was collected. Maximum length and quadrat number for each shell were recorded. Soft tissue was removed from the shell, which was then taken back to the laboratory at the School Ocean Sciences, Bangor University for analysis. They were rinsed clean with freshwater and air-dried at ambient temperature before embedding in resin. A subgroup of five shells of *P. depressa* per location was selected (total=30) for internal growth analysis (Table 4.1).

#### 4.2.4. Shell Embedding and Acetate Peels Preparation

A total of 10 shells of *Patella depressa* were used for annual line validation and 30 shells for age and growth analysis. These were all embedded in epoxy resin (Kleer-Set Type FF, Polyester Casting Resin, MetPrep Ltd, UK). Afterward, embedded shells were processed using a standard procedure described by Ekaratne & Crisp (1982, 1984).

In summary, the shells were cut using a Buehler ISOMET 5000 precision saw along their maximum growth axis from the anterior to posterior side of shells (cut rate 14 mm min<sup>-1</sup> and at 5000 rpm). One half of each resin block was then polished using progressively finer grinder pads P120, P400, P1200 and P1200/4000 (MetPrep Ltd, UK) and finally using a 2 µm diamond paste (Maiapul Polishing Cloth Diamond, Spectrographic Ltd, UK). Subsequently, acetate peels were prepared for each shell to enhance the visibility of growth lines. The exposed surface was etched for 30 seconds by immersion in HCl (5%). After that, each sample was rinsed with distilled water and air-dried at ambient temperature for 24 h in a fume hood. The dry shell sections were

flooded at the exposed surface with ethyl acetate and a 0.35 µm thick sheet of acetate film (Replication Material G255, Agar Scientific Ltd, UK) was applied to the etched shell surface and air-dried at ambient temperature for 45 minutes. The acetate peels were gently removed from the shells, trimmed, and mounted between microscope slides for visual analysis of shell increments under transmitted light microscopy.

High-resolution photographs of the whole acetate peel were taken using a Lumenera Infinity 3 camera (Infinity3-3URC 00199474, Canada) attached to a microscope (Meiji Techno co. MT8100, Ltd, Japan). The images were taken under an X5 magnification lens. The computer software ImagePro Premier® 9.1.4 (Built 5368, Media Cybernetics®) was used to generate photomontages and to catalogue each sample. Each peel (*i.e.*, a replicate from each shell) was stored and referenced for further measurements.

**Table 4.1.** Number and shells length range of *P. depressa* selected for age and growth analysis during June/July 2016 separated by location and region (n=30).

Region	Location	Samples	Size range (mm)
N-WALES	Shell Island	5	30.1 - 33.9
	Criccieth	5	30.2 - 36.4
S-WEST	Polzeath	5	30.8 - 36.5
	Trevone	5	36.6 - 43.1
S-EAST	Swanage	5	31.1 - 34.5
	Portland Bill	5	39.8 - 41.5

#### 4.2.5. Growth Line Validation

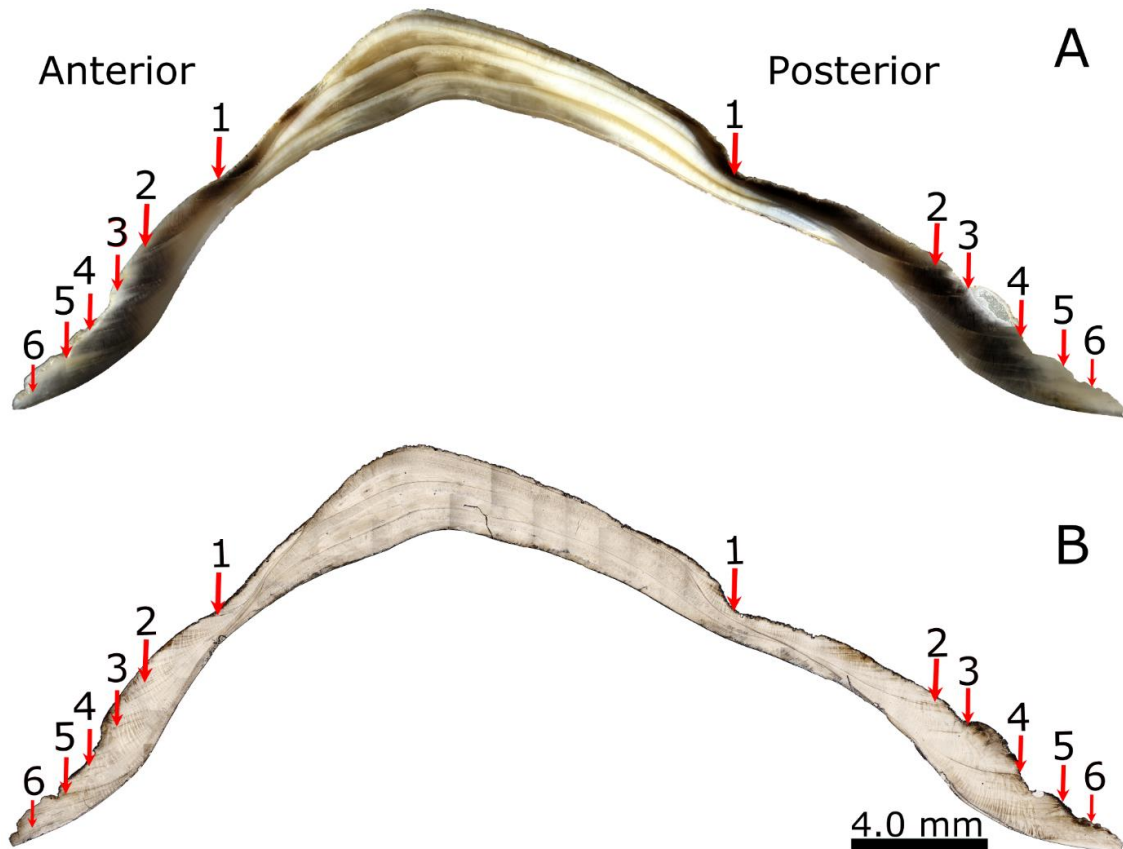
In order to validate the consistent selection of prominent annual lines and subsequent measurements of age and growth rates in *Patella depressa*, measurements recorded on tagged limpets from Shell Island (N-Wales) were compared against the maximum length measured for the last major growth line observed on peels (period 2015-16) from the margins (base) to the apex in shells. The major increment line was identified as the one that showed the highest contrast against the background features of the shell image on the peel (*i.e.*, the darkest line between the major increments, as well as using shell external features; Figure 4.1), which was examined under a microscope by using reflected and transmitted lights (Figure 4.3). Thus, once the notable annual line (period 2015/2016) was identified on both shell sides (*i.e.*, posterior and anterior; Figure 4.3), the maximum length between both shell margins was measured (Ekaratne & Crisp, 1983).

Comparisons between laboratory measurements and field measurements recorded in August 2015, November 2015 and March 2016 from tagged limpets were made using linear regression (Gotelli & Ellison, 2013). Additionally, the maximum length recorded when tagged limpets were collected in June 2017 was regressed against the length estimate from acetate peels. Parameters of the straight-line equation were calculated:  $y = mx + a$ , where  $m$  is the slope; and  $a$ , the intercept of the line on the y-axis, which corresponds to the error value of each measurement (Gotelli & Ellison, 2013). If the annual increment line was selected consistently then a close relationship would be expected between both measurements (field vs. laboratory), as denoted by a linear regression with a high coefficient of determination ( $R^2$ ) and the slope close to one. A non-zero intercept of the regression line can be interpreted as the inherent uncertainty of the field measurements (Gotelli & Ellison, 2013).

#### 4.2.6. Measuring of Maximum Length and Lines Number

In order to estimate age and growth rates of *Patella depressa*, annual lines in shells were identified and measured from samples collected in all three regions between June and July 2016 (Table 4.1). To support the selection of major lines and subsequent measurements of each sample, observations on the acetate peel as well as the resin block and morphological features of shells were matched (Figure 4.1 and Figure 4.3). Thus, once the notable annual lines were identified on both shell sides (*i.e.*, posterior and anterior) under microscope using reflected and

transmitted lights (Figure 4.3), the maximum length between both growing edges was measured (Ekaratne & Crisp, 1983). For each shell, the annual line number and its maximum length were appropriate to create von Bertalanffy growth curves for each location.



**Figure 4.3.** Shell cross-section of *P. depressa* indicating annual lines (arrows) identified under microscope by using both reflected light on the shell embedded in the resin (A) and transmitted light on the peel (B). External morphological traits were also useful to recognize and count annual lines number (Figure 4.1). Growth rates were calculated from the maximum length for each shell, which was measured once lines were identified at both sides of shells from the apex to the base (Figure 4.1).

#### 4.2.7. Von Bertalanffy Growth Curve: Ford-Walford Plot Approach

Von Bertalanffy growth parameters were estimated following the equation defined by:

$$L_t = L_{\infty} (1 - e^{-K(t - t_0)})$$

where  $L_t$  is the length at time  $t$ ;  $L_{\infty}$  is the theoretical maximum length that species would reach;  $K$  parameter is a growth coefficient which determines how fast the individual approaches its  $L_{\infty}$ . The von Bertalanffy growth curve often cuts the length axis at a value different from zero; hence,  $t_0$  is the theoretical age at zero length, which often has a small positive, or more usually, a small negative value (King *et al.*, 2007).

Ford-Walford plots were useful to estimate  $L_{\infty}$  and  $K$  (King *et al.*, 2007). A Ford-Walford plot shows the linear relationship between  $L_t$  against the length at  $t + 1$  ( $L_{t+1}$ ). From this relationship, which has a linear form,  $L_{\infty}$  and  $K$  can be calculated from the straight-line equation:  $y = mx + a$ ; where  $m$  is the slope, and  $a$ , the intercept of the line on the y-axis (King *et al.*, 2007). These parameters were useful to calculate  $L_{\infty}$  and  $K$  for each location, where  $L_{\infty} = a / (1 - m)$  and  $K = -\ln(m)$  (King *et al.*, 2007).

The remaining parameter in the von Bertalanffy growth equation,  $t_0$ , can be estimated if length at a particular annual line is known (see section 4.2.6 above). Therefore, from the von Bertalanffy equation,  $t_0$  may be calculated as follows (King *et al.*, 2007):

$$t_0 = t + (1 / K) * (\ln [(L_{\infty} - L_t) / L_{\infty}])$$

Von Bertalanffy growth curves were built using  $K$ ,  $L_{\infty}$  and  $t_0$  calculated for each location. Further, comparisons based on these parameters between locations and regions were made. In addition, as in fishes and invertebrates, whose growth process can be described by von Bertalanffy growth function, comparisons were also made through the overall growth performance index, *i.e.*,  $\Phi' = \log K + 2\log L_{\infty}$  (see Clarke *et al.*, 2004, Pörtner *et al.*, 2005 for details). According to Pauly (1979), the overall growth performance index describes the growth rate at the point of inflection of the Von Bertalanffy growth curve (*i.e.*, maximum growth rate; Heilmayer *et al.*, 2004).

The “TropFishR” package was used to build Ford-Walford plots and also to estimate the von Bertalanffy growth parameters in the CRAN R project (R Development Core Team 2014; Mildenerger *et al.*, 2017).

### 4.3. STATISTICAL ANALYSIS

In order to evaluate if the number of major increments (interpreted as age) varied among regions, an Analysis of Variance with two factors was performed (two-way, ANOVA; Gotelli & Ellison, 2013). Included in the ANOVA were the fixed factor Region, with three levels: N-Wales, S-West and S-East England; and Location nested in Region.

In order to examine whether individual K values (growth coefficient) of *Patella depressa* differed between regions, but also if there was a density-dependent effect, which can have an important influence on shell growth in limpets (Branch, 1974, 1975; Thompson *et al.*, 2000; Boaventura *et al.*, 2002, 2003), an Analysis of Covariance (ANCOVA) was applied (Gotelli & Allison, 2013). The factors included in the ANCOVA were Region, with three levels: N-Wales, S-West and S-East England; and Location nested in Region. The numerical explanatory variable considered was density of total limpets (number per 0.5 x 0.5 m). This continuous variable was the total limpet number recorded in the individual quadrats where shells were collected (June/July 2016). In addition, the coefficient of regression ( $R^2$ ) was calculated for each relationship between individual K values (growth coefficient) of *P. depressa* and density of total limpets (Gotelli & Allison, 2013).

Bartlett's tests were used to check the assumption of the residual variances before using both ANOVA and ANCOVA (Gotelli & Ellison, 2013). The “stats” package was used to run all analyses in the CRAN R project (R Development Core Team, 2014).

### 4.4. RESULTS

#### 4.4.1. Growth Line Validation

Line validation allowed the identification of annual lines from the base (margins) to the apex in shells of *Patella depressa* (Table 4.2 and Figure 4.4). Under high magnification, annual growth increments appear as bundles of closely spaced daily growth lines (Figure 4.3). Increments formed because of shell damage at the growing edge were generally less pronounced and associated with visible evidence of shell repair. Known as disturbance lines they are characterized by abruptly changing micro-growth increment widths and can occur when the animal is exposed to a sudden environmental stress, such as a major storm or an extreme cold period (Ekaratne & Crisp, 1982, 1983, 1984).



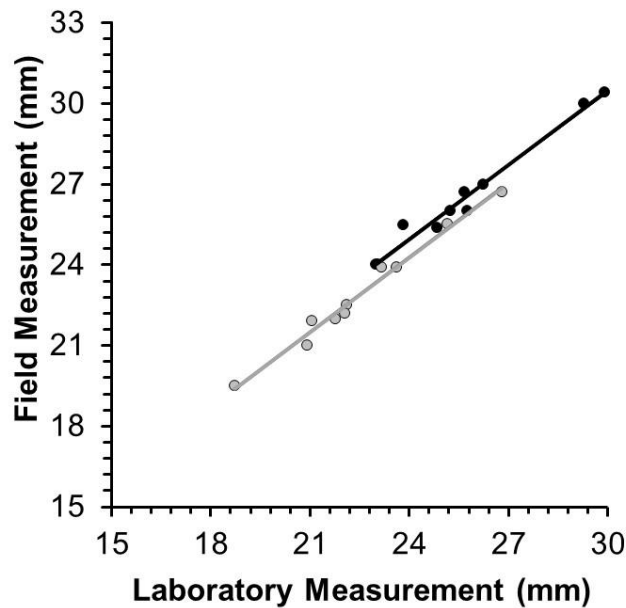
Parameters of linear regressions were useful to estimate the inherent uncertainty between field and laboratory (Figure 4.4). The maximum length of tagged limpets recorded in November 2015 was the closer measurement compared with the total length measured for the annual line identified on peels in the laboratory (period 2015/2016; Figure 4.4). The parameters of this relationship were  $m = 0.891 \pm 0.042$  SE,  $a = 2.906 \pm 0.941$  SE, and  $R^2 = 0.986 \pm 0.285$  SE (Figure 4.4). Parameters of the other relationships are shown in Table 4.2 (*i.e.*, August 2015 and March 2016). In addition, the relationship between the maximum length of tagged limpet collected in July 2017 against the length recorded from peels showed the following parameters  $m = 0.923 \pm 0.050$ ,  $a = 2.788 \pm 1.298$ , and  $R^2 = 0.977 \pm 0.354$  (Figure 4.4). Thus, these results suggest that the internal annual lines could have been formed at the end of the year (2015/2016) and indicate that the selection of annual lines together with external/internal morphological traits was made in a consistent manner.

#### 4.4.2. Measuring of Growth and Lines Number

All shells revealed pronounced annual lines, which allowed estimations of growth rates and age in shells (Figure 4.5 and Figure 4.6). Individuals of *Patella depressa* showed differences in the number of annual lines among regions (two-way ANOVA, Table 4.3; Figure 4.5). Individuals collected from N-Wales had a significantly higher number of annual lines (between nine and ten lines), when compared with individuals from S-West (between six and eight lines per shell) and from S-East (between six and seven lines per shell; Figure 4.5). However, these differences were not found between nested locations within each region (Table 4.3).

**Table 4.2.** Parameters of linear regressions to determine consistency in annual line selection and to estimate the uncertainty between measurements made in August 2015 and March 2016 on tagged limpets ( $n=10$ ) against the prominent line identified from their acetate peels (period 2015/2016). Parameters of the straight-line equation were calculated:  $y = mx + a$ , where  $m$  is the slope; and  $a$ , the intercept of the line on the y-axis, which correspond to the error value of each measurement.  $\pm$  SE = Regression Standard Error;  $m \pm$  SE = Slope Standard Error;  $a \pm$  SE = Intercept Standard Error.

Length Measurements (mm)						
Field	Laboratory	$y = mx + a$	$R^2$	$\pm$ SE	$m \pm$ SE	$a \pm$ SE
August 2015	Line 2015-16	$y = 0.857x + 3.315$	0.932	0.559	0.082	1.848
March 2016	Line 2015-16	$y = 0.505x + 13.998$	0.353	1.642	0.240	5.427



**Figure 4.4.** Relation between field and laboratory measurements of the maximum length (mm) of *P. depressa* individuals (n=20). Grey dots show the association between the measurement on tagged limpet in the field (November 2015) and the measurement for the last major annual increment identified (period 2015/2016) from the base to the apex in shells ( $y = 0.891x + 2.906$ ;  $R^2 = 0.986$ ). Black dots indicate the relation between the length recorded when tagged individuals were collected (July 2017) and its maximum length measured on each peel ( $y = 0.923x + 2.788$ ;  $R^2 = 0.977$ ).

#### 4.4.3. Von Bertalanffy Growth Curve: Ford-Walford Plot Approach

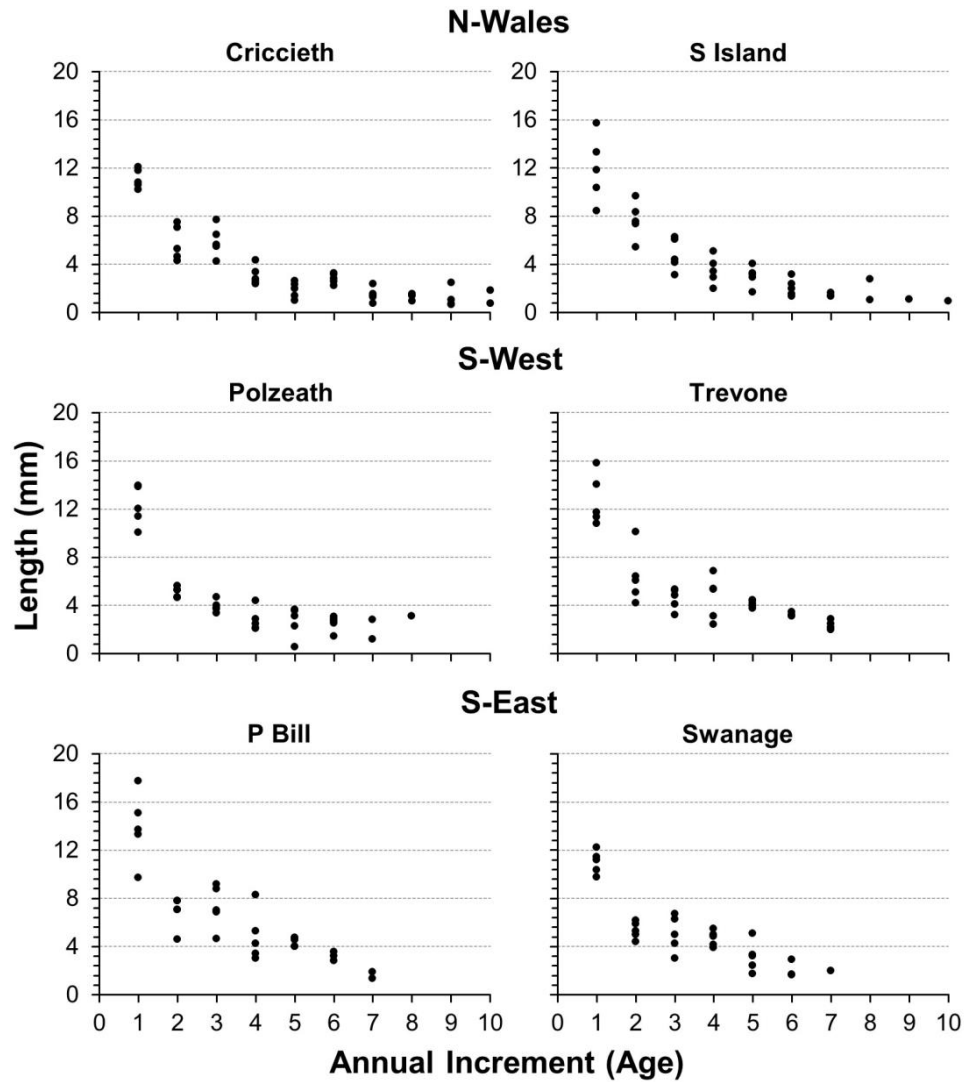
Ford-Walford plots were used to calculate von Bertalanffy growth parameters (Figure 4.6). Based on these parameters, von Bertalanffy growth curves indicated that growth decreased with increasing number of annual lines across shells (Figure 4.6; Table 4.4). Individuals of *P. depressa* from N-Wales and S-East England showed different growth patterns (Figure 4.6). Rapid growth was identified in shells collected from S-East England, where most individuals reached over 30 mm in length by the fourth or fifth annual increment at Portland Bill and by the sixth at Swanage (Figure 4.6). In contrast, shells collected from N-Wales showed slower growth and most shells only reached over 30 mm between the seventh and tenth annual line (Figure 4.6). This suggests slower annual growth rates in shells collected from N-Wales, which also have higher numbers of annual lines when compared to shells from S-East England (Figure 4.5 and Figure 4.6).

Comparisons of K (growth coefficient),  $L_{\infty}$  (maximum length) and  $t_0$  (theoretical age at zero length) as well as growth performance index ( $\Phi'$ ) are shown in Table 4.4. The calculated values of  $L_{\infty}$  (from 34.0 mm to 45.9 mm) were comparable to the maximum length recorded for each location (from 33.9 mm to 41.5 mm). Shells selected from S-East England indicated higher K values as well as  $t_0$  values compared to individuals from N-Wales (Table 4.4). In fact, K values for those individuals selected in N-Wales are very similar to those from S-West England (Table 4.3). Lower values of growth performance index were obtained from shells selected in N-Wales (Table 4.3). In contrast, performance index values of both S-West and S-East England tended to be equivalent, except for individuals selected in Portland Bill (S-East), which showed the highest value across locations.

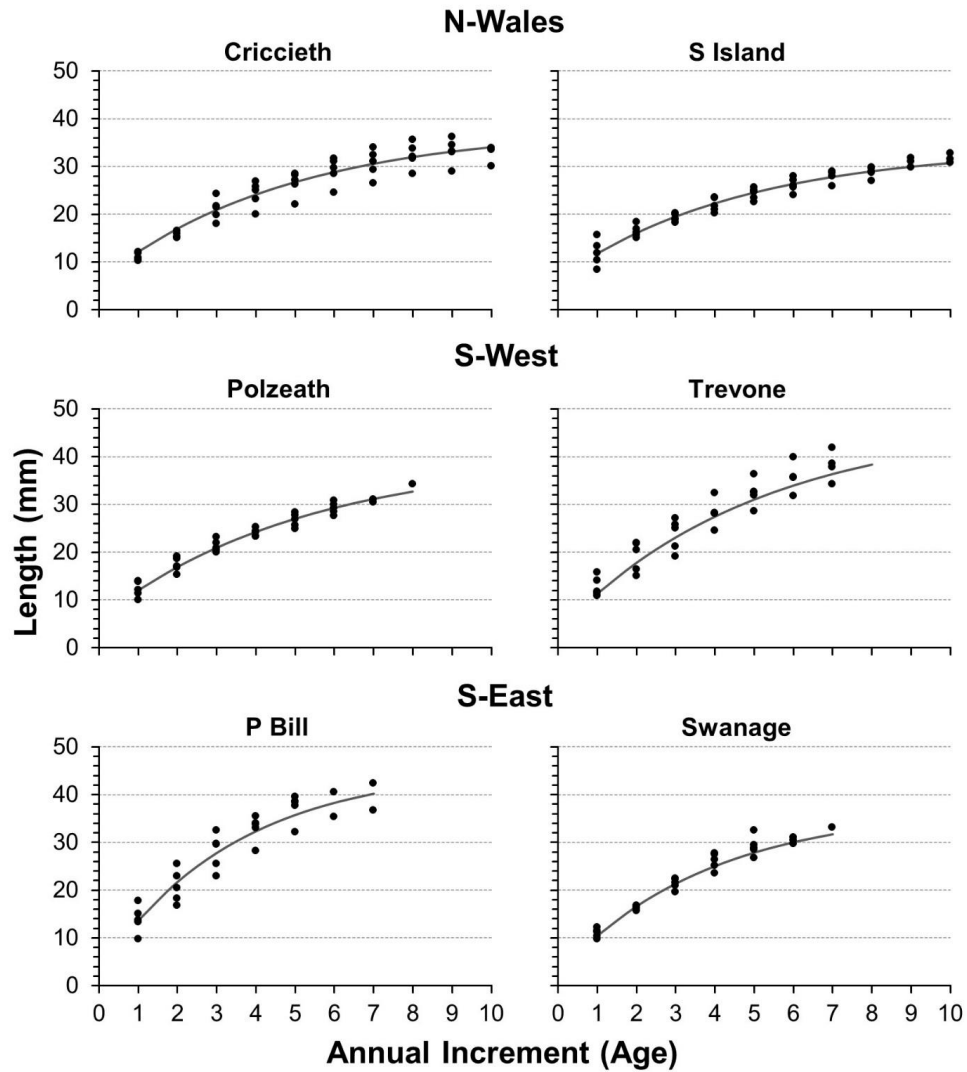
The ANCOVA analysis indicated that K values were significantly affected by the density of limpets recorded in each quadrat (two-way ANCOVA, Table 4.5 and Figure 4.7). Individuals with higher K values were found in lower densities of limpets across regions (Figure 4.7). They also differed between regions (Figure 4.6), but the interaction between density of limpets and region was not significant ( $P > 0.05$ ). Locations nested in region were marginally significant (Table 4.5), suggesting within region differences in limpet growth patterns.

**Table 4.3.** Two-ways Analysis of Variance (ANOVA) for the number of prominent lines identified on shells of *P. depressa* between Region (n=3) and Location (n=6), which is nested in Region (n= 2 per Region). DF= Degree of Freedom; SS= Sum Square; MS= Mean Square; F= F-Statistic; P= P-value ( $\alpha = 0.05$ ).

Source of Variation	DF	SS	MS	F	P-value
Region	2	34.2	17.1	13.86	$P < 0.005$
Location (Region)	3	1	0.3	0.27	0.85
Residuals	24	29.6	1.2		



**Figure 4.5.** Length (mm) and number of each increment identified from the apex (number 1) to the base (number 10) on shells of *P. depressa*. Five individuals were analysed at each location: N-Wales (Top) = Shell Island and Criccieth; S-West England (Middle) = Polzeath and Trevone; S-East England (Bottom) = Portland Bill and Swanage.



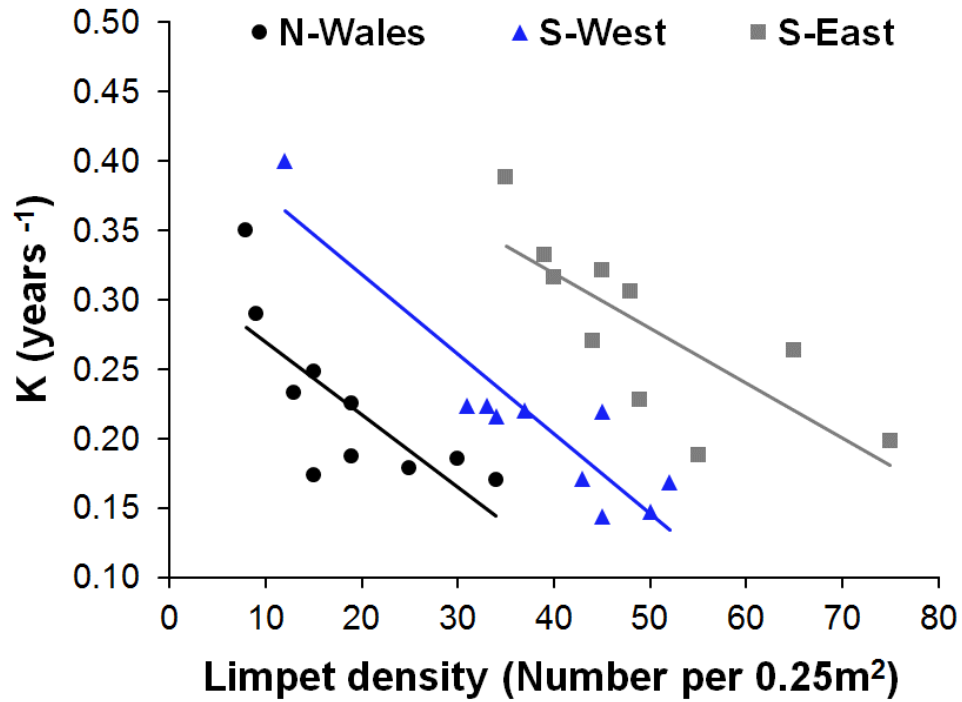
**Figure 4.6.** Von Bertalanffy growth curve based on the length and number of each annual line identified from the apex (1) to the base (10) on shells of *P. depressa*. Five individuals were analysed at each location: N-Wales (Top) = Shell Island and Criccieth; S-West England (Middle) = Polzeath and Trevone; S-East England (Bottom) = Portland Bill and Swanage. For each curve, von Bertalanffy growth parameters are shown in Table 4.4.

**Table 4.4.** Von Bertalanffy growth parameters ( $K$ ,  $L_{\infty}$  and  $t_0$ ) calculated using Ford-Walford plots for five shells selected in June/July 2016 at each location.  $L_{\infty}$  (mm) is the theoretical maximum length that species can reach;  $K$  ( $\text{year}^{-1}$ ) is a measurement of the rate at which the maximum size can be reached; and  $t_0$  is the theoretical age at zero length. The maximum length ( $L_{\text{max}}$ ) and the growth performance Index ( $\phi'$ ) are also indicated for each location ( $\phi' = \log K + 2\log L_{\infty}$ ). For each location, Von Bertalanffy growth curves are in Figure 4.6.

Region	Location	L max (mm)	$L_{\infty}$ (mm)	$K$ ( $\text{years}^{-1}$ )	$t_0$	$\phi'$
N-WALES	Shell Island	33.9	34.0	0.214	-0.994	2.29
	Criccieth	36.4	38.1	0.207	-0.849	2.28
S-WEST	Polzeath	36.5	40.1	0.191	-0.866	2.49
	Trevone	43.1	47.3	0.198	-0.381	2.65
S-EAST	Swanage	34.5	37.4	0.269	-0.247	2.58
	Portland Bill	41.5	45.9	0.299	-0.224	2.80

**Table 4.5.** Two-ways Analysis of Co-Variance (ANCOVA) for  $K$  values calculated from Ford-Walford plots for individuals of *P. depressa* selected at each Region ( $n=3$ ) and Location ( $n=6$ ), which is nested in Region ( $n= 2$  per Region). The co-variable was limpet density ( $N^{\circ}$  limpets per  $0.25\text{m}^2$ ) recorded at each quadrat from where shells were collected in the field (June and July 2016). DF= Degree of Freedom; SS= Sum Square; MS= Mean Square; F= F-Statistic; P= P-value ( $\alpha = 0.05$ ).

Source of Variation	DF	SS	MS	F	P-value
Region	2	0.027	0.013	10.72	$P < 0.005$
Density	1	0.077	0.077	62.27	$P < 0.005$
Location (Region)	3	0.011	0.004	2.89	0.05
Residuals	23	0.028	0.001		



**Figure 4.7.** Limpet density (N° limpets per 0.25m²) effects on each individual K value calculated for five shells of *P. depressa*. Total limpet density (irrespective of species) was recorded from each quadrat where shells were collected in the field (June and July 2016). Locations are nested by region: N-Wales (black dots;  $R^2 = 0.59$ ,  $P = 0.01$ ), S-West (blue dots;  $R^2 = 0.59$ ,  $P < 0.001$ ) and S-East England (grey dots;  $R^2 = 0.60$ ,  $P = 0.01$ ).

## 4.5. DISCUSSION

### 4.5.1 Overall Findings

My results showed that age, indicated by annual lines in shells, and growth performance, determined by their K values (growth coefficient) differed between populations of *Patella depressa* at their two leading edges in Britain (Figure 4.5, Figure 4.6 and Figure 4.7). Thus, my findings support the hypothesis that the two separate boundaries of *P. depressa* have differences in growth and age. Individuals of *P. depressa* from the range edge in S-East England showed a similar growth pattern when compared with individuals from more range central population in S-West England. In Chapter 3, I have shown that individual *P. depressa* have different growth rates between both leading borders in Britain, which is also supported by the results reported in this Chapter. Populations nearer to their poleward boundaries are generally characterized by older individuals (Williamson & Kendall, 1981; Kendall & Lewis 1986). This is the case for *P. depressa* at its northern boundary in N-Wales, but in S-East England, shells with fewer annual lines indicated less long-lived individuals. Advanced techniques such as sclerochronology in shells of *P. depressa* can confirm the structure of age in populations at their northern boundaries as well as the period (season) of annual line formation.

### 4.5.2. Growth Rates and Line Formation in *Patella* Species

In many mollusc species, external as well as internal incremental patterns of shells have been useful in determining the ages and growth rate estimations across different regions (see Sato, 1995; Richardson, 2001 for reviews). In my study, although growth of *Patella depressa* was higher in S-East England, values of growth coefficient (K) as well as the growth performance index ( $\emptyset'$ ) are still lower compared to other species of Patellidae family (Branch, 1981; Clarke *et al.*, 2004). This is true even within the central range of *P. depressa* in Portugal (Silva *et al.*, 2003) where growth rates of individuals are only slightly higher compared to those individuals on the British coast (see also Chapter 3). In some species of *Patella*, annual growth rates can reach between 22 and 70 mm during the first and fifth year (Branch, 1975, 1981). However, my results showed that the maximum growth rates recorded on individuals of *P. depressa* were between 8 and 16 mm over the first and second year (Figure 4.5). Additionally, it has been reported that in *Patella* species the growth performance index ( $\emptyset'$ ) generally declines with increasing latitude (see Clarke *et al.*, 2004; Pörtner *et al.*, 2005 for review). This



relationship, however, was not observed in *P. depressa* when comparing the S-West and S-East England (~50°) and N-Wales (~53°), where growth index values were almost the same (Table 4.4), except at Portland Bill in S-East England. These observations of growth performance in *P. depressa* using sclerochronological techniques are the same as those recorded from tagged limpets (Chapter 3). Thus, both tagging and growth lines analysis are useful techniques to estimate growth rates in *Patella* species in Britain, and have both demonstrated low growth performance values in *P. depressa* compared to other patellacean species around the world (see Branch, 1981; Clarke *et al.*, 2004 for review).

The present study has shown that growth patterns in *P. depressa* individuals tend to be more variable at locations in S-West and S-East England than locations in N-Wales, with shells showing both rapid and slow growth patterns at southern locations. This can be explained by the regional and inter-individual variations in the duration and intensity of both growth cessation and slowdown periods because of reproduction (Gutierrez-Zugasti *et al.*, 2017). In this context, the season of line formation may vary across the geographic range of species (Schackleton, 1973; Fenger, *et al.*, 2007; Surge *et al.*, 2013; Surge & Schoene, 2014; Prendergast & Schöne 2017). In general, formation of annual shell lines in mollusc species have been reported over winter periods in northern latitudes, *e.g.*, see Bachelet, (1980) for *Macoma baltica*, see both Williamson & Kendall, (1981) and Kendall, (1987) for *Monodonta lineata*, re-named as *Phorcus lineatus* (Affenzeller *et al.*, 2017), see Sato, (1995) for bivalve species. However, sclerochronological approaches in limpet species have shown that the formation of annual lines can vary even within individuals of the same species (Schackleton, 1973; Fenger *et al.*, 2007; Surge *et al.*, 2013; Prendergast & Schöne, 2017). For instance, Surge *et al.* (2013) found a mix between summer and winter annual lines in *Patella vulgata* shells from the English Channel, where the biogeographical boundary between the cold- and warm-temperate regions can be found (Lewis, 1964; Hiscock, 1998; Hiscock *et al.*, 2004). In contrast, in northeast Britain (a cold-temperate region; Hiscock, 1998; Hiscock *et al.*, 2004), where temperatures are cooler, shells have a slow growth rate and form a prominent annual line during winter (Fenger *et al.*, 2007; Surge *et al.*, 2013). Further south, individuals inhabiting the north of Spain (a warm-temperate region; Hiscock, 1998), form a noticeable annual line in summer presumably due to stress (Surge *et al.*, 2013). Hence, further growth analysis using sclerochronological techniques

on shells of *P. depressa* could elucidate the period of formation of growth lines in northern populations.

#### 4.5.3. Growth of Limpet Species at Northern Latitudes

In northwest Europe, *Patella vulgata* has been the model species to estimate growth patterns of limpet populations in northern latitudes (see Table 3.1 in Chapter 3 for details). In contrast, little information about growth patterns of *Patella depressa* is available close to its poleward limits in Britain. However, in Chapter 3, I showed that populations of *P. depressa* have different growth rates at their two leading edges. This difference in growth pattern was confirmed by the analysis of annual growth lines reported here, which allowed estimations of K values (growth coefficient) on shells of *P. depressa* from northern population. Thus, both approaches used in different Chapters (*i.e.*, tagged limpets and annual growth lines) are useful for estimating growth pattern and age structure of *P. depressa* at the poleward edges of its distribution. Both methods have shown lower growth in populations of *P. depressa* in N-Wales than in populations towards the S-East of England; both are range edges of its distribution. Similar growth patterns have been documented for warm-water intertidal species on British coasts (Williamson & Kendall, 1981; Lewis *et al.*, 1982; Kendall & Lewis, 1986; Herbert *et al.*, 2009). For example, slower growth rates of *P. lineata* individuals (ex *M. lineata*, Affenzeller *et al.*, 2017) were recorded in populations in N-Wales, when compared with individuals from the English Channel, which grew rapidly over a period of approximately seven years (Kendall, 1987). By contrast, higher growth rates in *G. umbilicalis* (re-named as *Steromphala umbilicalis*, Affenzeller *et al.*, 2017) can be found at the most northern location of its range distribution, due to lower intra-specific competition (Williamson & Kendall, 1981; Lewis *et al.*, 1982; Kendall & Lewis, 1986). Hence, such results indicate that growth may not be a limiting factor in intertidal species at their leading edges in Britain (Lewis *et al.*, 1982; Herbert *et al.*, 2009).

Northern populations of species are known to be characterized by short reproductive periods in summer and frequent recruitment failures (Hampe & Petit 2005, Bates *et al.*, 2014; Chuang & Peterson 2016). This can generate a latitudinal pattern, whereby marginal regions have an irregular age structure with missing year classes and often dominated by older and larger individuals (Lewis *et al.*, 1982; Lewis, 1986). For example, populations of *Patella vulgata* show this pattern, with large and old individuals more frequently found in populations towards its northern limit in north Norway (Bowman & Lewis, 1977; Lewis *et al.*, 1982; Bowman & Lewis,

1986). Similar patterns were seen for trochid gastropods at their northern limits in the cooler 1970s and early 1980s in Britain (Williamson & Kendall 1981; Lewis *et al.*, 1982; Kendall & Lewis, 1986). In my study, analysis of shells of *Patella depressa* suggest that individuals selected from N-Wales were between 9 and 10 years old; and between 6 and 8 years old in both S-West and S-East England (Figure 4.5 and Figure 4.6). This pattern indicates that older individuals of *P. depressa* may be more abundant at northern latitudes (N-Wales, ~53° North latitude) than southern ones (S-West and S-East England, ~50° North latitude). In fact, studies conducted on its congener *P. vulgata* have estimated a maximum life span from populations in the Isle of Man, to vary between 12 and 17 years old (Wright, 1977), and between 15 and 17 years in northeast England (Lewis & Bowman, 1975). By contrast, further south at its equatorward limit in Portugal, size-frequency data suggests that *P. vulgata* has a lifespan no longer than three or four years (Guerra & Gaudencio, 1986), indicating that latitudinal effects can be influencing population age-structure in limpet species (Lewis & Bowman, 1975; Wright 1977; Lewis *et al.*, 1982; Lewis, 1986; Guerra & Gaudencio, 1986). Similar lifespan estimates (3-4 years) have been reported for *P. depressa* along the Portuguese coast, at the centre range of its distribution (Guerra & Gaudencio, 1986; Lewis 1986). Therefore, the age patterns obtained here are not that far from those calculated for other limpet populations in Britain (Lewis & Bowman, 1975; Wright, 1977), supporting a gradient of increasing age of *P. depressa* from Portugal (~3 years old, Guerra & Gaudencio, 1986), to southern England (6-8 years old, this study) and N-Wales (9-10 years old, this study).

#### 4.5.4. Density Dependent Effects

Analysis of shell increments shows clearly that density of limpets (quadrat level) has affected growth patterns of individuals of *Patella depressa*. This pattern is supported by the significant negative relationship between growth performance (K values) of *P. depressa* and the total limpet density throughout the three regions. Based on previous surveys, limpet density can be one or two orders of magnitude higher in S-East England when compared with the other leading edge of *P. depressa* in N-Wales (Chapter 2). However, over a location scale, the high limpet density in S-East England does not reduce growth rates in *Patella* species (Chapter 3). In contrast, in a quadrat-scale, I also found a localised effect of limpet density on growth performance of *P. depressa* (this Chapter). This suggest that growth rates in limpet species is highly variable over different geographical scales. Previous studies have highlighted that *Patella*

species show stronger intra-specific competition than inter-specific competition, especially in terms of growth rates (Thompson *et al.*, 2000; Boaventura *et al.*, 2002, 2003; Moore *et al.*, 2007; Firth & Crowe, 2008; First *et al.*, 2009; Firth & Crowe, 2010). Hence, formal competition experiments on a large geographical scale between *Patella* species could be useful to understand the effects of competitive interactions on growth performance of limpet species.

#### 4.5.5. Concluding Comments

Growth is highly variable, subject to controls and limitations at various levels of biological organization (Pörtner *et al.*, 2005). Thus, the von Bertalanffy growth parameters should be considered as a general growth tendency, indicating general trends of species growth rates. Current results were consistent with growth patterns of *Patella depressa* obtained from tagged individuals, where slower growth rates were recorded in populations in N-Wales when compared with populations in the S-East England, both range edges of *P. depressa* in Britain. However, limpet density in quadrat-scale can also influence individual growth performance of *P. depressa*. In addition, growth line analysis in *P. depressa* suggests a population structure consisting of mainly older individuals in populations at N-Wales than S-East England. Hence, a better understanding of the timing of annual growth line formation of *P. depressa* over a large temporal scale could disentangle the mechanisms that underpin the opposing population dynamics seen at both poleward frontiers.

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## **CHAPTER 5:**

### **Abiotic modification of intra- and inter-specific competition between limpets in range-central and poleward-edge populations**

## 5.1. INTRODUCTION

In marine ecosystems, ecological patterns are determined by a complex interplay between abiotic factors (Hutchins, 1946) and species interactions (Connell, 1961). The strength and nature of biological interactions themselves are influenced by climate (Poloczanska *et al.*, 2008; Kordas *et al.*, 2011). If these interactions are sensitive to temperature, strong impacts on keystone species are expected (Sanford, 1999; Firth *et al.*, 2009) and therefore, noticeable changes on biological communities are highly probable (Leonard, 2000). Small changes in temperature may affect local populations by altering both trophic and non trophic interactions (Sanford, 1999). Climatic mediation of species interactions can control species abundance and distribution (Stachowicz *et al.*, 2002; Poloczanska *et al.*, 2008), but this interaction is still little understood (Louthan *et al.*, 2015). Thus, a better comprehension of the mechanisms by which climate and biology interact is crucial to interpret species distribution (Gilman *et al.*, 2010; Kordas & Dudgeon, 2011; Winz *et al.*, 2013), especially in those species that are showing changes in their geographic range limits (Chapter 2).

Population density over a latitudinal gradient may be a consequence of different levels of individual performance coupled with recruitment, which in turn will influence density-dependent processes, particularly competition (*e.g.*, Guo *et al.*, 2005). The hypothetical Gaussian shape (Brown, 1984; Abundance-Centre Hypothesis) in species abundance and distribution suggests that intra-specific competition may be strong in central populations, whereas towards marginal populations, inter-specific processes are typified by low numbers of individuals of a species (Guo *et al.*, 2005). The well-known biogeographic boundary in North-west Europe (Crisp & Southward, 1953; Crisp & Knight-Jones, 1954; Crisp & Southward, 1958; Herbert *et al.*, 2003; Hiscock *et al.*, 2004; Mieszkowska *et al.*, 2005, 2006, 2007; Hawkins *et al.*, 2008, 2009; Herbert *et al.*, 2009) where, southern warm-water species overlap at their northern range edges with central populations of boreal northern cold-water species (Forbes, 1854) has provided an interesting model system to assess the influence of competition between intertidal species over a large geographical scale (Poloczanska *et al.*, 2008; Firth *et al.*, 2009).

Shifts in biogeographic ranges are a biological manifestation of climate change (Southward *et al.*, 1995; Southward *et al.*, 2005; Mieszkowska *et al.*, 2006, 2007; Hawkins *et al.*, 2008; Poloczanska *et al.*, 2008; Hawkins *et al.*, 2009; Herbert *et al.*, 2009; Kordas *et al.*, 2011; Mieszkowska *et al.*, 2014; Herbert *et al.*, 2016; Poloczanska *et al.*, 2016). There is considerable

evidence that both the distributions of cold-species and warm-species are being affected by climate variability and more recent rapid anthropogenically-driven change (Southward *et al.*, 1995; Hawkins *et al.*, 2003; Hiscock *et al.*, 2004; Southward *et al.*, 2005; Mieszkowska *et al.*, 2006, 2007; Herbert *et al.*, 2009; Mieszkowska *et al.*, 2014). For example, the current range edge of the southern limpet species *Patella depressa* in North Wales has not fully recovered to the full extent occupied in the warm 1950s (Crisp & Knight-Jones, 1954; Crisp & Southward, 1958; see also Chapter 2). Nowadays breeding populations just reach the northern edge of Cardigan Bay and re-extension around the Lley Peninsula has not occurred (Chapter 2). On the other hand, the range of *P. depressa* has already extended along the English Channel to the east of the Isle of Wight (Fischer-Piette, 1936, 1948; Crisp & Southward, 1958; Kendall *et al.*, 2004; Mieszkowska *et al.*, 2005; Keith *et al.*, 2011; see also Chapter 2), with breeding populations occurring throughout the Isle of Wight and with scattered individuals occurring as far east as Beachy Head near Eastbourne (Chapter 2; Hawkins pers. comm). This is in contrast to the 1950s and 1980s, when *P. depressa* just reached Ventnor and Bembridge on the Isle of Wight, respectively (Kendall *et al.*, 2004). This change in distribution has been linked to warming (Mieszkowska *et al.*, 2006, 2007; Hawkins *et al.*, 2008; Moore *et al.*, 2011). Warming has also prompted an extended breeding season in *P. depressa* (Orton & Southward, 1961; Moore *et al.*, 2011); this has probably led to greater recruitment in Cardigan Bay in North Wales, increasing abundance compared to the colder 1980s (Chapter 2) and driving range extension in the English Channel at its other poleward range edge (Keith *et al.*, 2011).

*Patella* species are considered a keystone species because they have a strong impact on algal cover and influence patch dynamics of barnacles and macroalgae on exposed and semi-exposed rocky shores (Branch, 1981; Hawkins, 1981; Hawkins & Hartnoll, 1983ab; Hartnoll & Hawkins, 1985; Burrows & Hawkins, 1998; Jenkins *et al.*, 2005; Coleman *et al.*, 2006; Jonsson *et al.*, 2006). At mid-shore levels, *Patella vulgata*, a cold-water northern species and warmer-water *Patella depressa* are the most conspicuous grazers on South-west British rocky shores (Orton *et al.*, 1956; Orton & Southward, 1961; Hawkins & Hartnoll, 1983ab; Jenkins *et al.*, 2005; Moore *et al.*, 2007ab). *P. vulgata* is at the centre of its distributional range throughout Britain (Figure 5.1. A; Lima *et al.*, 2016), coinciding with poleward borders of *P. depressa* in North-west Wales and southern England (Figure 5.1A; Crisp & Knight-Jones, 1954; Crisp & Southward, 1958; Kendall *et al.*, 2004). In response to global warming, increasing abundance of



*P. depressa* in South-west Britain has been accompanied by local decline of *P. vulgata* (Southward *et al.*, 1995; Moore *et al.*, 2007ab; Hawkins *et al.*, 2008, 2009; Moore *et al.*, 2011; see also Chapter 2). As both limpet species share several niche characteristics and resource requirements during their foraging phase (Hawkins *et al.*, 1989; Thompson *et al.*, 2000; Jenkins & Hartnoll, 2001) inter-specific competition is probably occurring in South-west England (Moore *et al.*, 2007a; Firth *et al.*, 2009), as in Portugal (Boaventura *et al.*, 2002ab). There is small-scale local segregation modulated by temperature amelioration of microhabitats by fucoids: *P. vulgata* aggregates under *Fucus* clumps (Hawkins & Hartnoll, 1983b; Hartnoll & Hawkins, 1985) and moves or dies when these are removed (Moore *et al.*, 2007a). In contrast, *P. depressa* prefers open rock and does not aggregate under *Fucus* clumps (Moore *et al.*, 2007a). Therefore, this pattern suggests coexistence at larger spatial scales, but with an important local segregation due to interplay between temperature and competitive processes between both limpet species at small spatial-scales.

Canopy forming macroalgae are recognised as having key roles in structuring benthic communities by modifying physical environmental conditions (Santelices & Ojeda, 1984; Hawkins, 1983; Jenkins *et al.*, 1999; Leonard, 2000; Thompson *et al.*, 2004; Moore *et al.*, 2007a; Marzenelli *et al.*, 2012; Pocklington *et al.*, 2017). They can ameliorate thermal conditions by reducing extreme temperatures (Moore *et al.*, 2007a; Leonard, 2000; Marzenelli *et al.*, 2012) as well as reducing light levels (Reed & Foster, 1984; Jenkins *et al.*, 1999) which results in higher concentrations of biofilm beneath them (Thompson *et al.*, 2004). Canopy forming macroalgae can influence mortality and size of individuals of limpets providing better conditions to survive in places with extreme local conditions (Moore *et al.*, 2007a; Marzenelli *et al.*, 2012). Changes or loss of these habitats may influence biological interactions such as predation and competition as well as having consequences for community structure and ecosystem functioning (Sanford, 1999; Moore *et al.*, 2007a; Hawkins *et al.*, 2009; Jueterbock *et al.*, 2013).

Manipulative experiments have investigated competition in limpets species (Thompson *et al.*, 2000; Gilman, 2006; Moore *et al.*, 2007ab; Boaventura *et al.*, 2002b, 2003; First *et al.*, 2009; Marzenelli *et al.*, 2012; Aguilera *et al.*, 2018), producing contrasting results depending on geographic location (Thompson *et al.*, 2000; Boaventura *et al.*, 2002b). For example, at the North-east limit of *Patella depressa* in Britain, Thompson *et al.* (2000) evaluated intra-specific competition of *Patella vulgata* and *P. depressa*. They found that mortality rates of *P. vulgata*

increased at higher con-specific densities, while *P. depressa* was unaffected under similar densities (Thompson *et al.*, 2000). In contrast, further south towards the equatorward limit of *P. vulgata* in Portugal, *P. depressa* tends to be more susceptible to intra-specific competition (*i.e.*, central populations), whilst *P. vulgata* showed less negative density dependence, particularly in mortality rates (Boaventura *et al.*, 2002b). These patterns of mortality suggests that at the range edges of both patellid species (*i.e.*, the poleward limits of *P. depressa* in Britain and the trailing edge of *P. vulgata* in Portugal) intra-specific competition may be reduced (Guo *et al.*, 2005).

Species density may show large changes over geographical scales with implications for the relative levels of intra- and inter-specific competition (Guo *et al.*, 2005; Aguilera *et al.*, 2018). I hypothesized that individuals of *Patella depressa* towards the range edge in North Wales would be expected to be more influenced by inter-specific competition from its putative competitor *Patella vulgata*, than individuals in more central populations in South-west England (Orton *et al.*, 1956; Orton & Southward, 1961; Kendall *et al.*, 2004; Moore *et al.*, 2007ab; Borges *et al.*, 2015). In contrast, individuals of *P. vulgata* are expected to be influenced by intra-specific processes throughout the British Isles (Guo *et al.*, 2005), as it may be considered to be at the centre of its distribution (Southward *et al.*, 1995; Lima *et al.*, 2016). In addition, since both *Patella* species have different microhabitat preferences at small scales (Hawkins & Hartnoll, 1983b; Hartnoll & Hawkins, 1985; Moore *et al.*, 2007a), I investigated the effect of environmental conditions on the intensity of competition by simulating canopy shading. Hence, the main purpose of my study was to determine the importance of physical mediation of competition in overlapping zones of range distribution between both *P. depressa* and *P. vulgata* in Britain. I tested how intra- and inter-specific competition between *Patella* species varies in range central and range edge populations of *P. depressa* and how this is modulated by microhabitat differences in shading. The mechanisms explored were individual performance (growth rate) and population mortality of both *Patella* species, and shifts in available microalgal biofilm food as a consequence of both limpet density and local environmental conditions across regions (Thompson *et al.*, 2004). These experiments should provide insights into whether inter-specific competition can play a role in setting species range edges.

## 5.2. MATERIALS AND METHODS

### 5.2.1. Study Sites

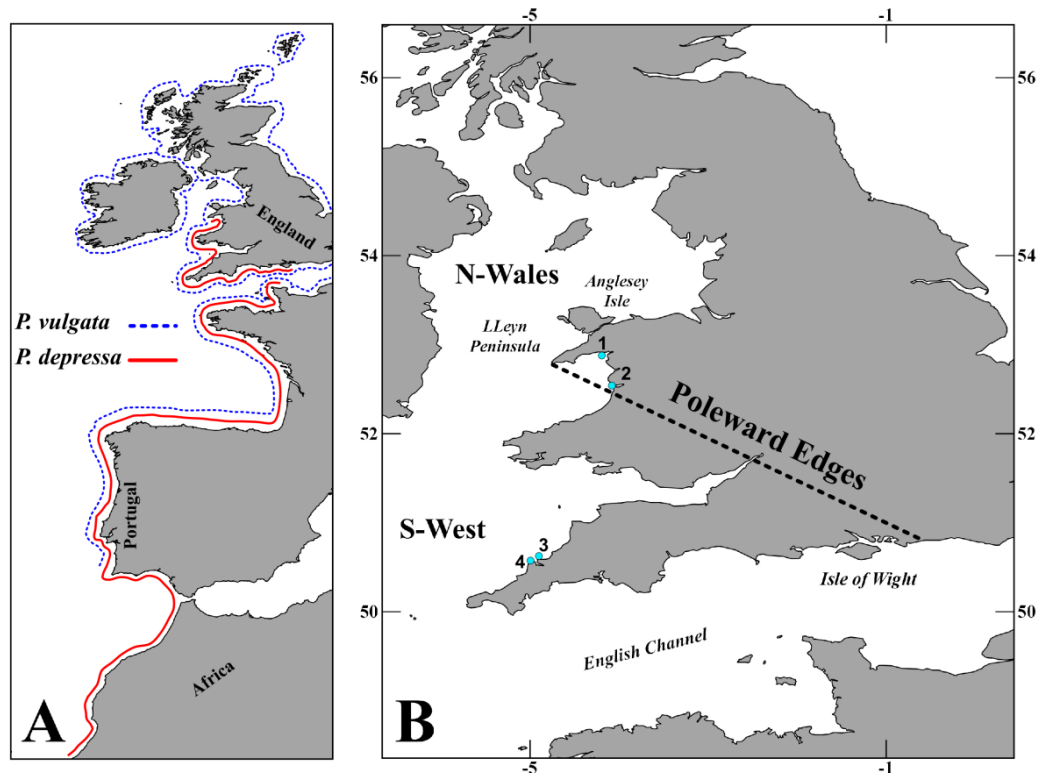
This study was carried out on the rocky shores of South-west England (hereafter S-West England) and North Wales (hereafter N-Wales) in Britain (Figure 5.1). Both regions can be considered in the centre of the distributional range of *Patella vulgata* in the British Isles (Southward *et al.*, 1995; Lima *et al.*, 2016). At the poleward limit of *Patella depressa* in N-Wales (Crisp & Knight-Jones, 1954; Kendall *et al.*, 2004), populations do not reach more than 20% of patellid populations, particularly in locations at the northern edge of Cardigan Bay (Chapter 2). In contrast, in S-West England, *P. depressa* has formed 50% or more of the limpet population over recent decades (Orton & Southward, 1961; Moore *et al.*, 2007ab; Hawkins *et al.*, 2008, 2009; Kendall *et al.*, 2004); these populations may be considered analogous to those in the range centre (*e.g.*, Portugal; Guerra & Gaudencio, 1986; Boaventura *et al.*, 2002ab, 2003; Borges *et al.*, 2015).

The experiment was run at two locations in each region: in N-Wales, Criccieth and Borth (Figure 5.1B). In S-West England, locations selected were Polzeath and Trevone (Figure 5.1B), which both have well-established populations of both *Patella* spp. species in Britain (Orton *et al.*, 1956; Orton & Southward, 1961; Moore *et al.*, 2007ab; Borges *et al.*, 2015). During June and July 2016, surveys of abundance were made at each location from approximately Mean High Water Neap (MHWN) to Mean Tide Level (MTL) where both limpet species reach their maximum abundances on both semi-exposed and exposed shores (Orton *et al.*, 1956; Orton & Southward, 1961; Hawkins & Hartnoll 1983a). Ten 30 x 30 cm quadrats were sampled along a transect parallel to the coastline, ~ 1 m apart, where the total number of both limpet species were counted. Barnacle cover in each quadrat was also recorded.

### 5.2.2. Competition Experiment between *Patella* Species in Britain

In order to determine the effects of intra- and inter-specific competition on *Patella* species in Britain across central and poleward populations of *Patella depressa* in Britain, different density treatments were created at each location. The central question addressed was to assess the role of inter-specific competition (under different environmental contexts) in setting the range limit of *P. depressa* in N-Wales, with a regional comparison made with S-West England (*i.e.*, central populations). For this reason, and in order to assure comparable density-

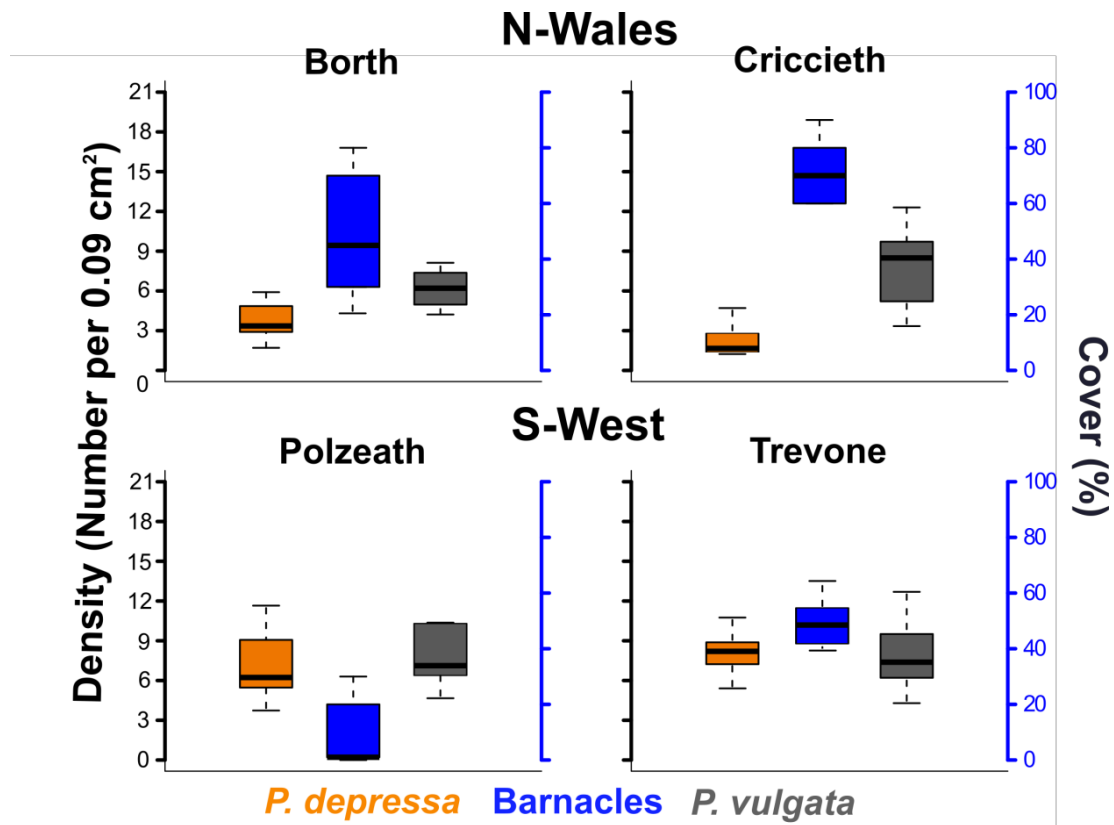
effects of *Patella* species (Underwood, 1986), the density of *P. depressa* in N-Wales was used as the baseline for the experiment. Previous abundance sampling showed that three limpets per plot (30 x 30 cm) was the mean *P. depressa* density (Figure 5.2), in poleward populations in N-Wales.



**Figure 5.1.** (A) Distributional range of *P. depressa* (red) and *P. vulgata* (blue) in the North West of Europe. (B) Locations (light blue circles) selected to measure intra- and inter-specific competition between *P. depressa* and *P. vulgata* in Britain. N-Wales: 1= Criccieth and 2= Borth; and in S-West England: 3= Polzeath and 4= Trevone.

During September and October 2016 different densities of *Patella* species were created by enclosing small limpet patches between MHWN to MTL (see above) at all 4 locations (Figure 5.1B). This was to avoid high mortalities of individuals due to removal and transplantation. Thus, the experimental design consisted of five density treatments: 1) Single-Species *P. depressa* (3 limpets per plot) and 2) Single-Species *P. vulgata* (3 limpets per plot), both of them considered as low density treatments. In addition, double density treatments were also considered: 3) double density of *P. depressa* (6 limpets per plot) and 4) double density of *P. vulgata* (6 limpets per

plot), both of them categorized as high density treatments. Furthermore, a fifth treatment consisted of mixed-species between *P. depressa* (n=3) and *P. vulgata* (n=3), categorized as treatments in high density of limpets (6 limpets per plot). Cages of 30 × 30 × 5 cm (PVC coated welded wire mesh, opening size 12×12 mm) were placed into limpet patches by drilling holes into the rocky substratum, using wall anchors, stainless steel washers, and screw bolts to attach the cage to the rock.



**Figure 5.2.** Mean of density (± Standard deviation) of each *Patella* species (black left-axis) and barnacle cover (blue right-axis) sampled in 10 quadrats of 30 x 30 mm before the experiment started (June/July 2016) in locations (n=4) at mid-shore levels.

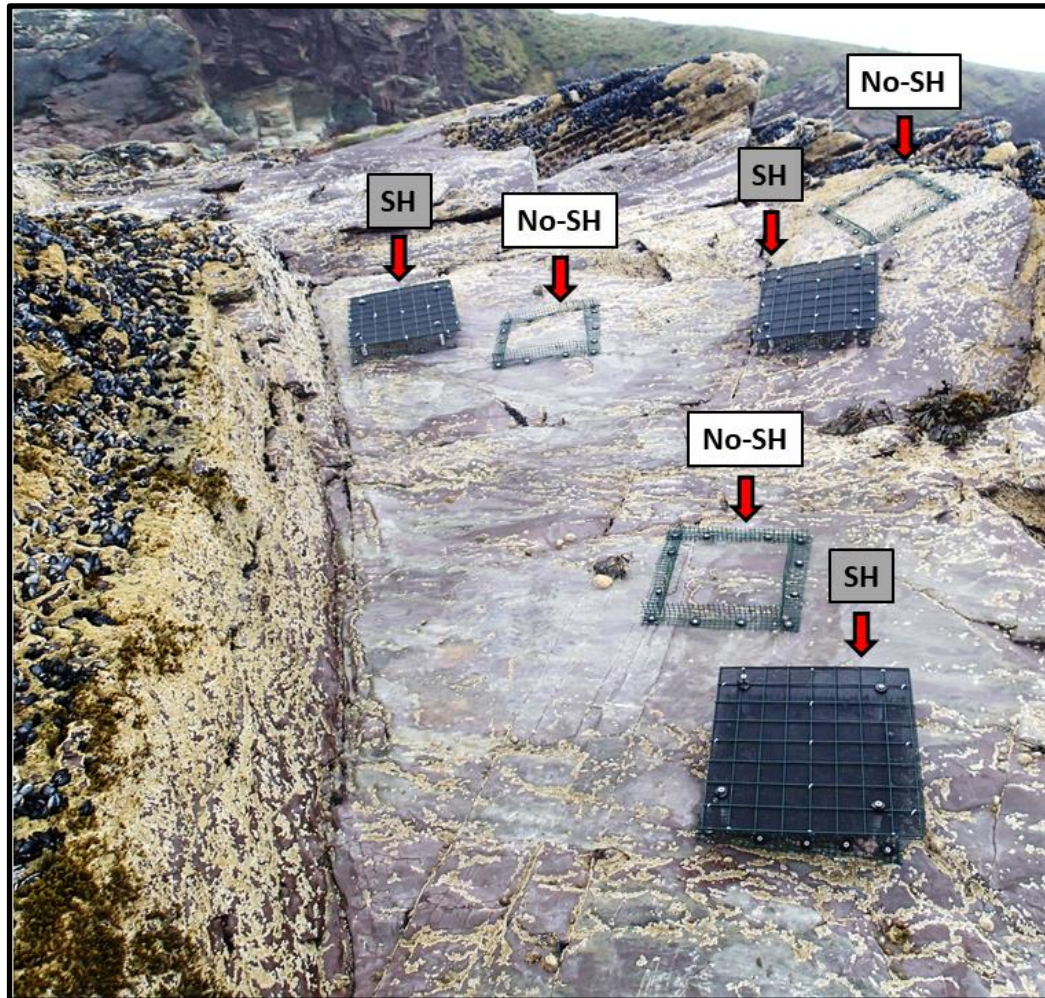
### 5.2.3. Effects of an Experimental Canopy on Limpet Interactions

In order to assess whether a thermal change has an impact on these competitive interactions of limpets at small-scales, temperature was manipulated with an experimental canopy. This approach has been widely used to modify natural conditions at small-scales (Wethey, 1984; Thompson *et al.*, 2004; Morelissen & Harley, 2007; Lamb *et al.*, 2014). The shades were made of a plastic mesh of 35 × 35 cm (opening size 2×1 mm; Netlon Insect Mesh, [www.tdponline.co.uk](http://www.tdponline.co.uk)) strapped to a PVC coated welded wire mesh (opening size 50×50 mm) with cable ties. The shades were attached to the rock ~ 7 cm above the substratum by means of stainless steel screw eyes anchored into the rock with wall anchors and cable ties. In each region, a temperature logger (Tidbit® v2 Temp, Onset HOB0, resolution 0.02 °C, USA) was attached inside a cage with and without experimental shade (*i.e.*, Criccieth in N-Wales and Trevone in S-West England). Thus temperature was recorded every 5 minutes over a year in both experimental units.

The experimental canopy was considered as a factor in the competitive experimental design (*i.e.*, Shade and No-Shade). Thus, five replicates per density treatment (10 treatments) were considered at each location (total number= 200 cages). Thus, 50 cages were monitored over one year-period at each location: 25 cages with Shade and 25 cages No-Shade (Table 5.1; Figure 5.3).

**Table 5.1.** Experimental design to evaluate both intra- and inter-specific competition between *Patella depressa* (PD) and *Patella vulgata* (PV) and the effect of an overlying shade simulating canopy (Shade / No-Shade) on these biological interactions. Low density= three limpets. High density= six limpets. Mix PD + PV = three PD + three PV (high density). Experimental layout was set up according to *P. depressa* densities in N-Wales, its poleward range edge in Britain.

Species	Shade / No-Shade			
	Single-Species PD		Mix PD+PV	Single-Species PV
Density Treatments	Low	High	High	Low      High



**Figure 5.3.** Picture of the experimental design in the field to evaluate both intra- and inter-specific competition between *P. depressa* and *P. vulgata* and the effect of an overlying shade simulating canopy (Shade [SH] / No-Shade [No-SH]) on these biological interactions. Plots with different limpet densities were  $30 \times 30 \times 5$  cm and placed into limpet patches at each locations (See section 5.2.2 and 5.2.3).

#### 5.2.4. Response Variables

The response variables measured over a period of 12-months were: 1) growth rates, 2) mortality, 3) available food measured as total biofilm chlorophyll concentration (*i.e.*, total biomass of green algae, cyanobacteria and diatoms). These three variables were used to quantify



the effects of intra- and inter-specific competition within and between *Patella depressa* and *Patella vulgata*.

In order to determine growth rates for both *Patella* species at different density treatments in each region, all individuals were double tagged using small waterproof numerical labels of 5 x 5 mm (Brady®, TMM-0-49-PK model, USA, <https://www.bradyid.com>). The initial size of individuals was measured at the beginning of the experiment (Sept/Oct 2016) with Vernier callipers to a resolution of 0.1mm. Two different colours of nail varnish were applied on shells for identification purposes. The maximum length of individuals was measured three-times over a period of ~12-months: 1) February/March 2017, 2) May/June 2017 and 3) September/October 2017.

In addition, after the experiment started (Sept/Oct 2016), densities were checked four-times in all treatment plots over same period of ~12-months: 1) November 2016, 2) February/March 2017, 3) May/June 2017 and 4) September/October 2017. Individuals lost through mortality were replaced by another limpet close to their same length, identified by the initial number assigned at the beginning of the experiment.

Furthermore, the concentration of microalgae was quantified with a benthic fluorometer BenthosTorch (see Aberle *et al.*, 2006; Resolution: 0.1 µg chl a / cm ; bbe-Moldaenke GmbH, Schwentinental, <https://www.bbe-moldaenke.de/en/>, Germany). Three sub-samples (area per measurement: 0.78 cm<sup>2</sup>) within each experimental plot were recorded three-times over a period of ~12-months: 1) February/March 2017, 2) May/June 2017 and 3) September/October 2017. For this variable, five additional un-manipulated plots were considered as controls around the area of the experiment at each location. Finally, at sampling date (*i.e.*, November 2016, February/March 2017, May/June 2017 and September/October 2017), other grazers and limpet recruits (if present) were removed from all plots.

#### 5.2.5. Comparisons between Intra- and Inter-Specific Competition

In order to distinguish the two types of competition between *Patella* species, comparisons among treatments were based on Underwood (1986). This was based on the assumption that the two species have similar resource requirements (Hawkins *et al.*, 1989; Thompson *et al.*, 2000; Boaventura *et al.*, 2002b, 2003) and resources are limiting (Jenkins & Hartnoll, 2001; Jenkins *et al.*, 2001; Boaventura *et al.*, 2002ab, 2003; Thompson *et al.*, 2004, 2010). Thus, to evaluate



intra-specific competition within limpet species, statistical analyses were based on comparisons between both low and high densities for single-species treatments (Table 5.2). Thus, these two intra-specific comparisons were: 1) Low-Single *P. depressa* vs. High-Single *P. depressa* and 2) Low-Single *P. vulgata* vs. High-Single *P. vulgata* (Table 5.2). In contrast, in order to assess inter-specific competition, statistical analyses were based on comparisons between both single- and mixed-species at high densities treatments (Table 5.2). Therefore, these two inter-specific comparisons were: 1) High-Single *P. depressa* vs. High-Mixed species; and 2) High-Single *P. vulgata* vs. High-Mixed species (Table 5.2).

**Table 5.2.** Experimental comparisons to distinguish both intra- and inter-specific competition between *Patella depressa* (PD) and *Patella vulgata* (PV) at different overlapping zones in Britain. These comparisons were based on Underwood (1986) to test competition for species that have similar resource requirements and when they are in short supply (Jenkins & Hartnoll, 2001; Jenkins *et al.*, 2001; Boaventura *et al.*, 2002ab, 2003; Thompson *et al.*, 2004, 2010). Statistical comparison for Shade and No-Shade treatments were made by separately.

		Experimental Treatments						
Competition		Single-Species PD			Single-Species PV			Mix PD+PV
Density	Intra- <i>spp.</i>	Low	vs.	High	Low	vs.	High	-
	Inter- <i>spp.</i>	High		vs.	High		vs.	High

### 5.3. STATISTICAL ANALYSIS

In order to determine whether growth and mortality rates as well as total biofilm concentration are affected by competitive interaction between both *Patella* species, Generalized Linear Mixed models (GLMMs) analyses were performed for each variable. Responses variables were analysed using different family errors: Gamma identity for growth rates and total biofilm concentration; and Binomial for mortality rates, respectively (Bolker *et al.*, 2009).

Temporal non-independence was included in the analysis (*i.e.*, repeated measures, Bolker *et al.*, 2009; Zuur *et al.*, 2009). The repeated measures analysis refers to multiple measurements made on the same experimental unit (over time or space) to account for the lack of independence between measurements (*i.e.*, each tagged limpet and each plot; Bolker *et al.*, 2009; Zuur *et al.*,

2009). Thus, for growth rate analysis, the repeated measures were both each tagged limpet (n=960) and each experimental plot (n=200). For mortality and biofilm analyses, the only repeated measure considered was each plot (n=200). These factors (repeated measures) were added as random factors into each analysis. In addition, three fixed factors were included: 1) Region, with two levels: N-Wales, S-West; 2) Species, with two levels: *P. depressa* and *P. vulgata* and 3) the experimental canopy, with two levels: Shade and No-Shade. Additionally, Location was a nested random factor within Region.

Diagnostic plots (*i.e.*, histograms of residuals and residuals vs. linear predictor) to evaluate both model fitness and statistical assumptions of residuals were used (Zuur *et al.*, 2009, 2010). For each response variable, when interaction terms were significant ( $\alpha = 0.05$ ), Tukey post-hoc tests were carried for multiple pairwise comparisons. All statistical analyses were done in the CRAN R project (R Development Core Team 2014). The “lme4” package (*i.e.*, Linear Mixed-Effects Models using 'Eigen' and S4) to fit each GLMM was useful. Tukey post hoc tests were carried out using the “emmeans” package (*i.e.*, Estimated Marginal Means, Least-Squares Means).

## 5.4. RESULTS

### 5.4.1. Initial Limpet Density and Size

Before the experiment started (June and July 2016), initial conditions of limpet density showed that the abundance of *Patella depressa* in poleward populations was lower compared to those in S-West England at mid-shore levels (Figure 5.2). The mean of individuals of *P. depressa* in its polewards populations was ~ 3 individuals in quadrats of 30 x 30 cm (Figure 5.2). In contrast, *Patella vulgata* occurred at higher densities than *P. depressa* across regions, but in locations in S-West England both species reached similar levels of abundance (Figure 5.2).

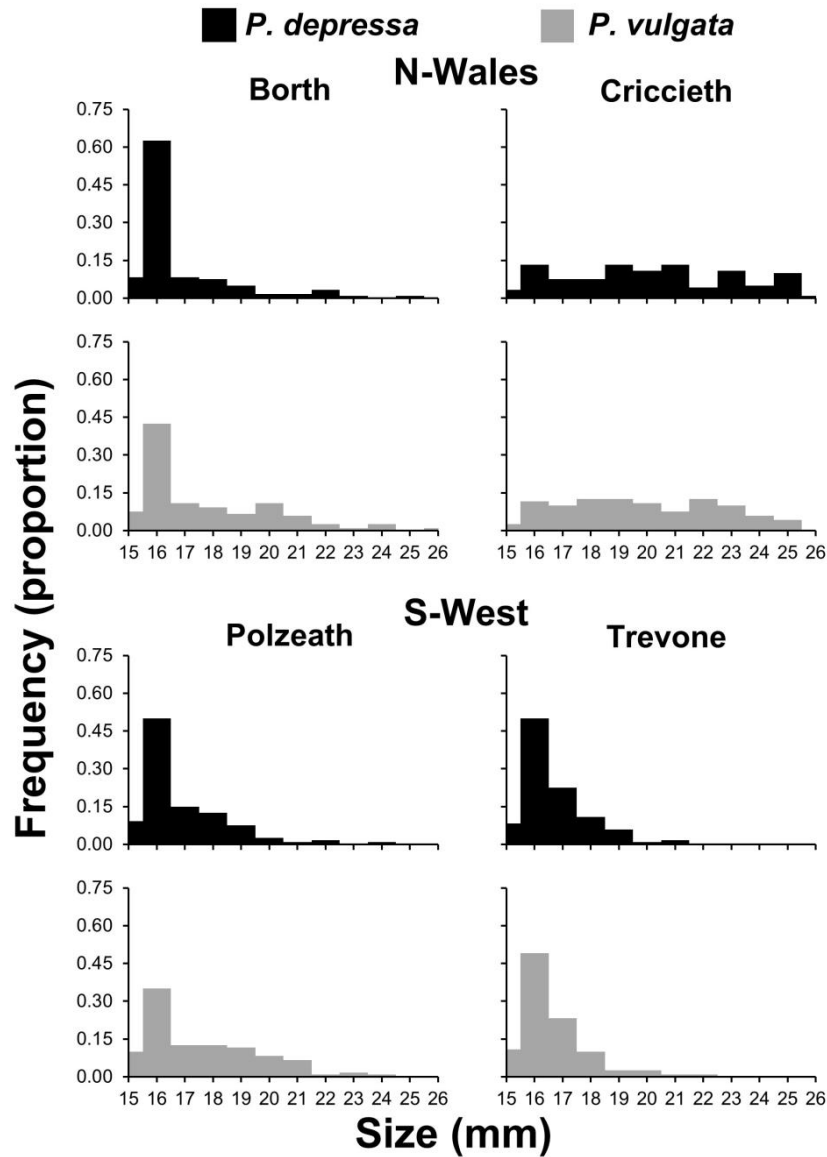
The size range of limpets selected to determine intra- and inter-specific effects in *Patella* species varied across poleward and central population of *Patella depressa* (Figure 5.4). However, frequency histograms showed that most of the individuals selected were between 15 and 20 mm in length at all locations (Figure 5.4). However, larger sizes were more common in N-Wales, particularly in Criccieth (Figure 5.4). Although *P. depressa* represents only 20% of limpet populations in North Wales (Chapter 2), the range of length between both *Patella* species was similar, between 15 and 25 mm (Figure 5.4).

### 5.4.2. Temperature in Shade and No-Shade Treatments

The temperature data loggers showed that at both locations temperatures were hotter and more variable in the open than under the shades which were cooler and less variable (Figure 5.5). There were less differences in minimum temperatures with shading (Figure 5.5). In N-Wales, the maximum temperature recorded between November 2016 and late-February 2017 under shading did not reach more than 10°C (Figure 5.5). In contrast, during the same period, in S-West England, shading treatment exceeded 10°C and even reaching temperatures close to 15°C.

### 5.4.3. Inter-Specific Effects on Growth and Mortality of *Patella* Species

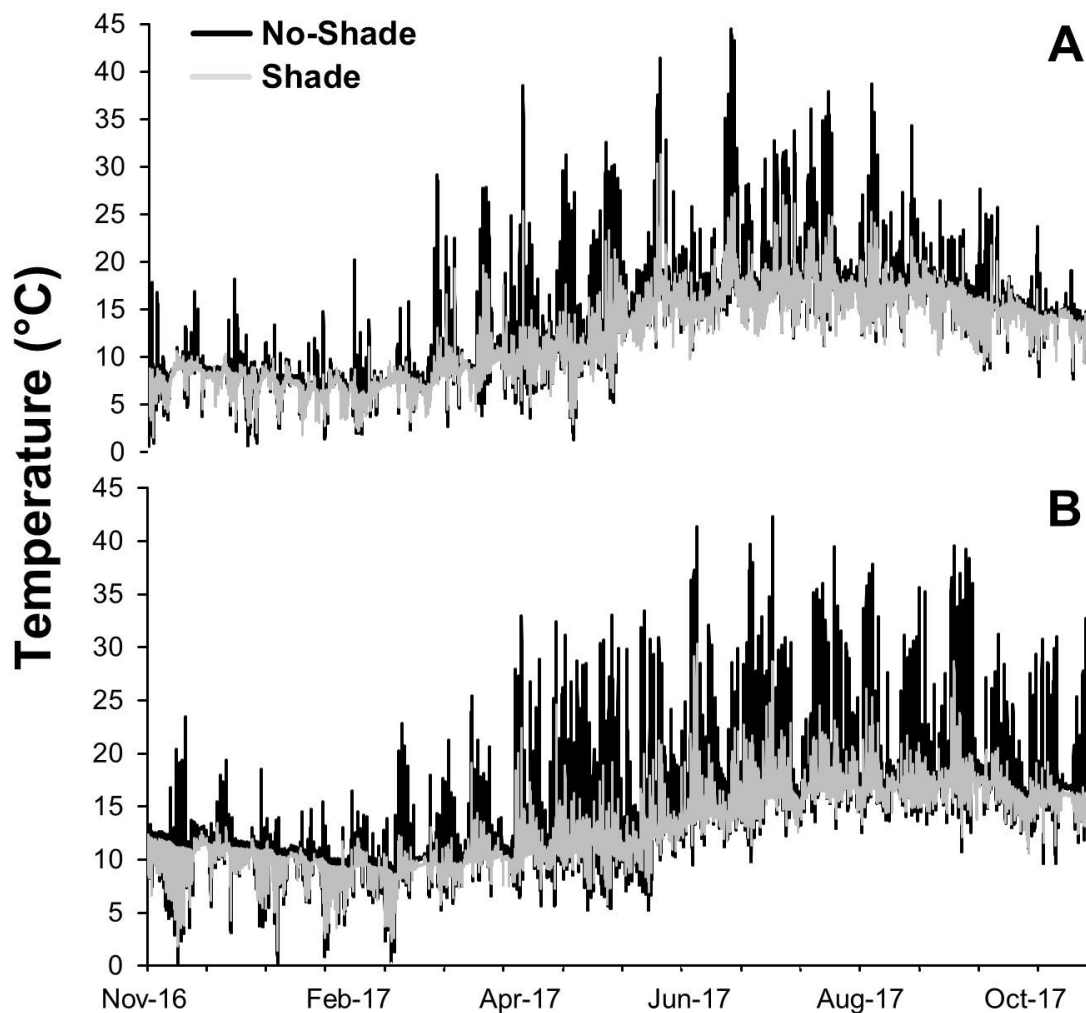
After a one year period of monitoring between October 2016 and October 2017 on the experiment across locations, inter-specific competition between *Patella depressa* and *Patella vulgata* affected the mean growth rates on both limpets species (Figure 5.6. A). The analysis showed a four-way interaction term among Region, Species, Shade and Focal species factors (Table 5.3). Thus, the comparison between mixed- and single-species treatments indicated that mean growth of *P. depressa* was strongly affected by the addition of its competitor *P. vulgata*,



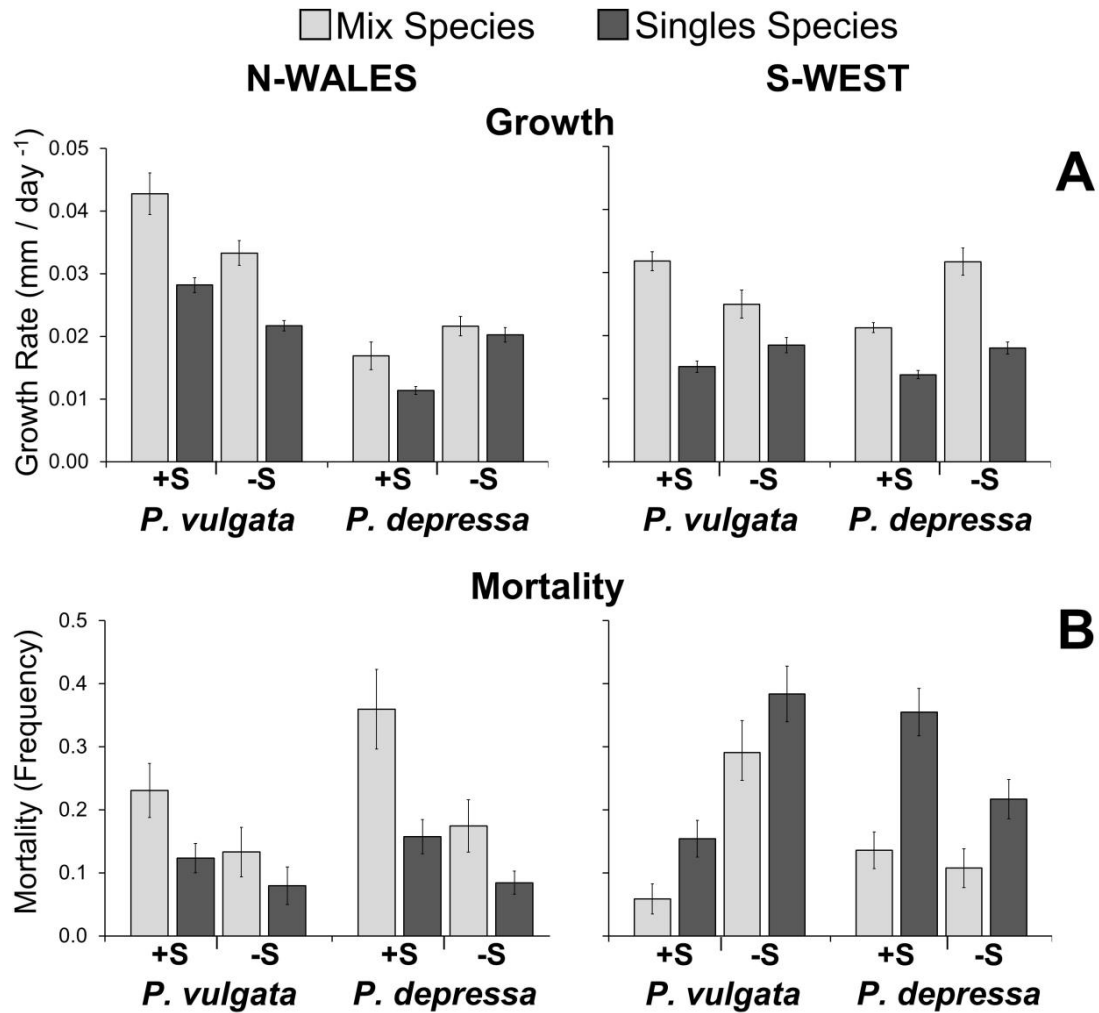
**Figure 5.4.** Frequency (proportion) of individual initial sizes (maximum length, separated by 1 mm) used to measure intra- and inter-specific competition between *P. depressa* and *P. vulgata* at each location separated by region (June/July 2016). n = 120 individuals per *Patella* species and location.

particularly on shading treatment in its range edge in N-Wales, when compared with plots in S-West England (Figure 5.6. A, Table 5.3). Although in single-species treatment the mean growth of *P. depressa* seems to be slightly reduced compared to mixed-species ones, the difference in growth of *P. depressa* is much higher in mixed -species treatment (Figure 5.6. A). In fact, individuals of *P. vulgata* beneath shading in N-Wales reached the greatest growth rate recorded

along the experiment, thereby, reducing growth in *P. depressa* (Figure 5.6. A). In contrast, *P. depressa* had lower growth performance in treatments with Shade, particularly in both mixed and single-species plots in N-Wales, when compared with more central populations (Figure 5.6. A, Table 5.3). Thus, these patterns suggest a strong effect of inter-specific competition on growth performance of individuals of *P. depressa* with its direct competitor *P. vulgata*, which is intensified by shade conditions in poleward locations of its distribution (Figure 5.6. A).



**Figure 5.5.** Temperature (°C) recorded every 5 minutes over a one year period under No-Shade and Shade conditions in (A) Criccieth (n=1; N-Wales) and (B) Trevone (n=1; S-West England). Tidbit® v2 Temp, Onset HOBO, resolution 0.02 °C, USA.



**Figure 5.6.** Effects of inter-specific competition (Mixed [light] versus Single [dark] species plots) on (A) mean growth rates ( $\pm$  SE) and (B) mean mortality ( $\pm$  SE) of both *Patella species* and its modulation by shading (+S and -S) in poleward (N-Wales) and more central populations (S-West England) of *P. depressa* in Britain. For growth rates, each bar corresponds to the mean of growth in length measured at three times after the experiment started (Sept/Oct 2016) over a year-period: 1) Feb/Mar 2017, 2) May/Jun 2017 and 3) Sep/Oct 2017. For mortality, each bar correspond to the mean of proportion of mortality measured in Nov 2016, Feb/Mar 2017, May/Jun 2017 and Sep/Oct 2017.

**Table 5.3.** Effects of inter-specific competition on growth rates in *Patella species* and its modulation by shading at poleward and central populations assessed by Tukey post-hoc test ( $\alpha=0.05$ ). Differences were indicates by a four-way interaction: Region (N-Wales and S-West), Species (*P. depressa* and *P. vulgata*), Shade (+ S and - S) and Focal species (Mix and Single). Significant terms are highlighted by **bold** and *italic type*.

Contrast				Combination				Estimate	SE	Zratio	P-value
Factor	Levels			Species	Shade	Focal-spp.	Region				
Region	S-West	vs.	N-Wales	<i>P. depressa</i>	- S	Mix		0.010	0.001	7.58	< <b>0.001</b>
				<i>P. vulgata</i>	- S	Mix		-0.009	0.002	-5.62	< <b>0.001</b>
				<i>P. depressa</i>	+ S	Mix		0.007	0.002	4.65	< <b>0.001</b>
				<i>P. vulgata</i>	+ S	Mix		-0.012	0.002	-5.54	< <b>0.001</b>
				<i>P. depressa</i>	- S	Single		-0.001	0.001	-0.89	1.000
				<i>P. vulgata</i>	- S	Single		-0.005	0.001	-3.14	<b>0.046</b>
				<i>P. depressa</i>	+ S	Single		0.002	0.002	1.09	0.996
				<i>P. vulgata</i>	+ S	Single		-0.013	0.002	-5.58	< <b>0.001</b>
Species	<i>P. vulgata</i>	vs. <i>P. depressa</i>		- S	Mix	N-Wales	0.014	0.001	12.13	< <b>0.001</b>	
				- S	Mix	S-West	-0.006	0.001	-4.28	< <b>0.001</b>	
				+ S	Mix	N-Wales	0.029	0.001	20.03	< <b>0.001</b>	
				+ S	Mix	S-West	0.010	0.002	5.87	< <b>0.001</b>	
				- S	Single	N-Wales	0.002	0.001	1.35	0.970	
				- S	Single	S-West	-0.001	0.002	-0.90	1.000	
				+ S	Single	N-Wales	0.016	0.002	8.86	< <b>0.001</b>	
				+ S	Single	S-West	0.001	0.002	0.54	1.000	
Shade	- S	vs.	+ S	<i>P. depressa</i>		Mix	N-Wales	-0.007	0.001	-6.08	< <b>0.001</b>
				<i>P. depressa</i>		Mix	S-West	-0.010	0.002	-6.34	< <b>0.001</b>
				<i>P. vulgata</i>		Mix	N-Wales	0.009	0.002	5.58	< <b>0.001</b>
				<i>P. vulgata</i>		Mix	S-West	0.006	0.002	3.05	0.064
				<i>P. depressa</i>		Single	N-Wales	-0.008	0.001	-5.45	< <b>0.001</b>
				<i>P. depressa</i>		Single	S-West	-0.004	0.002	-2.52	0.252
				<i>P. vulgata</i>		Single	N-Wales	0.006	0.002	3.44	<b>0.017</b>
				<i>P. vulgata</i>		Single	S-West	-0.002	0.002	-0.93	0.999
Focal spp.	Mix	vs.	Single	<i>P. depressa</i>	- S		N-Wales	-0.001	0.001	-0.98	0.999
				<i>P. depressa</i>	- S		S-West	-0.013	0.002	-8.43	< <b>0.001</b>
				<i>P. vulgata</i>	- S		N-Wales	-0.013	0.002	-8.52	< <b>0.001</b>
				<i>P. vulgata</i>	- S		S-West	-0.008	0.002	-4.60	< <b>0.001</b>
				<i>P. depressa</i>	+ S		N-Wales	-0.002	0.002	-1.42	0.954
				<i>P. depressa</i>	+ S		S-West	-0.008	0.002	-3.86	<b>0.003</b>
				<i>P. vulgata</i>	+ S		N-Wales	-0.016	0.002	-7.78	< <b>0.001</b>
				<i>P. vulgata</i>	+ S		S-West	-0.016	0.002	-6.92	< <b>0.001</b>

On the other hand, inter-specific effects on limpets mortality were not as clear as for limpet growth performance (Figure 5.6. B, Table 5.4). However, the analysis indicated three different significant terms (Table 5.4. A, B, C). Thus, the interactions between the factors: Region and Focal species (Table 5.4. A); Region and Shade (Table 5.6. B); Shade and Species (Table 5.4. C) showed significant differences in mortality proportion between both *Patella* species. Thus, mortality of both *Patella* species was higher in mixed-species than single-species treatment in N-Wales when compared with S-West England (Figure 5.6. B; Table 5.4. A). In

contrast, single-species treatment revealed higher mortality than mixed-species ones in S-West England than N-Wales (Figure 5.6. B). These patterns suggest inter-specific effects on mortality of limpet in N-Wales populations; in contrast, intra-specific effects in S-West England populations. (Figure 5.6. B). The experimental canopy showed opposite patterns of limpet mortality between regions (Figure 5.6. B; Table 5.4. B). In N-Wales, mortality of limpets were higher in Shade treatment, particularly for those individuals of *P. depressa* in mixed plots with *P. vulgata* (Figure 5.6. B). In contrast, in S-West England, no-shading treatment indicated greater limpet mortality, specifically for those individuals of *P. vulgata* in singles-species treatment (Figure 5.6. B). In addition, the experimental canopy also indicated opposite patterns of mortality between *Patella* species (Figure 5.6. B; Table 5.4. C). Whilst *P. depressa* had higher mortality of individuals in Shade than No-Shade treatments, *P. vulgata* showed lower mortality in cages with Shade than No-Shade (Table 5.4. C).

#### **5.4.4. Inter-Specific Effects of *Patella* Species on Microalgal Biofilm**

The microalgal biomass (biofilm) measured did not show differences between inter-specific treatments across all regions ( $P > 0.05$ ). However, the experimental shade was effective in modifying the biofilm biomass when compared with No-Shade treatments ( $P = 0.005$ ). Treatments under Shade showed higher concentration of biofilm measured as biomass, particularly in N-Wales (Figure 5.7).

#### **5.4.5. Intra-Specific Effects on Growth and Mortality of *Patella* Species**

Both *Patella* species showed lower growth rates in high density treatments in the two regions irrespective of whether shaded or not (Figure 5.8. A), suggesting intra-specific effects on limpets populations. The analysis did not, however, identify statistically significant intra-specific effects on growth rates of *Patella depressa* and *Patella vulgata* (Table 5.5). Thus, the analysis showed a three-way interaction term between Region, Species and Shade factors (Table 5.5). The comparison between regions indicated that individuals of *P. vulgata* had higher growth rates in N-Wales when compared with S-West England in Shade treatments (Figure 5.8. A; Table 5.5). Between *Patella* species, individuals of *P. depressa* showed lower growth rates in both No-Shade and Shade treatments than *P. vulgata* in N-Wales (Figure 5.8. A; Table 5.5). However, growth rates of *P. depressa* in shading were more affected when compared with no-shading treatment at its poleward limits in N-Wales (Figure 5.8. A; Table 5.5). In fact, in No-Shade



treatments, individuals of *P. depressa* have revealed greater growth rates in both central and northern populations (Figure 5.8. A; Table 5.5).

**Table 5.4.** Effects of inter-specific competition on mortality rates in *Patella species* and its modulation by shading at poleward and central populations assessed by Tukey post-hoc test ( $\alpha=0.05$ ). Differences were indicated by a four-way interaction: Region (N-Wales and S-West), Species (*P. depressa* and *P. vulgata*), Shade (+ S and - S) and Focal species (Mix and Single). Significant terms are highlighted by **bold** and *italic type*.

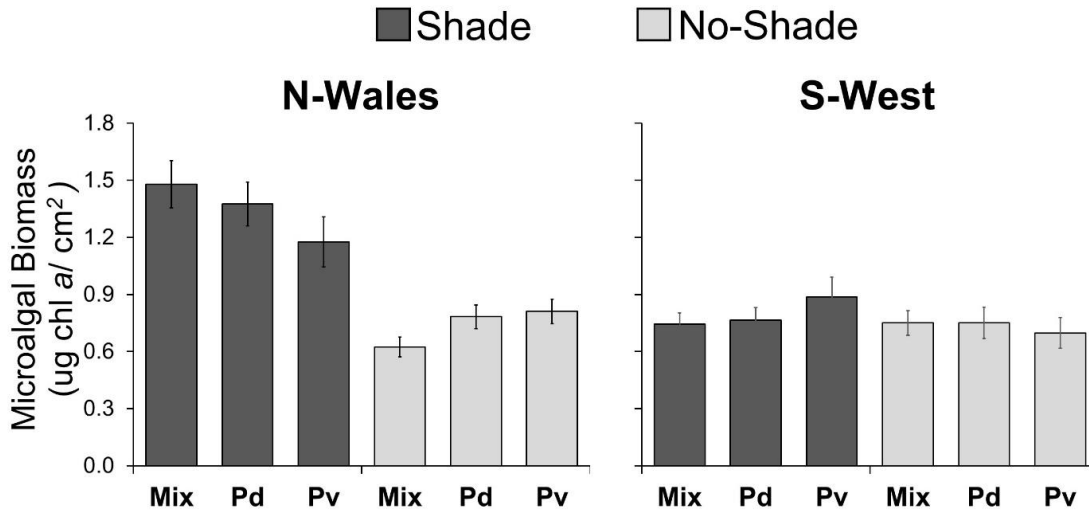
<b>A</b>								
Contrast				Combination				
Factor	Levels			Focal spp.	Region	Estimate	SE	P-value
Region	N-Wales	vs.	S-West	Mix		-0.426	0.263	0.316
				Single		0.923	0.227	< <b>0.001</b>
Focal spp.	Mix	vs.	Single		N-Wales	0.004	0.181	1.000
					S-West	1.353	0.178	< <b>0.001</b>

<b>B</b>								
Contrast				Combination				
Factor	Levels			Shade	Region	Estimate	SE	P-value
Region	N-Wales	vs.	S-West	- S		0.702	0.245	<b>0.016</b>
				+ S		-0.205	0.242	0.801
Shade	- S	vs.	+ S		N-Wales	0.556	0.183	<b>0.009</b>
					S-West	-0.351	0.171	0.135

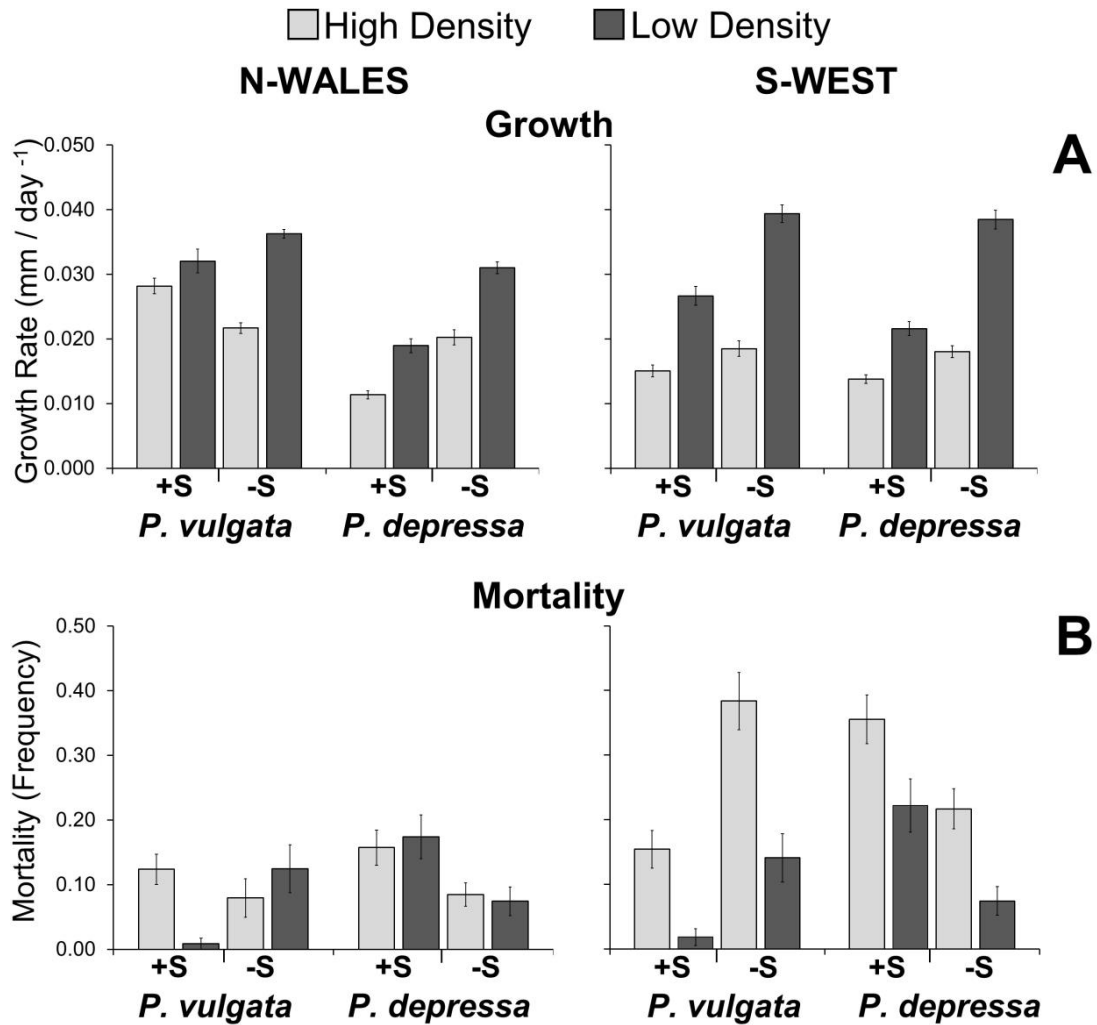
  

<b>C</b>								
Contrast				Combination				
Factor	Levels			Species	Shade	Estimate	SE	P-value
Shade	- S	vs.	+ S	<i>P. vulgata</i>		-0.346	0.171	0.141
				<i>P. depressa</i>		0.551	0.165	<b>0.003</b>
Species	<i>P. vulgata</i>	vs.	<i>P. depressa</i>		- S	0.357	0.158	0.082
					+ S	-0.540	0.153	<b>0.002</b>



**Figure 5.7.** Effects of inter-specific competition between both *Patella* species (Pd= *P. depressa*; Pv= *P. vulgata*) on mean microalgal biomass ( $\pm$  SE) and its modulation by shading (+S and -S) in poleward (N-Wales) and central populations (S-West England) of *P. depressa* in Britain. Each bar corresponds to the mean of microalgal biomass measured on three occasions after the experiment started (Sept/Oct 2016) over a year-period: 1) Feb/Mar 2017, 2) May/Jun 2017 and 3) Sep/Oct 2017.

In contrast to growth rates of limpets, intra-specific comparison showed an impact on limpet mortality. A three-way significant interaction term was found between Species, Density and Shade factors (Table 5.6). Although mortality rates in both *Patella* species seemed to be higher in S-West England than N-Wales (Figure 5.8. B), differences were not found between central and poleward populations of *P. depressa* (Table 5.6). Thus, individuals of *Patella vulgata* were more affected by mortality in high- than low- limpet density treatment, particularly in No-Shade treatment (S-West England; Figure 5.8. B, Table 5.6). This suggests an intense intra-specific competition between individuals of *P. vulgata* particularly in treatments with high density of conspecific in no-shading habitats. Further, individuals of *Patella depressa* were strongly affected by Shade factor either both high or low density treatments (Figure 5.8. B; Table 5.6).



**Figure 5.8.** Effects of intra-specific competition (High [light] versus Low [dark] densities) on (A) mean growth rates ( $\pm$  SE) and (B) mean mortality ( $\pm$  SE) of both *Patella species* and its modulation by shading (+S and -S) in poleward (N-Wales) and more central populations (S-West England) of *P. depressa*. For growth rates, each bar corresponds to the mean of growth in length measured at three times after the experiment started (Sept/Oct 2016) over a year-period: 1) Feb/Mar 2017, 2) May/Jun 2017 and 3) Sep/Oct 2017. For mortality, each bar correspond to the mean of proportion of mortality measured in Nov 2016, Feb/Mar 2017, May/Jun 2017 Sep/Oct 2017.

**Table 5.5.** Effects of intra-specific competition on growth rates in *Patella species* and its modulation by shading at poleward and central populations assessed by Tukey post-hoc test ( $\alpha=0.05$ ). Differences were indicates by a three-way interaction: Region (N-Wales and S-West), Species (*P. depressa* and *P. vulgata*) and Shade (+ S and - S). Significant terms are highlighted by **bold** and *italic type*.

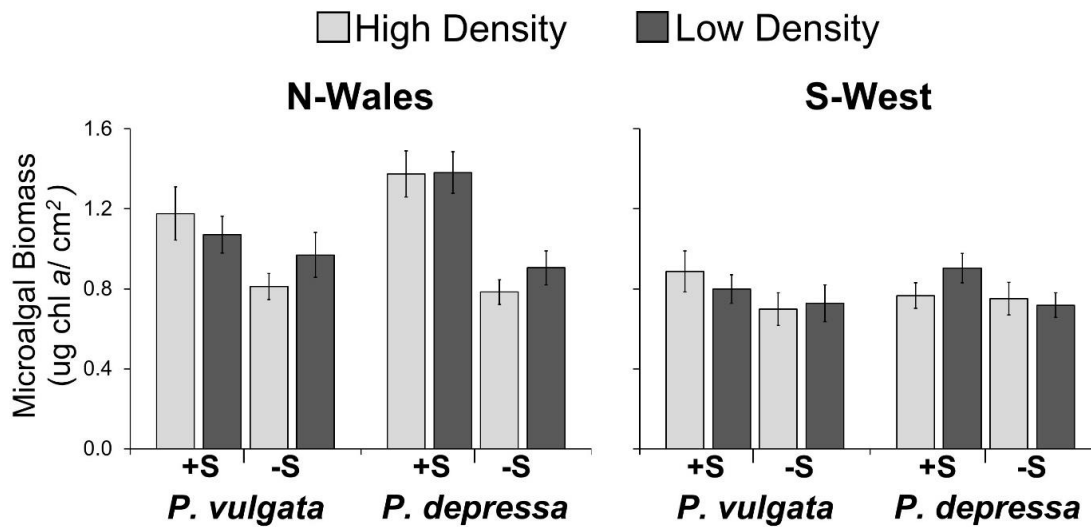
Contrast				Combination				Estimate	SE	Z ratio	P-value
Factor	Levels			Species	Shade	Region					
Region	S-West	vs.	N-Wales	<i>P. depressa</i>	- S			0.003	0.001	2.18	0.255
				<i>P. vulgata</i>	- S			-0.001	0.001	-0.94	0.965
				<i>P. depressa</i>	+ S			0.002	0.001	1.49	0.717
				<i>P. vulgata</i>	+ S			-0.009	0.002	-5.71	< <b>0.001</b>
Species	<i>P. vulgata</i>	vs.	<i>P. depressa</i>		- S	N-Wales		0.003	0.001	3.01	<b>0.028</b>
					- S	S-West		0.000	0.001	-0.29	1.000
					+ S	N-Wales		0.014	0.001	10.43	< <b>0.001</b>
					+ S	S-West		0.003	0.002	1.95	0.391
Shade	- S	vs.	+ S	<i>P. depressa</i>		N-Wales		-0.010	0.001	-8.91	< <b>0.001</b>
				<i>P. depressa</i>		S-West		-0.011	0.001	-7.60	< <b>0.001</b>
				<i>P. vulgata</i>		N-Wales		0.000	0.001	0.31	1.000
				<i>P. vulgata</i>		S-West		-0.007	0.002	-4.59	< <b>0.001</b>

**Table 5.6.** Effects of intra-specific competition on mortality rates in *Patella species* and its modulation by shading at poleward and central populations assessed by Tukey post-hoc test ( $\alpha=0.05$ ). Differences were indicates by a three-way interaction: Species (*P. depressa* and *P. vulgata*), Density (High and Low) and Shade (+ S and - S). Significant terms are highlighted by **bold** and *italic type*.

Contrast				Combination				Estimate	SE	Z ratio	P-value
Factor	Levels			Density	Species	Shade					
Species	<i>P. vulgata</i>	vs.	<i>P. depressa</i>	High		- S		0.410	0.179	2.29	0.182
				Low		- S		0.579	0.309	1.87	0.413
				High		+ S		-0.610	0.173	-3.53	<b>0.004</b>
				Low		+ S		-2.693	0.603	-4.47	< <b>0.001</b>
Density	High	vs.	Low		<i>P. depressa</i>	- S		-0.51595	0.2827	-1.83	0.447
					<i>P. vulgata</i>	- S		-0.34732	0.2242	-1.55	0.648
					<i>P. depressa</i>	+ S		-0.22869	0.1933	-1.18	0.875
					<i>P. vulgata</i>	+ S		-2.31183	0.5969	-3.87	<b>0.001</b>
Shade	- S	vs.	+ S	High	<i>P. depressa</i>			0.674822	0.1757	3.84	<b>0.001</b>
				Low	<i>P. depressa</i>			0.962081	0.2929	3.29	<b>0.010</b>
				High	<i>P. vulgata</i>			-0.34531	0.1814	-1.90	0.393
				Low	<i>P. vulgata</i>			-2.30982	0.6109	-3.78	<b>0.002</b>

#### 5.4.6. Intra-Specific Effects of *Patella* Species on Microalgal Biofilm

As for inter-specific competition, the microalgal biomass (biofilm) measured did not show differences between intra-specific treatments of limpets across all regions ( $P > 0.05$ ). However, the experimental shade was effective in modifying biofilm biomass when compared with No-Shade treatments ( $P = 0.002$ ). Treatments under Shade showed higher concentrations of biofilm measured as biomass, particularly in N-Wales, in plots where *P. depressa* was present (Figure 5.9).



**Figure 5.9.** Effects of intra-specific competition (High [light] versus Low [dark] densities) between both *Patella* species on mean microalgal biomass ( $\pm$  SE) and its modulation by shading (+S and -S) in poleward (N-Wales) and more central populations (S-West England) of *P. depressa* in Britain. Each bar corresponds to the mean of microalgal biomass measured on three occasions after the experiment started (Sept/Oct 2016) over a year-period: 1) Feb/Mar 2017, 2) May/Jun 2017 and 3) Sep/Oct 2017.

## 5.5. DISCUSSION

### 5.5.1. Overall Finding

My experimental testing of competition between two limpet species was made in the northern fraction of the geographic distribution of the warm-water species *Patella depressa* (Crisp & Knight-Jones, 1954; Kendall *et al.*, 2004). In Chapter 2, I have shown that the abundance of *P. depressa* differed between central and peripheral populations in Britain. In S-West England, populations of *P. depressa* can reach ~ 50% of total limpets or even more, whereas in marginal populations in N-Wales they only make up ~20 % of total limpets (Chapter 2). I found intra- and inter-specific effects on individuals of *Patella vulgata* and *P. depressa* in both central and poleward populations of *P. depressa* in Britain. However, depending on the species performance traits (*i.e.*, measured as individual growth and population mortality) the effects of both competitive interactions can vary across regions. Thus, my results confirm the initial hypothesis that populations of *P. depressa* towards the range edge in N-Wales are modulated by inter-specific competition but mediated by small changes in temperature at small spatial scales. By contrast, *P. vulgata* was not affected by inter-specific competition, but intra-specific effects were detected especially in no-shading treatments.

### 5.5.2. Inter-Specific Effects on *Patella* Species across Range and Central Populations

As expected at the beginning of the experiment, individuals of *Patella depressa* at their range edge (N-Wales) showed lower growth performance than their competitor *Patella vulgata* in mixed-species treatments with shading (Figure 5.6. A). In fact, individuals of *P. vulgata* beneath shading in N-Wales reached the greatest growth rate recorded over the whole of the experiment, thereby affecting growth performance of *P. depressa* which never grew as big as *P. vulgata* (Evans, 1947). This suggests that *P. depressa* may be an inferior competitor especially in populations at their poleward limit (Hawkins *et al.*, 2009). However, in S-West England, growth rates of individuals of *P. vulgata* were still higher than *P. depressa*, but the difference was not so great as when comparing individuals at the range edge in N-Wales in shade conditions (Figure 5.6. A). In a similar experiment but without shading effects, at the equatorward limit of *P. vulgata* in Portugal, Boaventura *et al.* (2002b) tested inter-specific competition where *P. depressa* and *P. vulgata* occurs at similar densities. After five months of monitoring, they did not find significant effects of the presence of the other species on limpet mean length (Boaventura *et*

*al.*, 2002b). However, Boaventura *et al.*, (2002b) used individuals over 25 mm in length at the beginning of their experiment (Boaventura *et al.*, 2002b). By contrast, in my study (a year-period), initial size used varied between 15 and 25 mm. In Chapter 3, I showed that individuals of limpets over 25-30 mm do not have an active growing phase. It is possible that limpets from Portugal did not show inter-specific competition because of the initial sizes used (Boaventura *et al.*, 2002b).

On the other hand, limpet mortality was higher in the mixed-species treatment when compared with single-species treatments, particularly in N-Wales, the range edge of *Patella depressa* in Britain (Figure 5.6. B). The addition of *Patella vulgata*, particularly in shaded treatments had a stronger effect on mortality of *P. depressa* in its range edge in N-Wales, when compared with the presence of *P. vulgata* in mixed-species treatment in S-West England. In addition, whilst *P. depressa* had higher mortality in Shade than No-Shade treatments, *P. vulgata* showed lower mortality in shaded habitats (Figure 5.6. B). These patterns confirm the results reported by Moore *et al.* (2007a), where a local segregation of both *Patella* species is modulated by temperature amelioration of microhabitats at small spatial scales (Marzinelli *et al.*, 2011; Lima *et al.*, 2016).

Similar relationships between patellid species have been reported. For example, on the Chilean coast the northern limpet *Scurria viridula* (analogous with the southern limpet *Patella depressa*) uses flat and open-rocks during low-tide, whereas its congener *Scurria zebrina* (analogous with the northern limpet *Patella vulgata*) is commonly seen resting beneath the red alga *Mazzaella laminaroides* (Aguilera *et al.*, 2013, 2018). However, as mortality is affected by shading in some limpet species (Moore *et al.*, 2007a), other microhabitats (*e.g.*, open-rocks vs rock-pools) can also have different species responses to inter-specific competition. Firth *et al.* (2009) made an inter-species approach to understand the consequences of climate warming, pre-empting the potential arrival of *P. depressa* on the Irish coast. After six months of experimental monitoring, they found similar growth and mortality between both *P. vulgata* and *Patella ullyponensis* (a warm-water species) in Ireland, where *P. depressa* is absent (Crisp & Southward, 1953). Additionally, in the presence of *P. depressa*, there was no effect on growth of *P. vulgata* when both species co-occurred on open rocks in southern England (Firth *et al.*, 2009). In contrast, when *P. depressa* co-occurred in rock-pools with *P. vulgata* and *P. ullyponensis*, there was a negative effect on the growth of *P. vulgata*. Thus, different types of habitat can be

considered as refuges for a particular species at small spatial scales (Chapperon *et al.*, 2016; Lima *et al.*, 2016; Seabra *et al.*, 2016), which may have an important effect on inter-specific competition between *Patella* species, highlighting the importance of microhabitat within a larger scale (Firth *et al.*, 2008, 2009, 2010; Aguilera *et al.*, 2013; Shanks *et al.*, 2014; Lima *et al.*, 2016).

### 5.5.3. Intra-Specific Effects on *Patella* Species across Range and Central Populations

Although statistical analysis did not show intra-specific effects on growth rates of *Patella depressa* and *Patella vulgata*, there was a trend for both limpet species to show lower growth rates in high density treatments in every case in both regions irrespective of whether shaded or not. Over a large geographical scale, Jenkins *et al.* (2001) found that limpet density can be one or even two orders of magnitude higher at southern latitudes (*i.e.*, S-West Portugal) than northern latitudes (*i.e.*, Isle of Man), which suggests density-dependent processes may be important at southern latitudes. Based on my central question, this experimental approach was run according to the mean density of *P. depressa* in N-Wales (mean=3 per treatment plot), its poleward range edge, which is dominated by older and large individuals (Chapter 2 and Chapter 4). In contrast, Boaventura *et al.* (2002b, 2003) tested intra-specific competition in Portugal, but their densities used were almost the double or triple when compared to my study. Therefore, it is highly likely to find intra-specific effects on growth of limpet species in Portugal (Boaventura *et al.*, 2002b, 2003), when compared with N-Wales populations, which is reflected by the smaller sizes of *Patella* species at southern latitudes than northern latitudes (Lewis *et al.*, 1982; Lewis, 1986).

In terms of mortality, intra-specific effects had an impact on *Patella vulgata*, particularly on individuals exposed to higher densities and no-shading conditions, which suggest the occurrence of strong intra-specific competition between individuals of *P. vulgata* in open habitats. Similar patterns have been described by Moore *et al.* (2007a) showing the consequences of *Fucus* removal in areas with high density of *P. vulgata* (*e.g.*, Marzinelli *et al.*, 2011). In contrast to *P. vulgata*, mortality of *Patella depressa* individuals were strongly affected by shading either in high or low density treatments. Others studies have suggested that effects of competition on survival of limpets may be indirect through exploitation of resources (*e.g.*, food or space; Branch, 1975, 1976, 1981) leading to increased mortality (Thompson *et al.*, 2000; Boaventura *et al.*, 2002b, 2003; Marzinelli *et al.*, 2011). Thus, if the quantity of resources in each area is equal, competition would be manifested by increases in mortality at higher densities



(Underwood, 1978). Further south in Portugal, Boaventura *et al.* (2003) found a reduction in mortality and higher growth rates at lower limpet density within or between size-classes of *P. depressa*. However, intra-specific effects were asymmetric between size-classes, showing greater effects of large limpets on both mortality and growth of small ones, but without any effect of small ones on larger ones. Their results suggest that the density of small limpets would be regulated by competitive interactions in areas where large limpets occur in high densities (Boaventura *et al.*, 2002b, 2003), as also occurs in populations of *P. vulgata* in Scotland (*e.g.*, Marzinelli *et al.*, 2011). However, these results differ from those described for the limpet *Cellana tramoserica* in southern Australia, where small limpets have a superior competitive ability compared to larger limpets (Marshall & Keough, 1994).

Limpet competitive interactions may also affect reproductive performance traits. The effect of competitive interactions on the output of gametes is likely to be important, due to possible influence on recruitment (Branch 1975, 1976, 1981). Intra-specific effects on phenological traits of *Patella* species suggest that neuter individuals (*i.e.*, individuals with no gonad development) form a greater proportion of the total population at high limpet densities, suggesting that the timing of the development of sexual maturity is sensitive to increases in abundance (Boaventura *et al.*, 2002b, 2003). The occurrence of only neuter individuals at high limpet densities suggests that competition suppresses the onset of reproduction, especially in individuals of *P. depressa* in Portugal (Boaventura *et al.*, 2002). Therefore, it is probable that gonadal development in *Patella* species is dependent on the intra-specific interactions, but is also modulated by climate variability (Moore *et al.*, 2011).

#### **5.5.4. Competitive Effects of Limpets on Microalgal Biofilm**

The availability of microalgal biofilm was assessed through determination of chlorophyll concentration (*e.g.*, Aberle *et al.*, 2006; Mrowicki & O'Connor, 2015). There was no evidence that food (*i.e.*, total of microalgal biomass) was a limited resource in all density treatments (*e.g.*, Boaventura *et al.*, 2002b, 2003; Marzinelli *et al.*, 2011). However, the highest concentration of biofilm was recorded in shade treatments in N-Wales, when *Patella depressa* was present, in both single- and mixed- species treatments. In general, shading effects modify local environmental conditions through reductions of light levels and stress by isolation (Reed & Foster, 1984; Jenkins *et al.*, 1999; Moore *et al.*, 2007a), resulting in higher concentrations of biofilm beneath them (Thompson *et al.*, 2004). In S-West England, there is evidence that *Patella*

*vulgata* has stronger effects in controlling macroalgal abundance than *P. depressa* (Moore *et al.*, 2007b), particularly during spring and summer when *P. depressa* is reproductively active (Orton *et al.*, 1956; Orton & Southward, 1961; Moore *et al.*, 2007b). In my study, higher concentration of biofilm can be explained by inter-specific effects on *P. depressa* in shaded plots in N-Wales. Thus, because it is a warm-water species, the lower temperatures in shade treatments may affect its growth and mortality, due to the lower metabolic rates under these conditions (Barry & Munday, 1959; Blackmore, 1969), when compared to individuals in unshaded areas (Moore *et al.* 2007a).

#### 5.5.5. Concluding Comments

Experimental approaches to tests the physical mediation of competition in setting species range edges remain scarce (Poloczanska *et al.*, 2008; Firth *et al.*, 2009; Coulson *et al.*, 2011). I examined experimentally the role of competition and shading effects in the current poleward range edge of the warm-water *Patella depressa* into the region occupied by its sibling cold-water species *Pulgata vulgata* in Britain. I showed that inter-specific competition with its closer competitor *P. vulgata* has reduced the performance traits of *P. depressa* mediated by lower temperatures at small-scales, which is expected to have an impact on populations to persist towards its leading edge in N-Wales. In northern latitudes, where warm- and cold-water species coexist, it is likely that the colder-water species may be competitively superior in terms of growth rates, and thereby in size (Hawkins *et al.*, 2009). This is certainly the case for barnacles and limpets: the cold-water barnacle *Semibalanus balanoides* grows faster and outcompetes warm-water species of *Chthamalus* (Connell, 1961; Poloczanska *et al.*, 2008), while *P. vulgata* grows faster and outperforms *P. depressa* (Evans, 1947; Thompson *et al.*, 2000; Boaventura *et al.*, 2002b; Moore *et al.* 2007ab).

Biotic interactions are not static in space and time (Gaston, 2009; Gilman *et al.*, 2010; Kordas & Dudgeon, 2011; Winz *et al.*, 2013) and can be linked with the impacts of changing climate (Sanford, 1999; Leonard 2000; Moore *et al.*, 2007b; Poloczanska *et al.*, 2008; Firth *et al.*, 2009; Aguilera *et al.*, 2018). In addition, they also can affect species response to abiotic changes, thereby determining large- and small-scale species distributions (Chappon *et al.*, 2016; Lima *et al.*, 2016; Seabra *et al.*, 2016). Therefore, a better understanding of the differences in competitive ability between *Patella* species over a large spatial scale, will improve our understanding of the influence of competition on species range dynamics.

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## **CHAPTER 6:**

### **Overview and Synthesis**

## 6.1. Overview

The intertidal zone of the European coast in general (see Phillipart *et al.*, 2011 for review), and the British and Irish coastlines in particular, present an excellent opportunity to study the effects of climate change on the geographic distribution of organisms for various reasons. The British Isles, Ireland and northern France sit astride a biogeographic boundary zone first described by Forbes (1858) (see also Hiscock, 1998; Hiscock *et al.*, 2004 for discussion). Climatic fluctuations over the last 120 years have been well described in the region, showing alternation of colder (1910s to 1920s, 1960s to 1980s) and warmer periods (1930s to 1950s; see Hawkins *et al.*, 2016) upon which recent anthropogenic warming has been superimposed (see Southward, 1980; Hawkins *et al.*, 2003; Hawkins *et al.*, 2016 for reviews). There is a rich historical record of species distributions and abundance on European continental coasts, with particularly detailed studies around Britain and Ireland (Forbes, 1858; Fischer-Piette, 1936, 1948; Crisp & Knight-Jones, 1954; Southward & Crisp, 1954ab; Southward & Crisp, 1956; Crisp & Southward, 1958; Crisp, 1964; Lewis, 1964). These include time series, albeit often interrupted (*e.g.*, Southward, 1967, 1991; Southward *et al.*, 1995, 2005) allowing effects of recent warming on marine systems (*e.g.*, Southward *et al.*, 1995). This has prompted re-surveys and restarts of time series showing responses to recent warming (Herbert *et al.*, 2003; Hiscock *et al.*, 2004; Mieszkowska *et al.*, 2005; Simkanin *et al.*, 2005; Helmuth *et al.*, 2006; Mieszkowska *et al.*, 2006; Herbert *et al.*, 2007; Mieszkowska *et al.*, 2007, Hawkins *et al.*, 2008; Herbert *et al.*, 2009; Mieszkowska *et al.*, 2009; Herbert, 2011; Philipart *et al.*, 2011; Wetthey *et al.*, 2011; Mieszkowska *et al.*, 2014; Firth *et al.*, 2015; Yesson *et al.*, 2015; Herbert *et al.*, 2016). The complex coastlines of France, the British Isles and Ireland (Forbes, 1858) provide multiple species range edges allowing additional insights into what ultimate and proximate factors are setting range edges (Hawkins *et al.*, 2009). This contrasts with the largely linear coastlines of North (Sagarin & Gaines, 2002a; Sagarin *et al.*, 2006) and South America (Broitman *et al.*, 2001), Southern Africa (McQuaid *et al.*, 2015) and Australia (Wernberg *et al.*, 2011).

As a consequence of global warming, complex interactions between factors in controlling species borders have been occurring (Bates *et al.*, 2014). Thus, recent studies of geographic ranges of species have turned towards their range edges because here species tend to be fragmented spatially (Mota *et al.*, 2014), reduced in abundances (Pearson *et al.*, 2009) and less diverse genetically (Eckert *et al.*, 2008; Nicastro *et al.*, 2013), and thereby more sensitive than

centre populations to environmental changes. Therefore, studying range-edge populations may be key in providing novel approaches in understanding how species are responding to rapid climate shifts (Gaston, 2003, 2009; Brown *et al.*, 1996; Helmuth *et al.*, 2006; Sexton *et al.*, 2009; Burrows *et al.*, 2014), enabling forecast (Hiscock *et al.*, 2004; Hawkins *et al.*, 2008, 2009) and prediction of future states (Svensson *et al.*, 2005; Lima *et al.*, 2007; Poloczanska *et al.*, 2008; Wetthey & Woodin, 2008; Kearney & Porte, 2009; Keith *et al.*, 2011; Jueterbock *et al.*, 2013; Poloczanska *et al.*, 2013, 2016).

It has long been widely accepted (Orton, 1920; Hutchins, 1947) that the abundance of a species reaches maximal values in the centre of its geographic range, where levels of physiological stress are assumed to be lowest, then decreasing towards the periphery (Brown, 1984). Thus, the Abundant-Centre Hypothesis (ACH; formalised by Brown, 1984) assumes environmental suitability is spatially auto-correlated such that species abundance is greatest where the environment is most favourable: at the species range centre. Direct empirical support for a decline in the abundance of species towards their distributional range-edges arises from studies of a diversity of taxa (*e.g.*, plants, insects, molluscs, fish, bird, mammals; see Gaston, 2003 for review). However observations do not always support this pattern (Sexton *et al.*, 2009). The underlying assumptions of the ACH (Brown, 1984) may be undermined by specific species life histories and environmental conditions which do not conform to the expected gradient with latitude (*e.g.*, Sagarin & Gaines 2002ab, Gilman, 2005; Rivadeneira & Fernandez 2005; Gilman, 2006ab; Helmuth *et al.*, 2006; Sagarin *et al.*, 2006; Herbert *et al.*, 2009; Hidas *et al.*, 2010; Fenberg & Rivadeneira, 2011; Herbert, 2011; Bates *et al.*, 2014; Ferreira *et al.*, 2015) as well as density-dependent processes acting at the population level (*e.g.*, Kendall & Lewis, 1986; Guo *et al.*, 2005; Jenkins *et al.*, 2005, 2008; Coulson *et al.*, 2011). There are a number of case studies, particularly on intertidal species (*e.g.*, Helmuth *et al.*, 2002, 2006), which have found conflicting patterns or less convincing evidence for the ACH (*e.g.*, Sagarin & Gaines 2002ab, Sagarin *et al.*, 2006). For example, Helmuth *et al.* (2002) have shown that patterns of local weather, wave height, and tidal regime interact between each other to create a thermal mosaic within a large scale along the west coast of the United States. Therefore, the ACH (Brown, 1984) may not be a good explanation of latitudinal patterns of abundance, particularly in those intertidal species, which do not show uni-modal abundance across their ranges (Helmuth *et al.*, 2002; Sagarin & Gaines, 2002ab; Helmuth *et al.*, 2006; Sagarin *et al.*, 2006) as predicted by Brown (1984).

I used patellid limpet species as model organisms to test the ACH (Brown, 1984) and explore what sets the range edge of *Patella* species in the North-East Atlantic (Lewis, 1964; Southward *et al.*, 1995). I focussed on the warm-water species *Patella depressa*, which reaches its northern limit in northern Europe and its congener, and putative competitor, the cold-water species *Patella vulgata*. I took advantage of the multiple range edges of *P. depressa* in the British Isles to test the ACH (Brown, 1984) at the both the individual and population level. I also tested the geographic variation in competitive interactions with its congener, *Patella vulgata* in Britain. In the remainder of this concluding chapter, I summarize my main findings and discuss potential explanations of what factors are setting poleward range edges in Britain with a special focus on *P. depressa*.

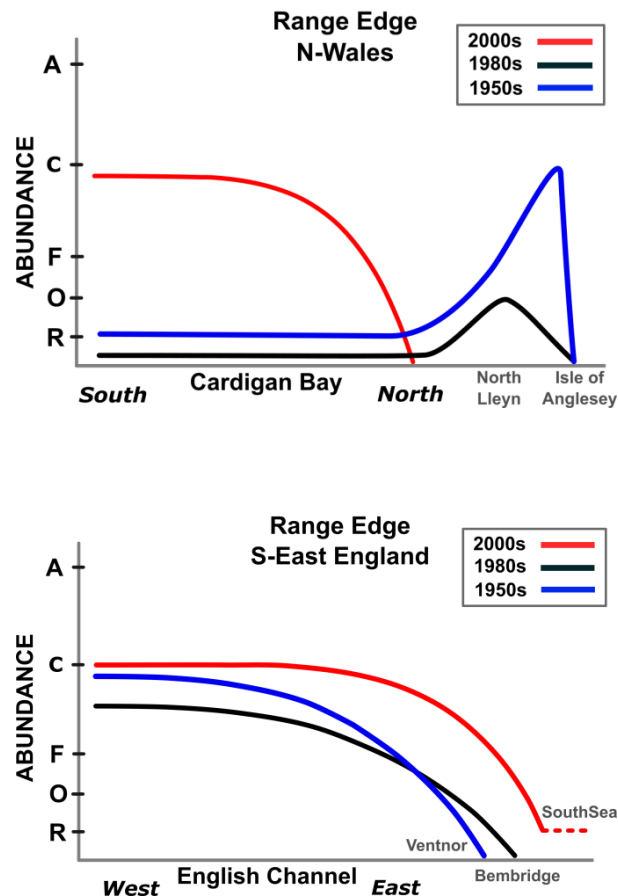
## 6.2. Summary of Main Findings

In Chapter 2, I have shown that at each of the poleward limits of the warm-water species *Patella depressa*, shifts have occurred in different ways over the past decades, evidenced by historical and current abundances in Britain. The Figure 6.1 shows changes in abundance and distribution of *P. depressa* towards both of its poleward edges in the last 60 years. Thus, the current range edge of *P. depressa* in North Wales (hereafter N-Wales) has not fully recovered to that occupied in the warm 1950s after the cooler 1960s to early 1980s (Crisp & Knight-Jones, 1954; Crisp & Southward, 1958). Nowadays breeding populations just reach the northern edge of Cardigan Bay and have not re-extended around the Llyn Peninsula. Scattered individuals are no longer found on Anglesey as in the early 1980s (Figure 6.1). On the other hand, in the English Channel, although abundance of *P. depressa* was less towards its range edge in the 1980s compared to the 1950s, its range has now extended on the east of the Isle of Wight (Fischer-Piette, 1936, 1948; Crisp & Southward, 1958; Kendall *et al.*, 2004; Keith *et al.*, 2011), now forming a breeding population at Southsea with scattered individuals being occasionally found further east as far as Beachy Head in the last decade (Figure 6.1; Hawkins comm. pers.).

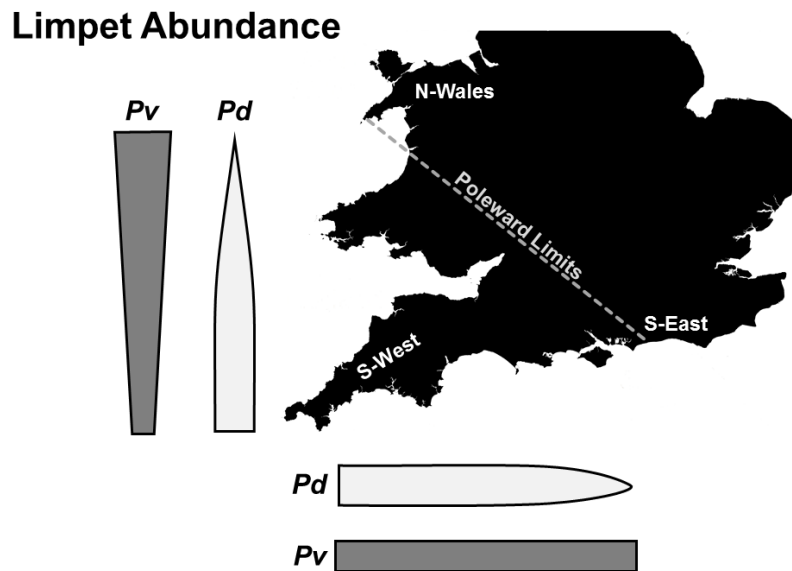
In addition, measures of limpet abundance (1980/2016) indicate that *Patella depressa* has had different abundance patterns towards the two leading edges in Britain (Figure 6.2). These different patterns of abundance of *P. depressa* show declines from central populations (ACH; Brown, 1984) but densities are much higher towards South-east England (hereafter S-East England) than N-Wales. *P. depressa* has been much less abundant in N-Wales when compared with population in S-East England in the last 35 years. In fact, in S-East England, the abundance



of *P. depressa* has been one or even three orders of magnitude higher than northern populations. In South-west England (hereafter S-West England), which represents central populations of *P. depressa*, comparable to its centre range in Portugal (Boaventura *et al.*, 2002, 2003), both *Patella* species tend to have equivalent patterns of abundance (Figure 6.2). For *P. vulgata*, there is a slight increase in abundance in N-Wales populations compared to the South-west England (Figure 6.2).

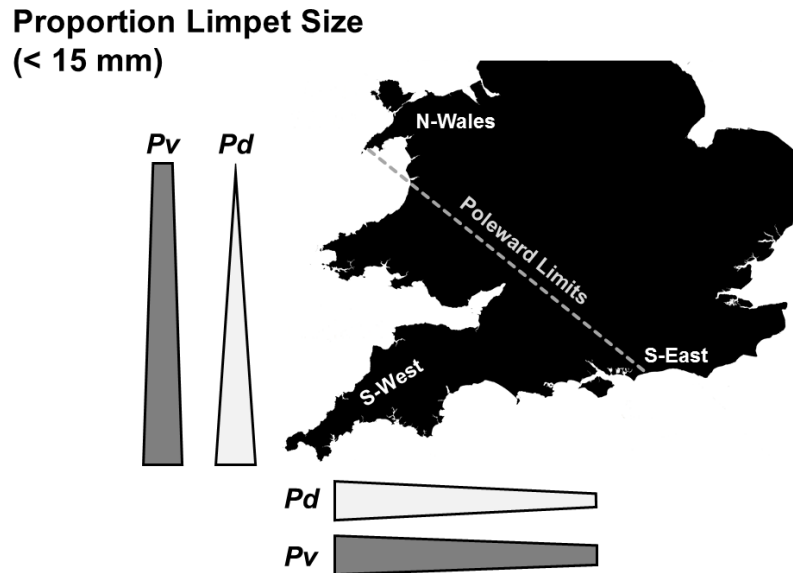


**Figure 6.1.** Schematic diagram of abundance and distribution of *P. depressa* in both poleward range edges in Britain. Abundance of *P. depressa* (y-axis) is represented by five ACFOR scale categories (A= abundant; C= Common; F= Frequent; O= Occasional; R= Rare) adapted from Crisp & Southward (1958) and reported by Kendall *et al.*, (2004) for both warmer 1950s and cooler 1980s, and by this study and pers. comm. from Prof SJ Hawkins (2000s, 2010s). In N-Wales (top), the x-axis represents populations from south to north within Cardigan Bay (range edge of *P. depressa* in 2000s) until the Isle of Anglesey (the range edge of *P. depressa* in 1950s). In S-East England (bottom), the x-axis represents populations from west to east in the English Channel towards Isles of Wight (*i.e.*, Ventnor and Bembridge, both *P. depressa* range edges in 1950s and 1980s, respectively) until Southsea (the range edge of *P. depressa* in 2000s).



**Figure 6.2.** Schematic diagram of abundance patterns of both *Patella* species toward both poleward limits of *P. depressa* in Britain. Patterns of abundance were evaluated by both short (2015) and long term data-sets (1980/2016). *Pv*= *P. vulgata*; *Pd*= *P. depressa*.

My short-term surveys have shown that the range limit of *Patella depressa* was found on the north coast of Cardigan Bay in N-Wales. Here, populations of *P. depressa* tend to be dominated by larger individuals than in other regions. In Chapter 4, older individuals were found in N-Wales than at its other leading range edge in S-East England. In contrast to North Wales, reasonably dense numbers of individuals of *P. depressa* were found at the leading edge in the English Channel (Chapter 2). Populations now extend to the east of the Isle of Wight at Southsea on the mainland, where the last breeding population in the English Channel is now to be found (Hawkins comm. pers.). In the English Channel, I found a significant fraction of individuals of *P. depressa* with less than 15 mm in length indicating consistent recruitment (Figure 6.3). Here, selected individuals for age analysis (Chapter 4) were younger than those ones in the range edge in N-Wales populations. Therefore, short-term abundance patterns together with age analysis of individuals of *P. depressa* indicates consistent recruitment in southern England, potentially influenced by its close proximity to central populations (*i.e.*, S-West England). For *P. vulgata*, the proportion of individuals of less than 15 mm in length were similar across regions (Figure 6.3).

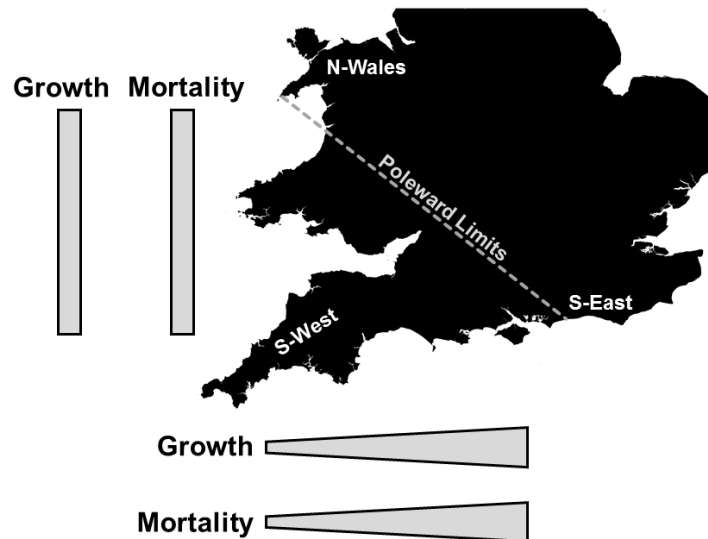


**Figure 6.3.** Schematic diagram of limpet size patterns for those individuals with less 15 mm in length of both *Patella* species toward both poleward limits of *P. depressa* in Britain (2015). *Pv*= *P. vulgata*; *Pd*= *P. depressa*.

I found that growth and mortality rates do not differ substantially between *Patella depressa* and *Patella vulgata* across regions in Britain (Chapter 3, summarised in Figure 6.4). However, both growth and mortality rates of both limpet species were higher at the range edge of *P. depressa* in S-East England, when compared with populations in the range edge in N-Wales and in central populations in S-West England (Figure 6.4). Thus, performance traits (measured as individual growth and population mortality rates) of *P. depressa* differ between the two separate poleward boundaries, meaning the separation between more central populations (S-West England) and range edge populations in Britain (N-Wales and S-East England) was not consistent. Surprisingly, *P. vulgata*, which may be considered at its centre range of distribution in the British Isles, showed patterns very similar to *P. depressa*. Therefore, these patterns of growth and mortality of both *Patella* species do not support the ACH (Brown, 1984). They demonstrate the primacy of local factors, which over-ride any abundant-centre effects on species geographic distribution at local spatial scales (Guo *et al.*, 2005).

In Chapter 4, I confirmed the finding that populations nearer to their poleward boundaries are generally characterized by older individuals (Hutchins, 1947; Williamson & Kendall, 1981; Kendall & Lewis, 1986). This is the case for *Patella depressa* at its northern boundary in N-Wales. In addition, growth performance (von Bertalanffy K growth coefficient) calculated by using annual lines on shells supported the results of limpet growth in Chapter 3; similar growth performance values were obtained by using both labelling and annual growth line approaches. I also found that *P. depressa* growth patterns were influenced by density-dependent effects over different spatial scales (*i.e.*, shore vs. quadrat scales). Thus, over a shore scale within a region, high limpet density does not necessarily lead to a reduction in growth rates in *Patella* species (Chapter 3). In contrast, at a quadrat-scale, I found a localised effect of limpet density on growth performance of *P. depressa* (Chapter 4). These patterns suggest that growth rates in limpet species are highly variable (Chapter 3 and 4), subject to drivers and limitations at various levels of geographical scale, with local processes being important.

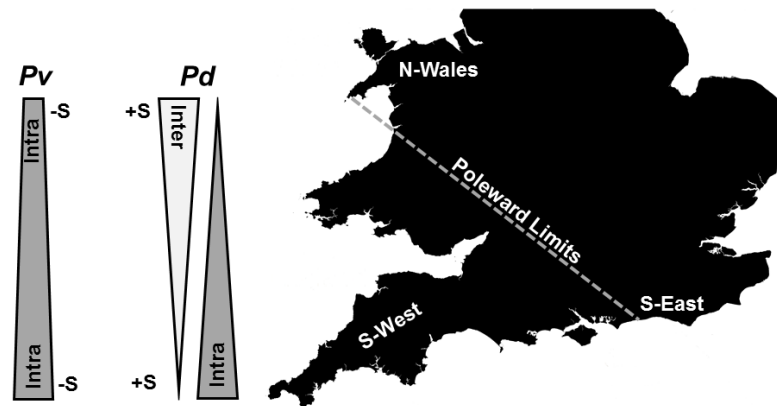
### Limpet Species Performances



**Figure 6.4.** Schematic diagram of growth and mortality patterns of both *Patella* species toward both poleward limits of *P. depressa* in Britain (2015/2016).

In chapter 5, I have tested intra- and inter-specific competition between both *Patella* species in central and marginal populations of *Patella depressa* in Britain under contrasting environmental conditions (with and without a shade canopy). Individuals of *P. depressa* were strongly affected by inter-specific competition at its range edge in N-Wales, particularly in mixed plots with *Pulgata vulgata* under shade treatments (Figure 6.5). By contrast, its congener, *P. vulgata* was affected by intra-specific competition in no-shading plots, particularly in populations in S-West England. These results suggest that both biological and physical factors are modulating the range edges of *P. depressa* in populations in N-Wales.

### Limpet Competition



**Figure 6.5.** Schematic diagram of competitive interactions showing the strength on species performance traits (measured as growth and mortality) of both *Patella* species at both central and marginal populations of *P. depressa* in Britain (2016/2017). It is also indicated the shading effects (-S and +S) for each *Patella* species. *Pv*= *P. vulgata*; *Pd*= *P. depressa*.

### 6.3. Ultimate and Proximate Factors Acting on Range Edges of Species

The geographic range of a species can be seen as a product of population dynamics (Guo *et al.*, 2005; Gaston, 2009; Fordham *et al.*, 2013; see also Box 1.3, Chapter 1). It represents the area over which the rate of establishment of local populations is not exceeded by the rate of extinction, with its boundary defined by the point at which this ceases to be so (Gaston, 2009). However, the distributional limit of a species may be mediated by complex interactions between

multiple factors (Keith *et al.*, 2011; Bates *et al.*, 2014; Bennett *et al.*, 2015; Chuang & Peterson, 2016). Local and regional factors can lead to complex patterns of species distribution rather than simple species range shifts (Helmuth *et al.*, 2006). Unfortunately, the effects of multiple interacting factors on the limits to species are difficult to study in the field (Brown *et al.*, 2011, 2016). Given the temporal variation of many abiotic and biotic factors, the identities of the factors and their interaction may change through time and space (Poloczanska *et al.*, 2008; Kordas & Dudgeon, 2011; Kordas *et al.*, 2011). Thus, the identities of limiting factors on species range edges may change from one part of a geographic range to another (Gilman *et al.*, 2010; Leonard, 2010; Kordas & Dudgeon, 2011; Wisz *et al.*, 2013; Bates *et al.*, 2017).

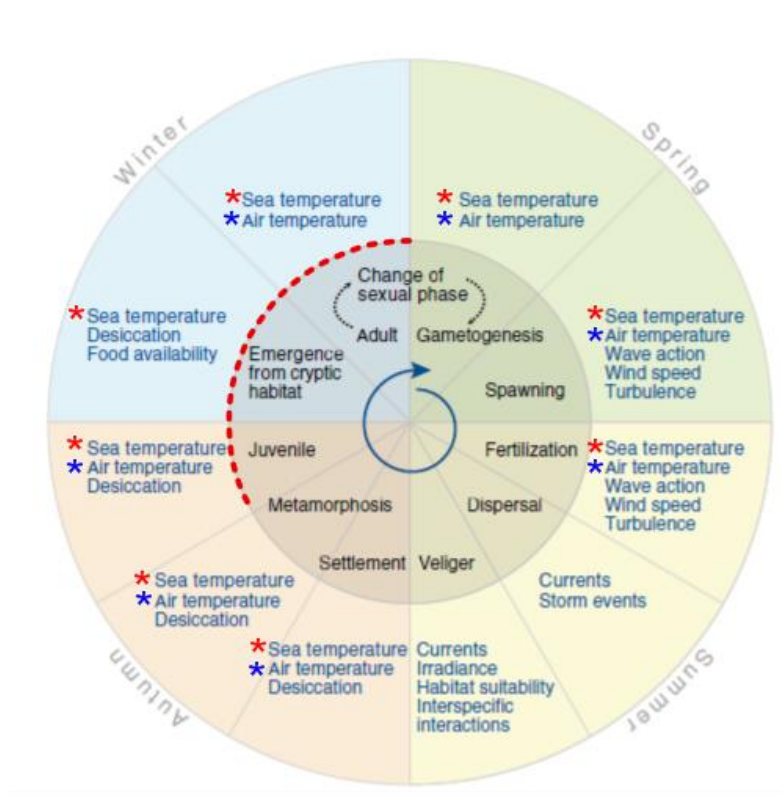
Numerous hypotheses have been proposed to explain the geographic limits of species (see Gaston, 2003, 2009 for review). Early marine biogeographic studies linked species distributions with temperature (usually measured as Sea Surface Temperature, hereafter SST) in setting their distributional limits (Orton, 1920; Hutchins, 1947; Frank, 1975). This still forms the basis to explain species ranges distribution in ecology (Gaston, 2003, 2009). In marine ecosystems, SST is the ultimate factor driving geographic distributions of marine organisms including intertidal species (Orton, 1920; Hutchins, 1947) through its regulation of metabolism (Barry & Munday, 1959; Blackmore, 1969; Wright, 1977). Water temperature has shown to have strong effects on metabolism and growth (Bayne *et al.*, 1973; Phillips, 2005), feeding behaviour (Petrakis, 1992; Sanford, 1999, 2002), reproduction (Hutchins, 1947; Philippart *et al.*, 2003) and rates of larval development (Anil *et al.*, 2001; Hoegh-Guldberg & Pearse, 1995; Luppi *et al.*, 2003) of intertidal and subtidal organisms. Direct effects of temperature occur when thermal conditions are unsuitable for survival or reproduction beyond the boundaries of a species geographic range. Hutchins (1947) distinguished two general ways in which this might occur, emphasizing the important role of reproduction and recruitment in setting species distributions. Thus, climatic conditions, through their effects of temperature, may impose a boundary by directly killing individuals or because they are unsuitable for reproduction or the successful completion of life cycles (Hutchins, 1947). Both observations were made with particular reference to winter and summer temperatures, which have generally been considered the most important group of climatic variables limiting the northern limits of warm-water species in Britain (Crisp & Knight-Jones, 1954; Crisp & Southward, 1958; Crisp, 1964; Lewis, 1964; Keith *et al.*, 2011; Firth *et al.*, 2015).

However, various aspects of performance and survival of intertidal organisms can be influenced by ultimate and proximate factors (Fordham *et al.*, 2013; Bates *et al.*, 2014; Bennett *et al.*, 2015; Chuang & Peterson, 2016). Thus, multiple hypotheses can be related to species performance traits because they have a variety of impacts on different stages of species life history and different levels of organisation influencing either individuals (*i.e.*, growth, reproduction) and populations (*i.e.*, recruitment and mortality) (Helmuth *et al.*, 2006). For example, Helmuth *et al.* (2006) proposed a set of physical and biological factors, which have been linked with physiological performance and survival throughout the life history of warm-water *Patella depressa* (Figure 6.5). They suggested most of the stages from gametogenesis to adult are controlled by sea temperature, which is expected to have an impact on its reproductive output leading to changes in abundances (Moore *et al.*, 2011). As a proximate factor, Helmuth *et al.* (2006) indicate that air temperature can exert high stress when the tide is out particularly during settlement periods (Lewis & Bowman, 1975). Wave action has also been proposed as proximate factor prompting spawning (Orton *et al.*, 1956; Orton & Southward, 1961). In my study, however, I did not consider all life history stages of *P. depressa* (Figure 6.5).

My work covered the fraction from juveniles to adults (Figure 6.5). Therefore, final conclusions from each chapter must be restricted to those life stages in *Patella depressa* as well as for *Patella vulgata*. Thus, as the British Isles are affected by different weather conditions (*i.e.*, manifestation of temperature, Chapter 2), species performance traits vary, leading to regional variations in limpet abundance and consequently variation in the level of density-dependent interactions (Chapter 3 and Chapter 4). In addition, limpet competitive interactions and local physical conditions must be considered as important local drivers within a large geographical scale (Chapter 5). Thus, my results do not support the ACH (Brown, 1984) for most aspects considered in this study for the two *Patella* species. Therefore, as *Patella* species have been proposed as climate indicator species (Southward *et al.*, 1995; Mieszkowska *et al.*, 2005; Hawkins *et al.*, 2008, 2009), the effects of climate must therefore be considered in terms of both limpet life-history traits and the interactions of ultimate (*i.e.*, sea temperature) and a multitude of local proximate factors (Figure 6.5; Helmuth *et al.*, 2006).

Additionally, all biotic interactions between species take place within a landscape of varying abiotic conditions (Gilam *et al.*, 2010; Wisz *et al.*, 2013), but surprisingly few studies have examined both abiotic and biotic interactions at species range limits (Sexton *et al.*, 2009).

The importance of abiotic and biotic factors in determining range limits has been much debated (Poloczanska *et al.*, 2008; Gilman *et al.*, 2010; Kordas *et al.*, 2011; Wisz *et al.*, 2013; Louthan *et al.*, 2015). Two divergent viewpoints can be distinguished (Louthan *et al.*, 2015). On the one hand, at the edge of its geographic range, stresses caused by abiotic factors can be seen as potentially reducing the competitive ability of a species, and increasing its vulnerability to predation or its susceptibility to pathogens. Thus, biotic factors may become an important limitation (Louthan *et al.*, 2015). On the other hand, at the edge of its range abiotic factors may commonly render a species too scarce for biotic factors to have any marked effect (Louthan *et al.*, 2015). Based on my results (Chapter 5), it seems that *Patella depressa* is affected by inter-specific competition in synergy with small changes in temperatures at small scales. Hence, both factors can thus be considered the main influences on the range edge of *P. depressa* in N-Wales.



**Figure 6.5.** Importance of multiple climatic and biological factors on physiological performance and survival of *P. depressa* during different stages of limpet life history (Modified from Helmuth *et al.*, 2006). Dashed red line show the life stages of *P. depressa* covered in my study. It is also indicated the effects of the sea (\* in red) and air (\* in blue) on each stages. Subsequent work (Borges *et al.*, 2015) has shown that *P. depressa* in the British Isles is unlikely to be protandrous.



#### 6.4. Others Proximate Factors: Physical Barriers and Habitat Availability

Physical barriers exemplify the multiple levels of causality of range edges (Gaston, 2003). They may themselves be seen as resulting directly in species range edges (Adams *et al.*, 2014). Commonly, the presence of physical barriers is reflected in the co-occurrence of the range limits of a number of species (Rapoport, 1982), which may reflect a discontinuity between biogeographic provinces in Britain (Crisp & Knight-Jones, 1954; Crisp & Southward, 1958). However, the impacts of barriers are closely linked with species dispersal abilities influenced by hydrographic patterns and habitat requirements at range edges (Keith *et al.*, 2011; Adam *et al.*, 2014). Thus care must be taken when attributing range edges to physical barriers as a variety of other factors are likely to be operating (Gaylord & Gaines, 2000).

Connectivity amongst populations of rocky shore species is interrupted by barriers to larval transport (Crisp & Southward, 1953; Herbert *et al.*, 2009; Keith *et al.* 2011). Dispersal limitation is likely to be more important at barriers for those species with poor dispersal abilities (Kinlan & Gaines, 2003), which it seems to be the case for *Patella depressa* towards both of its range edges in Britain (*e.g.*, Crisp & Southward, 1953; Crisp & Knight-Jones, 1954; Keith *et al.*, 2011). For example, at both the Llyn Peninsula in North Wales (Crisp & Knight-Jones, 1954) and the Isle of Wight towards the east of the English Channel (Keith *et al.*, 2011) the abundance of *P. depressa* suddenly drops. In addition, as larvae may reach great distances from their parent populations (Gaines *et al.*, 2007), the absence of *P. depressa* in Ireland (Crisp & Southward, 1953; Firth *et al.*, 2009) could be an indicator of a poor spreader when compared with both of its sibling species *Patella vulgata* and *Patella ulyssiponensis*, both of which are present on the Irish coasts (Crisp & Southward, 1953; Firth *et al.*, 2009). The Llyn Peninsula and associated hydrography appears to still be acting as a hard barrier to re-establishment of populations northwards to its previous limit at the tip of Anglesey - probably a hydrographic barrier setting the then northern limit (Crisp & Southward, 1953; Crisp & Knight-Jones, 1954). In contrast the previous barrier of the Isle of Wight appears to be more porous - perhaps aided by greater reproductive output in southern England (Moore *et al.*, 2011) - coupled with artificial habitat enabling modest eastward extension.

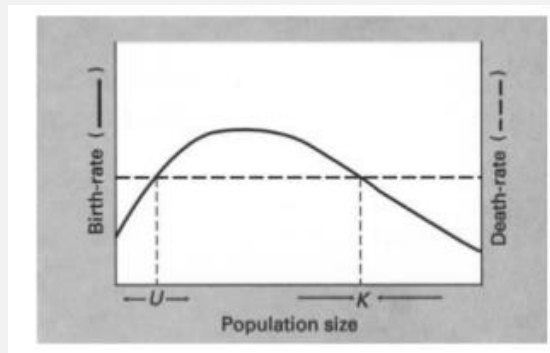
As a consequence of limitations in dispersal traits of *Patella depressa*, it would be expected to experience Allee effects at range edges in Britain (Allee, 1931; see Box 6.1). These have been suggested for equator-ward populations of *P. vulgata* in Portugal (Borges *et al.*, 2015)

and also for poleward populations of *Chthamalus stellatus* in the English Channel (Herbert *et al.*, 2009). Low densities of spatially dispersed and isolated individuals are typical at species range edges (Herbert *et al.*, 2009; Borges *et al.*, 2015). In this context, *P. depressa* reach only 20% of the total limpet population in N-Wales (Chapter 2). Because adult densities become so low at the range limit, especially in populations in N-Wales, Allee effects would be expected (Allee, 1931; see Box 6.1) due to low concentration of sperm and eggs necessary for fertilization in northern populations. However, it is probable that local and circular currents at the northern edge of Cardigan Bay (*i.e.*, eddies; Robins *et al.*, 2013) could be acting as a larval retention zone together with the physical barrier of Llyn Peninsula in N-Wales, which could reduce any Allee effects on populations of *P. depressa* in Cardigan Bay. Similar processes may occur to the west of St. Catherine's Point on the Isle of Wight and in Lyme Bay.

#### Box 6.1

##### Allee Effects

Allee (1931) observed that aggregation had positive effects on the survival of land isopods, which were subject to rapid desiccation when isolated. Allee effects are broadly defined as a decline in individual fitness at low population size or density, that can result in critical population thresholds below which populations crash to extinction (Figure 6.6).



**Figure 6.6.** The 'Allee effect'. Density-dependent birth at moderate and high densities leads to a stable carrying-capacity (K) but the change to inversely density-dependent birth at low densities leads to an unstable equilibrium (U) below which the population will decline to extinction (Allee, 1931). Figure adapted from Begon *et al.*, (1996).

Limitations in habitat availability can have strong effects on the likelihood of range shifts in a species distribution (Poyry *et al.*, 2009). Range edges may be set by a lack of unsuitable habitats (Crisp & Southward, 1958; Hiscock, 1998; Herbert & Hawkins, 2006) or by habitat-

modifying species (Ling, 2008; Shank *et al.*, 2014). For example, the north-eastern range edge of southern species of barnacles, limpets and top-shells in the English Channel has been attributed (Crisp & Southward, 1958; Hiscock, 1998; Herbert & Hawkins, 2006; Herbert *et al.*, 2009; Keith *et al.*, 2011) to the lack of extensive rocky intertidal habitat, being dominated by intertidal chalk platforms, sandy or shingle beaches, coupled with strong offshore currents (Herbert *et al.* 2009; Kieth *et al.*, 2011). However, in the east of the Isle of Wight many locations are characterized by artificial structures, which have been proliferating in recent years (Firth *et al.*, 2016). The population at Southsea is on a totally artificial rocky shore, and scattered individuals found at Brighton and Elmer were on artificial sea defences. These stepping stones may have facilitated the expansion of *Patella depressa* eastwards but not in sufficient numbers to form breeding populations (Mieszkowska *et al.*, 2005, 2006; Hawkins *et al.*, 2008; Kieth *et al.*, 2011).

### 6.5. Multiple Factors Limiting Southern Species Distribution in Britain

Keith *et al.* (2011) showed that mean annual SST has provided the best indicator of the historical distribution for southern species in Britain. The study considered southern species such as *Osilinus lineatus*, *Gibbula umbilicalis* (both re-named as *Phorcus lineatus* and *Steromphala umbilicalis*, respectively; Affenzeller *et al.*, 2017), *Patella depressa* and *Chthamalus montagui*. These southern species have different pelagic larval durations: *G. umbilicalis*  $\leq 7$  days, *O. lineatus*  $\leq 7$  days, *P. depressa*  $\leq 14$  days, and *C. montagui*  $\leq 28$  days (Burrows *et al.*, 1999; Keith *et al.* 2011). Although top-shells probably have shorter pelagic larval duration (maybe one to two days) than *P. depressa*, both species populations have passed physical barriers such as the Lleyn Peninsula in north Wales (e.g., *O. lineatus* and *G. umbilicalis*). It is possible that the Menai Straits provides a by-pass for larvae around Anglesey (Mieszkowska *et al.*, 2006, 2007). Similar extensions have occurred beyond the Isle of Wight in the English Channel in *G. umbilicalis*, perhaps using artificial habitats as stepping stones. *O. lineatus* has recently spread around the barrier of Portland Bill, and is now very common in Weymouth Bay, with individuals being found on the Isle of Wight (Hawkins pers. comm.). Both of these species have experienced increased reproductive success with increased temperature at their northern range edge aiding recruitment (Mieszkowska *et al.*, 2006, 2007). The shorter larval life of trochids may allow small extensions to be made and consolidated without Allee effects, in contrast to limpets and barnacles with longer-lived larvae (Keith *et al.* 2011). Combinations of ultimate and proximate factors are acting on populations of trochids, *P. depressa* and *C. montagui* to the east of the Isle

of Wight, which set idiosyncratic species-specific geographic limits and differential spread poleward (Sexton *et al.*, 2009; Keith *et al.* 2011). These factors potentially could be related with habitat availability, dispersal traits and hydrographic features (Crisp & Southward, 1953; Crisp & Southward, 1958; Hiscock, 1998; Herbert *et al.*, 2009; Keith *et al.*, 2011; Phillipart *et al.*, 2011). However, a combination of these factors in controlling species range edges in limpets and barnacles has not been formally tested yet.

### 6.6. Limitations and Recommendations for Further Work

Demographic attributes of populations play a major role in establishing species boundaries (Brown, 1984; Caughley *et al.*, 1988; Brown *et al.*, 1996; Guo *et al.*, 2005; Chuang & Peterson, 2016). The factors that limit the geographic range of a given species at a particular place are often difficult to predict without detailed knowledge of the biology of species and the prevailing environmental conditions (Gaston, 2003). In this context, although I have measured mortality rates of *Patella depressa* in different chapters, mortality by predation on limpets can directly affect the structure and spatial distribution of limpet populations (Lewis & Bowman 1975; Coleman *et al.*, 1999; Silva *et al.*, 2004, 2008, 2010; Nagarajan *et al.*, 2015). Oystercatchers, crabs and fishes are the major predator of *Patella* species (Lewis & Bowman, 1975; Coleman *et al.*, 1999; Silva *et al.*, 2004, 2010, 2008; Nagarajan *et al.*, 2015). However, although it seems to be that crabs have not a significant effect on the structure and abundance of limpet communities (Silva *et al.*, 2004, 2008), oystercatchers and fishes seem to be the main predator on limpets species (Silva *et al.*, 2010). They can attack both *Patella vulgata* and *P. depressa* with higher preference on solitary limpets than clumped limpets (Coleman *et al.*, 1999; Nagarajan *et al.*, 2015) and larger sizes than smaller ones (Silva *et al.*, 2010). In my study, mortality of limpets by predation was not measured. However, denser patches of limpets were selected avoiding solitary limpets, which would reduce mortality by predation (Coleman *et al.*, 1999).

Additionally, although I have measured growth rates of *P. depressa* through different methods, one recommendation for further studies could be consider reproductive traits towards both range edges of *P. depressa* could be useful to understand the impacts on individual performance living in the edge of its distribution. Species channelling energy exclusively into reproduction will simultaneously reduce the budget for growth (Wright & Hartnoll, 1981; Sato, 1995; Pörtner *et al.*, 2005; Ling *et al.*, 2008).

Another recommendation, which it can be a valuable way to disentangle the effects of different factors that are controlling the geographic ranges of *Patella depressa* in Britain, is to carry out transplant experiments (Gilman, 2006b), introducing individuals beyond their present limits. *P. depressa*, for example, could be transplanted to the Isle of Anglesey, where it was categorized as a common species ~ 60 years ago by Crisp & Knight-Jones (1954). However, this approach is difficult because of the ethical concerns to transplant species from one place to another.

### 6.7. Concluding Remarks

Finally, the work developed through this PhD project allowed exploration of range edge effects on performance traits of a warm-water *Patella* species with two poleward borders in Britain. The knowledge gained on both *P. depressa* and *P. vulgata* performance patterns across regions in Britain, combined with observational and experimental approaches in the field as well as in the laboratory, is expected to have a contribution in terms of future comparisons of species which are showing range extension or range contraction within their geographical distribution and also in a context species adaptation to the current climate change scenarios (IPCC, 2018). Not only are processes at range edges very species specific, my work has shown how even in the same species different processes can be operating - although dispersal and habitat availability seem to be key proximate factors setting range edges. Temperature is the ultimate influence on individual performance in ectothermic invertebrates, but at the population level recruitment and density dependence seem to drive population dynamics (Jenkins *et al.*, 2008). Comparisons between central and marginal populations of keystone species are expected to be crucial in revealing the consequences of climate change to intertidal ecosystem functioning.

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