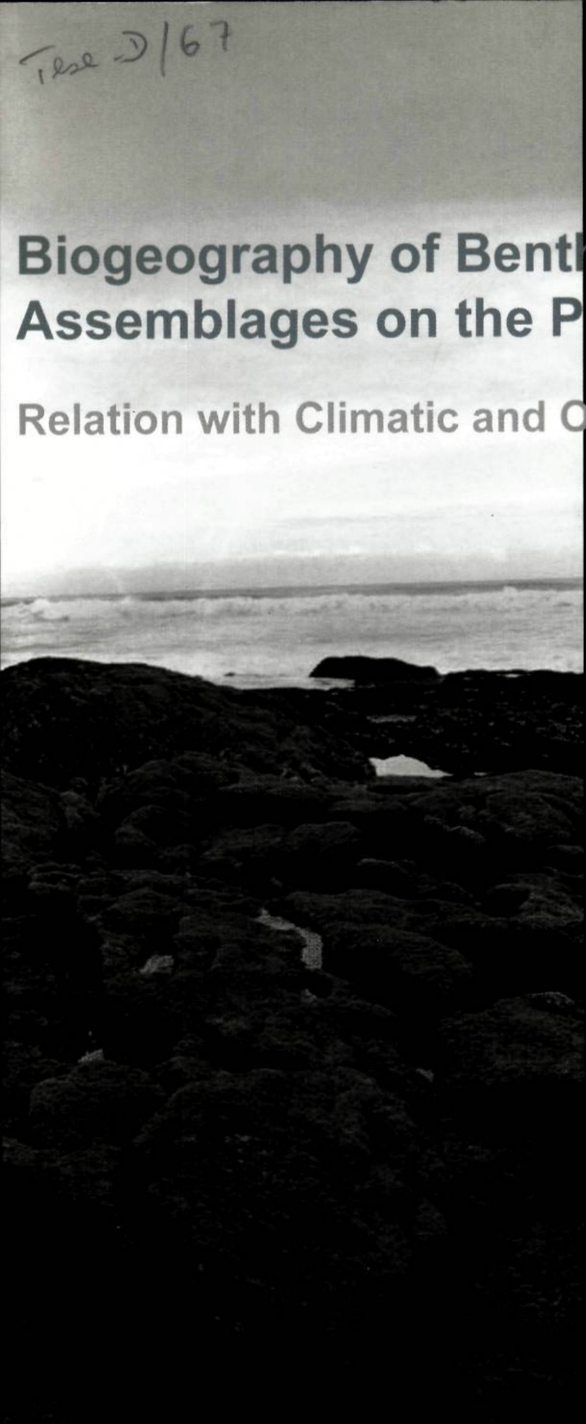

Biogeography of Benthic Invertebrate Assemblages on the Portuguese Coast

Relation with Climatic and Oceanographic Patter

PhD Thesis

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Biogeography of Benthic Invertebrate Assemblages on the Portuguese Rocky Coast: Relation with Climatic and Oceanographic Patterns

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Em todas as publicações decorrentes deste trabalho é devidamente referido que as instituições de origem do doutorando Fernando Pádua Silva e Lima são:

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- Marine Biological Association of the United Kingdom, Plymouth, United Kingdom.

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To my Mother and Father

Climate plays an important part in determining the average numbers of a species, and periodical seasons of extreme cold or drought, I believe to be the most effective of all checks.

Charles Darwin, *On the Origin of Species*

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Abstract

A decade ago, climate change was only a conjecture. Nowadays, with temperature limits being exceeded every year, there is a scientific consensus on its reality and anthropogenic origin. Furthermore, acceleration is expected to occur during this century. Although terrestrial and marine species have already been reported to be responding to changing climatic conditions, substantial research is still required. Rocky shore species are particularly useful in this task since they are sensitive indicators of climatic changes and their historical distribution limits and abundances are reasonably well known.

The first chapter sets the context of this thesis by introducing both climate change and its biological and ecological effects. The general introduction ends with an outline of the rationale and with a list of manuscripts that compose the thesis.

The second chapter addresses the present geographical distribution patterns of intertidal species along the Portuguese rocky coast, in the European context. The need to objectively define biogeographic discontinuities along the coastline for a high number of species resulted in the development of an analytical tool which proved to be of great utility in locating multivariate boundaries in one-dimensional and unevenly distributed data. The relation between patterns of distribution of crustacean epifauna and conspicuous macroalgal species was for the first time investigated along the Portuguese coast. It was shown that epifaunal abundance and diversity are probably not related with geographical changes in the dominant algal species, but are most likely linked to physical factors.

In the third chapter, the contemporary biogeographic patterns were compared with historical data. The observed modifications were studied in the light of the current theories on species responses to climate change. In a parallel task, the past 50 year trend of the climatic and oceanographic conditions along the SW European coast was assessed. Although a significant number of warm-water species is currently expanding their distribution ranges (thus matching the expected northward migration in response to the warming environment), it was shown that the same generalization cannot be made for the cold-water species group, which showed no consistent pattern. Data from several groups of organisms suggested that not all evidence of change is related to the distributional limits of species. On the contrary, the majority of climate-related distribution modifications were observed within the species' geographic domain. Several probable explanations of the processes driving temporal modifications on species' abundances and distributions were advanced. In addition, transplant experiments have raised the question of the effect of biological interactions on the mediation of species' responses to the warming environment.

In the fourth chapter, species-based models were used to hindcast past distributional modification in species ranges. Environmental envelope modelling proved to be useful to investigate the relative importance of climate and dispersal in establishing species distributional limits.

A general discussion integrates and synthesizes the work in this thesis. It is suggested that modifications in distributional ranges are complex and highly variable in intensity, direction and causal factors from species to species. Therefore, generalizations about poleward range shifts due to increasing temperature should be made with caution.

Resumo

Até à década passada, as mudanças climáticas globais não eram mais que conjecturas. Actualmente, com os níveis de temperatura a atingir novos recordes todos os anos, assiste-se a um consenso científico acerca da existência e da origem antropogénica do fenómeno do aquecimento global. É também consensual que o seu efeito se intensificará nas próximas décadas. Embora existam bastantes estudos sobre os efeitos das mudanças climáticas em espécies terrestres e marinhas, é ainda necessária investigação adicional nesta área, uma vez que muitos processos estão por compreender. No entanto, as espécies intertidais de substrato rochoso têm vindo a ser reconhecidas como particularmente sensíveis a essas mudanças. Além disso, como a abundância e os limites de distribuição destas espécies estão razoavelmente bem documentados para o passado recente, são de grande utilidade neste tipo de estudos.

Assim, o primeiro capítulo da presente dissertação introduz e contextualiza o fenómeno das alterações climáticas globais e dos seus efeitos sobre a biologia, a ecologia e a distribuição das espécies. Introduz ainda o problema base da tese e a lista de trabalhos que a constituem.

O segundo capítulo apresenta o estudo do actual padrão de distribuição

das espécies intertidais em Portugal, à luz do contexto Europeu. A necessidade de definir objectivamente descontinuidades biogeográficas ao longo da linha de costa para um grande número de espécies resultou no desenvolvimento de uma nova ferramenta analítica, que demonstrou ser de grande utilidade para a identificação de fronteiras baseadas em dados multivariados e desigualmente distribuídos. Pela primeira vez, investigou-se a relação entre os padrões de distribuição dos crustáceos e das macro-espécies de algas na costa Portuguesa. Este estudo permitiu concluir que, possivelmente, o padrão geográfico observado na abundância e diversidade de epifauna não está relacionado com a identidade e a distribuição das algas dominantes, mas sim com factores físicos.

No terceiro capítulo, os padrões contemporâneos de distribuição e abundância das espécies intertidais foram comparados com dados históricos das décadas de 1950 e 1960. Paralelamente, a análise das alterações das temperaturas do mar e do ar, ao longo da costa sudoeste Europeia nos últimos 50 anos, forneceu uma estimativa precisa do processo de aquecimento. Assim, as diferenças nas distribuições foram avaliadas e posteriormente interligadas com as modificações das variáveis climáticas e oceanográficas. Apresentaram-se, também, algumas possíveis explicações sobre os processos que controlam as alterações temporais dos processos biogeográficos. Verificou-se que embora a distribuição de um número significativo de espécies típicas de águas quentes se esteja a expandir para norte, não se observa uma retracção consistente nas distribuições dos organismos típicos de águas frias. Adicionalmente, experiências recorrendo a translocação de espécies ao longo da costa Portuguesa sugeriram que algumas das modificações nas distribuições geográficas em resposta ao aquecimento global são significativamente mediadas por interacções biológicas. Dados recolhidos em vários grupos de organismos também sugerem que, em muitos casos, e contrariamente ao que se julgava, as modificações relacionadas com alterações climáticas ocorrem primeiramente dentro dos limites gerais da sua distribuição e não nas fronteiras de distribuição.

No quarto capítulo, a modelização de factores ambientais permitiu demonstrar que a capacidade de dispersão pode ser 333extremamente importante para o estabelecimento de limites de distribuição das espécies intertidais. Além disso, a relativa importância deste factor parece ser variável de região para região.

O último capítulo constitui a discussão geral onde se sintetiza o trabalho desenvolvido na tese. Por fim, salienta-se que as generalizações em relação à migração para norte nos limites de distribuição das espécies em resposta às alterações climáticas globais devem ser propostas com cautela, uma vez que as excepções a esta regra parecem ser numerosas.

Résumé

Il y a une décennie, le changement climatique était seulement une conjecture. De nos jours, avec les records de températures qui sont brisées d'année en année, il y a un consensus scientifique sur la réalité de son origine anthropogène et sur son intensification dans les décennies à venir. Bien que des espèces terrestres et marines aient déjà été abondamment rapportées comme répondant aux conditions climatiques changeantes, une recherche substantielle est néanmoins toujours requise. Les espèces des côtes rocheuses sont des indicateurs particulièrement sensibles à ces changements. En outre, plusieurs études historiques présentent un niveau de référence robuste sur les abondances des espèces et leurs limites de distribution.

Ainsi, le premier chapitre de cette thèse introduit et met en contexte le phénomène des changements climatiques globaux et ses effets sur la biologie, l'écologie et la distribution des espèces. On introduit aussi le thème de la thèse et la liste des travaux qui la constituent.

Le deuxième chapitre présente la description des modèles géographiques actuels dans la distribution des espèces intertidales sur les côtes rocheuses du Portugal, dans un contexte Européen. La nécessité

de définir objectivement des discontinuités biogéographiques le long du littoral, pour un grand nombre d'espèces, a résulté dans le développement d'un outil analytique qui s'est avéré à être de grande utilité en localisant des confins multivariables dans des données unidimensionnelles et inégalement distribuées. Le rapport entre les modèles de la distribution de l'épifaune crustacée et les espèces de macroalgue a été étudié pour la première fois pour les côtes Portugaises. Au cours de cette étude il a été démontré que les modèles géographiques d'abondance et diversité d'épifaune observés ne sont pas reliés aux changements géographiques de l'identité de l'espèce d'algues dominante, mais est probablement lié aux facteurs physiques.

Dans le troisième chapitre, la tendance de la température côtière de l'air et de la mer des derniers 50 années sur la côte sud ouest d'Europe a été réévaluée, fournissant une estimation précise du processus d'échauffement. Des modèles contemporains de la distribution et de l'abondance des macro-espèces ont été comparés aux données historiques des années 50 et des années 60. Les changements ont été évalués et ont été reliés avec les modifications des variables climatiques et océanographiques. Quelques explications possibles aux processus conduisant les modifications temporelles sur les modèles biogéographiques ont été avancées. On a vérifié que bien qu'un nombre significatif d'espèces d'eau chaude augmentent actuellement leur limite de distribution répondent ainsi à ce fait de migration du nord prévue en réponse à l'échauffement de l'environnement, la même tendance parmi le groupe des espèces d'eau froide n'a pas été observée. Les expériences de greffe employant des algues ont souligné l'importance des interactions biologiques en réponse d'espèces de médiation à l'échauffement de l'environnement. Les données rassemblées de plusieurs groupes d'organismes suggèrent que non seulement toute l'évidence de changement se soit produite aux marges nord ou sud des limites des espèces, mais aussi que la majorité de modifications associées au climat sont susceptibles de se produire premièrement dans des poches d'absence distributionnelles dans le principal domaine géographique des espèces.

Dans le quatrième chapitre, la modélisation de l'enveloppe environnementale s'est avérée utile pour étudier l'importance de la dispersion en établissant les limites distributionnelles des espèces intercotidales. On a suggéré que plus probablement, l'importance relative de ce facteur soit fortement dépendante de la région géographique considérée.

Le dernier chapitre traite de la discussion générale qui résume le travail développé pendant cette thèse. On remarque que les généralisations au sujet de déplacement des limites vers les pôles dus à la température croissante devraient être faites avec prudence.

Contents

Chapter 1

General Introduction

The climate of the Earth has been in a continual state of change, with the last thousands of years being characterized by a succession of ice ages and interglacial periods (Petit *et al.*, 1999). Direct and indirect assessments of the climate history showed that rapid and widespread changes have occurred repeatedly in the past (Alley, 2000a; Overpeck and Webb, 2000; Shackleton, 2001; Alley *et al.*, 2003), particularly during warming periods (Martrat *et al.*, 2004). For example, during ice-ages abrupt step-like shifts have taken place over decades or less (Overpeck and Webb, 2000). Additionally, through the last glacial periods the Earth has experienced global temperatures up to 5 °C cooler, while some interglacial ages were 2 °C warmer that current climate (Overpeck and Webb, 2000; Zachos *et al.*, 2001). These changes had profound effects on ecosystems and species, which have moved and evolved in response to the climatic variability (Hulme, 2003). However, although the prehistoric changes in climate were clearly of natural origin, contemporary climate change is dominated by human perturbation of the atmosphere (Mann *et al.*, 1998; Zwiers and Weaver, 2000; Karl and Trenberth, 2003).

The rate of present day warming already exceeds anything experienced

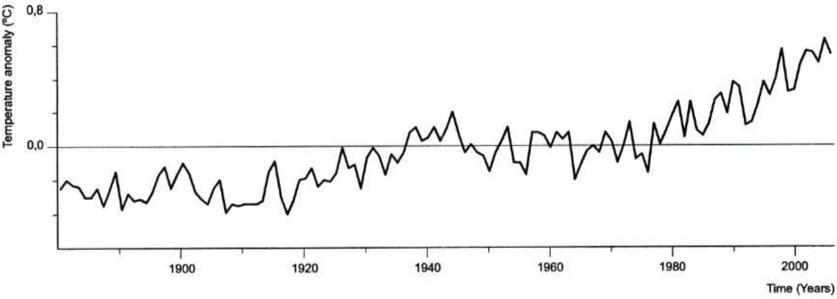

Figure 1.1 Line plot of global mean land-ocean temperature anomaly index (in relation to 1951-1980 period), from 1880 to present. Data obtained from the Goddard Institute for Space Studies, NASA. http://data.giss.nasa.gov/

in the last centuries (Hulme, 2003), and 11 years between 1995 and 2006 are among the 12 warmest since 1850 (Figure 1.1, Hansen *et al.*, 2002; IPCC, 2007). A milestone in the understanding of these unprecedented climatic alterations was the 2001 Intergovernmental Panel on Climate Change assessment (IPCC, 2001). Developed with the contribution of more than 1,200 scientists from approximately 120 countries, it quickly became a standard reference and consolidated the scientific consensus about global warming. While a decade ago it was just a conjecture, it is now largely accepted by the scientific community that climate change is of anthropogenic origin (Oreskes, 2004).

In fact, humans have significantly modified global biogeochemical cycles, altered the global environment, transformed land and enhanced the mobility of organisms. In the near future, greenhouse gases will probably cause the most abrupt climate change experienced in the last 18,000 years, since the end of the last glaciation (Chapin III *et al.*, 2000). Therefore, understanding and forecasting responses of species to climate change and to habitat loss are, today, among the greatest scientific challenges in the fields of ecology and conservation biology (Root and Schneider, 1995; McCarty, 2001; Travis, 2003).

In this thesis, the response of intertidal species to climate change is considered from a biogeographical perspective. In the remaining of this general introduction the scene for the rest of the thesis is set by reviewing climate change, before considering biological responses to climate change. The use of modelling in predicting climate change responses of marine species is reviewed. The intertidal system is introduced finally considering the sources of historical information. The general introduction concludes with an outline of the rationale of the thesis and a list of publications or manuscripts that form the chapters.

1.1 The climate change

The most recent period of warming has been nearly ubiquitous and widespread over the globe (Oerlemans, 2005; Hansen *et al.*, 2006), but the largest increases in temperature have occurred over the mid and high latitudes of the Northern Hemisphere (Jones *et al.*, 2001; Hansen *et al.*, 2006). The increase in temperature observed in the 20th century is likely to have been the largest in the past 1,000 years, with a particularly high rate of warming over the last 40 years (Mann *et al.*, 1998; Crowley, 2000; IPCC, 2001; Jones *et al.*, 2001). The total temperature increase from 1850-1899 to 2001-2005 was 0.76 ± 0.19 °C (IPCC, 2007).

In the Northern Hemisphere, lakes and rivers are now in average freezing 5.8 days later per 100 years, and ice break-up is happening 6.5 days later per 100 years (Magnuson *et al.*, 2000; Sagarin and Michell, 2001). There is also evidence that glaciers are melting and retreating. All these changes are probably anthropogenically driven (Dyurgerov and Meier, 2000). The dramatic loss of Arctic and Greenland sea ice (Meier *et al.*, 2005; Chen *et al.*, 2006) is now widely followed by climate scientists, policy makers, and by the public (Francis and Hunter, 2006).

A substantial portion of the climate variability in the Atlantic sector is associated with the North Atlantic Oscillation (NAO - Hurrell, 1995; Visbeck *et al.*, 2001; Hurrell *et al.*, 2003) which is known to be a major influence on wintertime temperatures of the Northern Hemisphere (Marshall *et al.*, 2001). Over the last three decades, NAO has been shifting to a predominantly positive phase (Visbeck *et al.*, 2001; Woolf *et al.*, 2003). It seems increasingly likely that greenhouse gases resulting from human activities are playing a significant role (Paeth and Hense, 1999; Visbeck *et al.*, 2001).

1.1.1 A warming Ocean

Due to the specific heat capacity and high density of seawater, the ocean is able to store and transport large amounts of heat, thus having a critical buffering role in the variability of Earth's climate system. It is also a key element in the carbon cycle, and it has been estimated that nearly half of the total carbon released by human influence since pre-industrial eras has been captured by the ocean (Sabine *et al.*, 2004). Additionally, it has absorbed approximately 84% of total heating of the Earth climate system (Levitus *et al.*, 2000; Levitus *et al.*, 2005). Nonetheless, because of its high volume and thermal inertia, the observed mean increase in sea surface temperature (SST) has not exceeded more than half of the average temperature increment in the terrestrial atmosphere (IPCC, 2001).

The global ocean heat content is particularly well documented since the late 1950s, when the first adequate observations of sub-surface ocean temperatures have been gathered, although it is known that its increase has a previous onset (Cane *et al.*, 1997). The increase was approximately 14.5 x 1,022 Joules, representing an absolute mean warming of 0.037 °C (Levitus *et al.*, 2005). Furthermore, the warming has been observed not only at the surface (Hansen *et al.*, 2006) but also inside the water column. The layer between 0 and 300 m has suffered a global mean temperature increase of approximately 0.31 °C since 1955 (IPCC, 2001). Waters between 800m and 2,500m depth have also warmed over recent years and the warming since 1957 is remarkably uniform, at least across the east-west extent of the North Atlantic (Mikolajewic *et al.*, 1990). Intermediate waters between 1,000 and 2,000 meters have increased ~0.5 °C in temperature during the 20th century (Arbic and Owens, 2001). This warming in the inner ocean contrasts with surface changes predicted by some computational models (Mikolajewic *et al.*, 1990). Thus, the deep ocean is not in a equilibrium state and has changed significantly under the forcing conditions of the past decades (Parrilla *et al.*, 1994).

Recent evidence have shown that the Atlantic, Pacific and Indian Oceans exchange heat and that they have undergone a net warming since the 1950s (Levitus *et al.*, 2000). Since it is free of continental barriers, the Southern Ocean plays a critical role in this exchange process, transmitting climatic signals between several Ocean basins (Gille, 2002). Complex teleconnections between the major climatic systems in the Pacific and Atlantic systems, the El Niño - Southern Oscillation (ENSO) and the NAO, are now known to have occurred frequently during the 20th century (Diaz *et al.*, 2001; Kucharski *et al.*, 2006). Changes in the Western Equatorial Pacific oceanographic regimes (widely known as El Niño/La Niña), such as the recent warming which raised the temperature close to its maximum in the past million years (Hansen *et al.*, 2006), propagate to the global ocean, affecting the climate in many different regions of the Earth (Knippertz *et al.*, 2003; Yasunaka and Hanawa, 2005). Another example of the fundamental role of the Ocean in mediating the global climate change is the recent finding that melting sea ice in the Arctic might cause some counter-intuitive effects, slowing the global warming by allowing a higher oceanic absorption of carbon dioxide from the atmosphere. The ice retreat over the last three decades has tripled the amount of CO2 that the Arctic Ocean can absorb (Bates *et al.*, 2006).

Warming in the last century has probably contributed significantly to the observed sea level rise, through thermal expansion of sea water and widespread loss of terrestrial ice (Cabanes *et al.*, 2001; Church, 2001; IPCC, 2007). Data from coastal tide gauges and from altimeter satellites have shown that global average sea level rose between 0.1 and 0.2 meters during the 20th century (IPCC, 2001; Miller and Douglas, 2004; IPCC, 2007). Furthermore, increasing wave heights during the recent decades have also been described for the North-Eastern Atlantic and North Sea (Woolf *et al.*, 2003).

1.1.2 Causes of recent climate change

The extensive and generalized fossil-fuel combustion and deforestation triggered a 30% increase in the CO_2 content of the atmosphere during the past three centuries, with more than half of this increase occurring since the 1960s (Chapin III *et al.*, 2000). The atmospheric concentration of this gas in 2005 exceeds by far the natural range over the last 650,000 years (IPCC, 2007). Warming in the 20th century has been mainly studied by reconstructing Northern Hemisphere temperatures and testing various mechanisms of climate change. The use of diverse modelling approaches based in different climate forcings allows the comparison between several natural and anthropogenic factors (Crowley, 2000).

The agreement among observed and simulated temperature variations strongly suggests that forcing from anthropogenic activities, although moderated by variations in solar and volcanic forcings, has been undoubtedly the main driver of climate change during the past century (Mann *et al.*, 1998; Tett *et al.*, 1999; Zwiers and Weaver, 2000; Barnett *et al.*, 2001; Meehl *et al.*, 2004). Given that the heat penetration in depth varies from ocean to ocean, worldwide historical records of subsurface warming provide a fingerprint that simulation models must match. It has been found that the particular patterns in ocean warming could only be accurately mimicked by including anthropogenic greenhouse gases as a climate driver (Barnett *et al.*, 2005). Enhanced greenhouse effect may have caused the Earth to heat by an extra amount equivalent to a supplementary 1% of the total solar input, and this amount is increasing (Cicerone, 2000). These and other evidences suggest that it is very likely that greenhouse effect has established itself above the level of natural variability in the climate system (Crowley, 2000; IPCC, 2007).

1.1.3 Projections for the future

It is certainly impossible to predict the exact climate 50 years from now, but it is still easier to assess the relative likelihood of different long-term trends than the chaos of a regular short-term weather forecast for the next week (Allen and Ingram, 2002). The unpredictability regarding both the course that the global economy will take and the future innovations in technology is perhaps the most important source of uncertainty in the task of quantifying the future climate change. To overcome this problem, a variety of scenarios for future emissions of CO_2 and other important gases (such as methane and aerosols) are usually used to run GCMs (General Circulation Models, also known as Global Climate Models) which are then used to project future changes. These models have traditionally shown a wide variety of responses, ranging from relatively moderate warming (Mahlman, 1997) to projections that far exceed the natural variability of the past 1,000 years and are greater than the estimate of global temperature change for the last interglacial period (Crowley, 2000). More recently, model sensitiveness have started to converge, and the current eight most important scenarios predict a warming rate spanning from 2.6 to 4.0 °C until 2100 (Kerr, 2004). However, this range might be underestimated since contemporary aerosol cooling is predicted to decline relatively to greenhouse gases due to the shorter life of aerosols and to the social consciousness in seeking a cleaner atmosphere. Thus, the future climatic warming, free from aerosol restraints, may even exceed the upper limit of the forecasted range (Andreae *et al.*, 2005). Recent models suggest that anthropogenic warming and sea level rise would continue for centuries due to the timescales associated with climate processes and feedbacks, even if greenhouse gases were to be stabilized (IPCC, 2007). Another major concern with a potential ongoing change in climate is that extreme events have a greater probability of occurrence (Easterling *et al.*, 2000; IPCC, 2001; 2007), including extreme high and low temperatures, and intense precipitation and drought episodes.

While recent attention has mainly focused on the climatic consequences of greenhouse gas emissions and on their impacts on the Earth, less attention have been given to the possibility that widespread changes in climate might occur rapidly. Nonetheless, some models confirm the likelihood of abrupt climate changes in the near future (e.g., Manabe and Stouffler, 1995). The fast increase in the influence of anthropogenic forcing might amplify the probability of crossing a particular threshold, and hence triggering an abrupt climate change (such as shutting down the oceanic Thermohaline Circulation). This would result in rapid cooling as occurred in the Younger Dryas period (Alley, 2000b) with far drastic consequences than the majority of published studies have predicted (Alley *et al.*, 2003; Hansen *et al.*, 2004).

1.1.4 Regional models

Regional climate change information has been characterized by a relatively high level of uncertainty. In reality, the high complexity of the processes determining regional climate, their integration over a descending hierarchy of spatial and temporal scales, and the difficulty in extracting fine-scale regional information from coarse resolution coupled GCMs have proved to be the main obstacles (IPCC, 2001). Therefore, the majority of studies related with climate change have focused on global patterns and, consequently, have produced global forecasts. Nonetheless, a minority of regional studies and reports (e.g., Santos *et al.*, 2002; Rowel, 2005) have been strengthening the idea that consequences of global changes might be different from region to region (IPCC, 2001).

Other studies indicate that at finer scales the changes can even be highly divergent in magnitude and/or in the direction of change, when compared with global forecasts. For example, the global heating caused by the rising greenhouse effect has the potential to disrupt some of the major oceanic currents (like the Thermohaline Circulation) from which the distribution of heat on the planet depends. In case it happens, some regions such as Europe may possibly stop receiving a significant amount of heat, causing a catastrophic and abrupt decay in temperature as high as 10 °C (Manabe and Stouffler, 1995; Kerr, 1998). Although with a high degree of uncertainty, some data show that this process might have already been started (Hansen *et al.*, 2001; Dickson *et al.*, 2002; Hansen *et al.*, 2004; Bryden *et al.*, 2005; Quadfasel, 2005).

1.2 Biological responses to recent climate change

Many physiological processes are under tight control by particular thresholds of temperature or humidity (Theede, 1973; Easterling *et al.*, 2000). Hence, species distribution within and across ecosystems can be largely explained by the physical and chemical conditions of the environment (IPCC, 2001; Clarke, 2003). Variations in that environment are thought to have a profound influence on a variety of physiological and ecological processes and, consequently, to cause changes in patterns of species abundance (Hurrell *et al.*, 2003).

Long-term studies indicate that some species are already responding to recent climate anomalies. However, there are some inevitable limitations in the interpretation of such evidence. First, both submission and publishing of positive trends are encouraged by the nature of scientific publishing, to the detriment of negative or inconclusive results.

Second, the apparent strength of those trends is highly dependent of the particular time interval chosen for the analysis. Finally, the character of long-term studies implies that the majority cannot be independently controlled, and thus several possible causes for the observed patterns are confounded. These restrictions mean that no single study can be taken as a certain evidence of an anthropogenic-driven change. Instead, it is the cumulative amount of examples that is becoming persuasive (Hughes, 2000). In fact, the idea underlying global conclusions on biological alterations is parallel to the logic applied to global climate change itself. With climate change, the attribution of modern warming trends to anthropogenic drivers comes from analysis of global patterns, not from detailed data derived from individual meteorological stations. Likewise, the global pattern of change is much more important than any single study for the assessment of biological impacts (Parmesan and Yohe, 2003). The consistency between distinct studies, the observed correlation with climate data and a variety of background experimental work strengthens the hypothesis that changes in species ranges are truly related to recent climatic warming (Parmesan *et al.*, 2005).

The observed influences of climate change on biological and ecological processes can be grouped in three main categories: phenological responses, changes in abundance and in distribution ranges, and finally changes in community structure and dynamics. The phenological changes are sensitive and easily traceable indicators of biotic changes in response to climate warming (Peñuelas and Filella, 2001). They include changes in the timing of plant unfolding, flowering, growing and decline phases (Bradley *et al.*, 1999; Menzel *et al.*, 2001; Ahas *et al.*, 2002). Responses in the timing of bird breeding, egg laying and migration have also been commonly reported (Crick *et al.*, 1997; Crick and Sparks, 1999; Sillet *et al.*, 2000; Beaumont *et al.*, 2006). Phenological effects also extend to other groups of animals such as insects, amphibians and mammals (Inouye *et al.*, 2000; Wuethrich, 2000). An enormous and systematic phenological network data set of 542 plant and 19 animal species in 21 European countries showed that, from 1971 to 2000, the average advance of spring/summer events was 2.5 days per decade (Menzel *et al.*, 2006a). Another meta-analysis revealed a mean advancement of spring events by 2.3 days per decade (Parmesan and Yohe, 2003). In marine ecosystems, substantial trends in the length of phytoplankton season have been related with global warming (Reid *et al.*, 1998; Edwards and Richardson, 2004; Chiba *et al.*, 2006). Phenological changes related to climate signals have also been shown for squid (Sims *et al.*, 2001) and fish (Sims *et al.*, 2004).

Perhaps the most pervasive change documented in biological systems has been the shift in geographical ranges of species (Rivadeneira and Fernández, 2005). The poleward movement in latitude or upward in altitude has been predicted and observed, in different geographic regions, for many species' ranges, including terrestrial plants and animals (Parmesan, 1996; Parmesan *et al.*, 1999; Hughes, 2000; Stenseth *et al.*, 2002; Walther *et al.*, 2002; Parmesan and Yohe, 2003; Root *et al.*, 2003; Franco *et al.*, 2006; Hickling *et al.*, 2006). There is a consistent temperature-related shift in species ranging from invertebrates to mammals and from grass to trees. More than 80% of the species that showed changes in distribution are shifting in the direction that is expected based on their known physiological constraints (Root *et al.*, 2003).

A high number of studies indicate past modifications in climate as being implicated in abundance and/or geographical range changes of both pelagic and sessile marine species (Southward and Crisp, 1952; Southward and Crisp, 1954; Crisp, 1964; Southward, 1967; Southward, 1975; Southward *et al.*, 1975; Southward, 1980; 1991; Southward and Boalch, 1994; Southward *et al.*, 1995; Dynesius and Jansson, 2000; Sims *et al.*, 2001; Beaugrand *et al.*, 2002; Stenseth *et al.*, 2002; Beaugrand, 2003; Beaugrand and Reid, 2003; Chavez *et al.*, 2003; Hawkins *et al.*, 2003; Sims *et al.*, 2004; Sabates *et al.*, 2006). Hence, it is reasonable to expect that contemporary and forthcoming accelerated warming in global climate will continue to cause significant perturbations in the distribution of marine life. In fact, some evidence of the effects of current global warming on marine organisms is already being reported (Holbrook *et al.*, 1997; Sims *et al.*, 2001; Stachowicz *et al.*, 2002; Hawkins *et al.*, 2003; Genner *et al.*, 2004; Perry *et al.*, 2005; Harley *et al.*, 2006).

In the intertidal environment, increasing evidence has also been accumulating. Globally, intertidal species have shown to be migrating towards the north at a rate up to 50 km per decade, which is much faster than most recorded shifts of terrestrial species (Helmuth *et al.*, 2006). The northward migration of the northern range edge of the gastropod

Kelletia kelletii in the North-East Pacific coincided with the steady increase in coastal SST that occurred during the second half of the twentieth century (Zacherl *et al.*, 2003). During the last three decades, the blue mussel *Mytilus edulis* has jumped a historical oceanographic barrier in northern Europe, extending its distribution by 1,000 km towards the north (Weslawski *et al.*, 1997; Berge *et al.*, 2005). The expansion was attributed to an anomalously large northward transport of warm Atlantic water into the Greenland (Berge *et al.*, 2006).

The distribution of intertidal organisms has also been extensively studied throughout the British Isles during the last century. Northern and eastern range extensions have been observed for several species of southern gastropod and barnacle species (Herbert *et al.*, 2003; Mieszkowska *et al.*, 2005; Mieszkowska *et al.*, 2006). The eastern limit of the southern (warm-water) algae *Bifurcaria bifurcata* has re-extended along the English Channel in the past four decades (Helmuth *et al.*, 2006). The poleward-range contraction of the cold-water algae *Alaria esculenta* at its southern limit in Britain is thought to be following the poleward shift of the summer 16ºC SST isotherm (Helmuth *et al.*, 2006). Furthermore, resurveys in the British Isles (Herbert *et al.*, 2003; Mieszkowska *et al.*, 2005) and in the North-Eastern Pacific (Barry, 1995; Sagarin, 1999) showed that, generally, the community composition has been changing with abundance ratios now favouring warm-water species. These comparisons showed that increases in the abundance of southern species of pelagic fishes, trochids, limpets, anthozoans, and barnacles occurred in parallel to significant raise in summer coastal SST.

Changes in physiology, phenology and in the distributional ranges will indubitably modify interactions between species, with repercussions to local abundance and distributions (Hughes, 2000). Changes in temperature patterns are expected to affect these interactions even more strongly (Walther *et al.*, 2002), since they alter the synchrony between many species' life cycles (Harrington *et al.*, 1999; Peñuelas and Filella, 2001; Stenseth *et al.*, 2002; Menzel *et al.*, 2006b). Unfortunately, most studies have concentrated on the effects of a single variable (usually temperature) on just one life-stage or one species, ignoring the complexity of possible relations within and between the abiotic and biotic constituents of climate change (Harrington *et al.*, 1999; Przeslawski *et* *al.*, 2005). There are, however, some exceptions which have shown that species interactions in the intertidal zone may be sensitive to even subtle changes in climate (e.g. Southward and Crisp, 1954; Southward, 1991; Leonard, 2000). In the North-East Pacific, increasing sea temperature derived from upwelling relaxation has been used to document changes in the strength of the interaction between a keystone predator and its prey (Sanford, 1999). It is also very likely that the warming sea temperature was the driving factor behind the increases in abundance of the starfish *Asterias forbesi*, thus causing the decline in the cold-water congener *Asterias vulgaris* in the North-West Atlantic (Harris and Tyrrell, 2001). In the same region, it was shown that competitive interaction between two barnacle species (*Chthamalus fragilis* and *Semibalanus balanoides*) is drastically influenced by small alterations in microclimate, which could benefit one or another species, depending on the direction of the change (Wethey, 2002). In the Bering Sea, variations in atmospheric circulation and ocean currents influence the abundance of walleye pollock, an important foraging fish for many other species (Wespestad *et al.*, 2000). Thus, the climatic influence affecting the basal species is subsequently propagated throughout the entire food web (Ciannelli *et al.*, 2005). This effect was also recently reported for plankton-based food webs in North-Eastern Atlantic (Richardson and Schoeman, 2004). A final example can be found in coral reefs from tropical seas. Drastic community changes are commonly observed when mass coral bleaching occurs (due to sea warming, for example) since the majority of organisms associated with corals depend on the reef for shelter and as their primary energy source (Hoegh-Guldberg, 1999).

Although it is clear that climate has and will continue to have a large influence on different species in rocky intertidal ecosystems, it should not be expected to observe climate change impacts everywhere (Helmuth *et al.*, 2006). Recent evidence indicate that the distributional limits of many intertidal species are not exhibiting the same trend or extension of poleward expansions, with some species showing little or no change despite exposure to warming sea and air temperatures (Rivadeneira and Fernández, 2005; Halpern and Cottenie, 2007). Furthermore, it is unlikely that climate change will produce a similar increase in temperature at global scale (see section 1.1.4). It will most likely involve geographically-specific changes in diurnal and seasonal patterns of sea and air temperatures and other atmospheric and oceanographic conditions (Helmuth *et al.*, 2005). Thus, global warming may not generate poleward shifts in the distribution of intertidal organisms as previously suggested (Walther *et al.*, 2002), but may instead cause localized extinctions at series of hot-spots (Helmuth *et al.*, 2002). It is very important to note that many of these potential alterations in abundance and/or distribution can only be detected by continuous monitoring, as they can occur abruptly and without warning. Moreover, the challenge here is not simply to examine responses, but to the use existing knowledge in an effort to forecast future changes and to comprehend how and when such responses are related to climatic variability (Araújo and Rahbek, 2006; Helmuth *et al.*, 2006).

1.3 Species modelling as a tool for understanding the effects of climate change

Potential impacts of the projected climate change on biodiversity have been often assessed using single-species bioclimatic envelope models. Over the last years, these models have become commonplace in biogeographic studies (Araújo and Guisan, 2006). After having identified a species' climate envelope, the application of future climate scenario data enables potential redistribution of the geographic domain of the species to be estimated (Pearson and Dawson, 2003). These bioclimatic models are not only useful first filters for identifying locations and species that may be at greater risk (Pearson and Dawson, 2003; Thuiller *et al.*, 2005) but may also be informative in investigating the likelihood that a particular change in climate affect species' distributions (Araújo *et al.*, 2006a). Their application to climate change analyses was recently highlighted by an impressive study considering the possibility of future mass extinction at a global scale (Thomas *et al.*, 2004).

Methodological advances in this area have been growing exponentially (Guisan and Zimmermann, 2000), and a remarkable diversity of modelling tools is now available to be used depending on the particular nature of the variables considered in each study. The statistical evaluation of models and model outputs have also been improved in different ways (Guisan and Thuiller, 2005). It is important to become aware that not all methodologies are appropriate for all conditions (Guisan and Thuiller, 2005). In fact, the uncertainty that arises from choosing different analyses, spatial resolutions, scales, modelling techniques and evaluation methods is sometimes greater than the variability originated by the use of different climate change scenarios (Thuiller, 2004). However, the choice of the correct statistical method, which seems to be the most critical factor influencing the results (Johnson and Omland, 2004), is nowadays sustained by numerous comparisons (Moisen and Frescino, 2002; Segurado and Araújo, 2004). Still, the decision of which model to use has generally been *ad hoc* (Araújo and Rahbek, 2006). Multicollinearity and data autocorrelation can also influence model selection and thus deserve careful consideration, but have been ignored in most studies (Guisan and Thuiller, 2005).

The sudden increase in the number of publications focusing on methodological aspects of distribution models allowed substantial progress to be made, but on the other hand, concealed some of their characteristic limitations within the bulk of new information (Guisan and Thuiller, 2005). Undeniably, there are still essential conceptual ambiguities and also some reserve regarding most biotic processes and algorithmic aspects in the modelling process that must be properly explored prior to fully entrusting model outputs (Araújo and Guisan, 2006). Thus, due to their different sources of uncertainty, the models and the results they yield should be applied whilst also recognizing their limitations (Pearson and Dawson, 2003; Thuiller, 2004; Araújo *et al.*, 2005a; Araújo *et al.*, 2005b). Although a wide range of statistics is being increasingly used in an attempt to validate models by comparing predictions with resampled observations within the training data set (resubstitution), it is very important to acknowledge that the predictive accuracy of climate envelope models can only be fully assured by direct contrast of model predictions with independent observations in time or space (Araújo *et al.*, 2005a). Nevertheless, such validation has been limited by the inevitable lack of data against which projections of future ranges can be tested (Araújo *et al.*, 2005b).

Finally, the validity of climatic envelope approaches has been recently questioned, since many factors other than climate (such as biological interactions, adaptive genetic variation or dispersal limitation) can significantly determine species distributions and influence the dynamics of distribution changes (Davies *et al.*, 1998; Pearson and Dawson, 2003; Hampe, 2004). Furthermore, current species distributions are not necessarily in phase with the contemporary climate and thus may discredit any attempt to predict future distributions (Pearson and Dawson, 2003). Nonetheless, these models can present a quick and useful tool for the identification of key relationships between species and the factors controlling their distribution (Huntley *et al.*, 2004) especially at large scales (e.g. continental and global) where the importance of climatic forcing is higher (Pearson *et al.*, 2002; Pearson and Dawson, 2003). Furthermore, when the physiological factors that limit the range of the studied species are poorly known, these methods may represent the best possible approach (Crumpacker *et al.*, 2001).

In conclusion, although the use of bioclimatic envelopes is highly appealing, their novelty means they had not yet been sufficiently tested and hence more empirical evidence needs to be gathered in order to reinforce the confidence on them and on their predictions (Araújo *et al.*, 2005b).

1.4 The rocky intertidal habitat

Rocky intertidal habitats owe their existence to the cyclic effect of tide in the contact region between the terrestrial and marine domains. Organisms inhabiting this zone comprise an ideal model for studying the effects of large-scale climatic drivers due to several reasons. They are periodically exposed to rapidly fluctuating and extreme temperatures and desiccation regimes, living close to their thermal tolerance (Helmuth *et al.*, 2002; Tomanek and Helmuth, 2002). Intertidal species respond more rapidly than their terrestrial equivalents to environmental changes because of their usually short life-span associated with sessile adult stages (Southward *et al.*, 1995). Unlike marine organisms such as fish, most rocky shore species are generally free from intense human harvesting (thus the confounding effect of exploitation can normally be neglected) and their ecologies are relatively well-known (Simkanin *et al.*, 2005).

For these reasons, intertidal species have been suggested as sensitive early warning systems for the impacts of climate change (Barry, 1995; Southward *et al.*, 1995; Thompson *et al.*, 2002; Hawkins *et al.*, 2003; Harley *et al.*, 2006). Furthermore, surveys of intertidal organisms can be easily made since they are generally conspicuous, slow moving or sedentary, and their ranges are roughly one-dimensional, conveniently defined by the coastal endpoints (Sagarin and Gaines, 2002). In conclusion the study of intertidal communities has the potential to provide a unique perspective on the relationships between the changing environment and the physiology and the ecology of organisms (Helmuth *et al.*, 2006).

1.5 The Portuguese coast

The Portuguese coast is particularly well suited for the study of the putative effect of climate warming on species distribution for several reasons. First, the clear north–south orientation of the coastline is the most appropriate for this type of analysis (Rivadeneira and Fernández, 2005). Second, it is a contact region between warm- and cold-water species, where both northern and southern boundaries of several organisms can be found (Fischer-Piétte, 1959; Fischer-Piétte and Gaillard, 1959; Fischer-Piétte, 1963; Ardré, 1970; Santos, 2000). Finally, shifts in species distribution have been described since the 1950s, not only for this particular stretch of coastline but also for the Iberian Peninsula (Fischer-Piétte and Forest, 1951; Fischer-Piétte, 1957a; Fischer-Piétte and Kirsch, 1957; Fischer-Piétte and Prenant, 1957; Ardré, 1971; Santos, 2000).

The main sources of historical information on intertidal species distribution and abundance for the Portuguese coast are the comprehensive works of Nobre (1931a; 1931b; 1936; 1938; 1940), Miranda (1934), Palminha (1951), Dizerbo (1954), Fischer-Piétte (Fischer-Piétte, 1957b; 1957a; 1958; 1959; 1963) Fischer-Piétte and Forest (1951), Fischer-Piétte and Prénant (1957), Fischer-Piétte and Gaillard (1959) and Ardré (1970; 1971). When considered together, these studies provide an extensive and detailed picture on the abundance of a wide range of intertidal species, from algae to molluscs and crustaceans, between the decades of 1930 and 1960.

On the other hand, during the last decades, the majority of the Portuguese rocky coast has been neglected by marine ecologists working on biogeography (Santos, 2000; Boaventura *et al.*, 2002b). Most of the studies were performed over a limited geographical area (e.g., Saldanha, 1974; Santos, 2000; Araújo *et al.*, 2005c; Araújo *et al.*, 2006b), studied a restricted taxonomic group (Guerra and Gaudêncio, 1986; Lopes *et al.*, 1993; Marques and Bellan-Santini, 1993), or when covering a large areas, covered only a small number of macrospecies (Boaventura *et al.*, 2002b). As a result, none of them provides sufficient data to obtain a global picture of the current distribution and abundance of intertidal organisms. Therefore, in addition to difficulties in integrating them into current research, it is very hard to make comparisons with historical data.

1.6 General objectives

The present study can be conceptually divided into three main sections. The first part was aimed at describing geographic patterns in the distribution of several intertidal species along the Portuguese rocky coast, within the European context (e.g., section 2.2). The relationship between patterns of distribution of crustacean epifauna and conspicuous macroalgal species was for the first time investigated in this area (section 2.1). The need to objectively define biogeographic discontinuities along the coastline for a high number of species resulted in the development of an analytical tool to characterize multivariate boundaries in one-dimensional and unevenly distributed data (section 2.3).

The second section emphasizes the comparison of contemporary biogeographic patterns with historical data. The observed modifications were studied considering the current theory on species responses to climate change. Thus, the hypothesis that boundaries would be in general shifting northwards in response to current warming was explicitly tested using data on intertidal algae (section 3.2). On the other hand, the past 50-year trend on the climatic and oceanographic conditions along the South-Western European coast was also assessed. Plausible theories to explain the observed changes, like changes in upwelling regimes, sea surface and air temperatures or coastal current patterns were discussed, and whenever possible, testable explanatory models were suggested (e.g., section 3.1). To examine the possible effects of the warming sea temperature during the reproductive period of the intertidal algae *Himanthalia elongata* (a cold-water species which is known to be retreating its distributional range towards the north), the reproductive growth of individuals transposed beyond the present southern boundary was compared with growth from individuals measured within the northern stable populations (section 3.3).

Finally, the third and last part of the work intended to use a single-species bioclimatic envelope approach to gain some insights into the factors driving the distribution of a marine gastropod, *Patella rustica*, in the northeast Atlantic (chapter 4). The model was implemented to understand the likely mechanisms governing the distribution of this limpet rather than to predict its future distribution.

1.7 Submitted and published manuscripts

The present thesis encompasses results from a project which was developed during the last four years. The thesis is presented as a series of linked chapters, each including one or more sections. Each section is a paper or a manuscript (in submission or in preparation). A general discussion integrates and synthesizes the work in the thesis.

The complete list is as follows:

Pereira S. G., **Lima F. P.**, Queiroz N. C., Ribeiro P. M. and A. M. Santos (2006). Biogeographic patterns of intertidal macroinvertebrates and their association with macroalgae distribution along the Portuguese coast. *Hydrobiologia*, **555**:185-192.

Lima F. P., Queiroz N. C., Ribeiro P. M., Xavier R., Hawkins S. J. and A. M. Santos (Submitted). First record of *Halidrys siliquosa* (Linnaeus) Lyngbye in the Portuguese coast. *Botanica marina*.

Lima F. P., Santos A. M. and S. J. Hawkins (In preparation). Detection of boundaries in one-dimensional unevenly distributed ecological data using split moving window gradient analysis (SMWGA).

Lima F. P., Queiroz N. C., Ribeiro P. M. Hawkins S. J. and A. M. Santos (2006). Recent changes in the distribution of a marine gastropod, *Patella rustica* Linnaeus, 1758, and their relationship to unusual climatic events. *Journal of Biogeography*, **33**:812-822.

Lima F. P., Ribeiro P. M., Queiroz N. C., Hawkins S.J. and A. M. Santos (Submitted). Do long-term changes in intertidal algae assemblages in the northeast Atlantic reflect warming? *Global Change Biology*.

Lima F. P., Queiroz N. C., Ribeiro P. M., Felga Ana C., Pereira Rui, Pinto Isabel S., Hawkins S. J. and A. M. Santos (Submitted). Transplant experiments on the retreat of the southern distribution limit of *Himanthalia elongata* (Linnaeus) S.F. Gray in the northeast Atlantic. *Journal of Biogeography*.

Lima F. P., Ribeiro P. M., Queiroz N. C., Xavier R., Tarroso P. , Hawkins S.J. and A. M. Santos (Submitted). Modelling past and present geographical distribution of the marine gastropod *Patella rustica* as a tool for exploring responses to environmental changes. *Global Change Biology.*

Chapter 2

Spatial analysis of biogeographic patterns

Section 2.1

Biogeographic patterns of intertidal macroinvertebrates and their association with macroalgae distribution along the Portuguese coast

2.1.1 Abstract

Geographical patterns in the distribution of epifaunal crustaceans (Amphipoda, Isopoda and Tanaidacea) occurring with dominant macroalgal species were investigated along the Portuguese rocky coast. Three regions, each encompassing six shores, were studied. Algal species were selected according to their geographical distribution: *Mastocarpus stellatus* and *Chondrus crispus* (north); *Bifurcaria bifurcata* (north-centre); *Plocamium cartilagineum* and *Cystoseira tamariscifolia* (centre-south); *Corallina* spp. and *Codium tomentosum* (entire coast). Multivariate techniques were used to test for differences in crustacean assemblage composition between sub-regions and host algal species. A clear gradient of species substitution was observed from north to south. Differences in abundance and diversity of epifaunal crustaceans were observed between southern locations and the remaining sites. Four species were recorded for the first time in the Portuguese coast. Among the 57 *taxa* identified, southern distribution limits were observed for three species and northern distribution limits were observed for four

species. Interestingly, the observed geographical patterns in epifaunal abundance and diversity were not related with geographical changes in the indentity of the dominant algal species.

2.1.2 Introduction

Understanding the causes driving species distribution is a major challenge of modern biogeography. The analysis of the relation between patterns of distribution of organisms and physical or biological factors is usually the first step towards this goal (Hoffman and Blows, 1994). In the marine environment, most large to medium scale studies were primarily focused on the importance of physical factors in the distribution of species (van den Hoek, 1984; Cambridge *et al.*, 1987; Zacharias and Roff, 2001).

Marine algae are known to provide habitats for a wide range of animal species (Williams and Seed, 1992). Several studies addressed the role of seaweeds as determinants of epifauna diversity (Kitching, 1981; Kelaher *et al.*, 2001; Parker *et al.*, 2001; Chemello and Milazzo, 2002; Christie *et al.*, 2003). However, few attempts have been made to investigate the relation between geographical changes in algae composition and patterns of macroinvertebrate diversity (Arrontes and Anadón, 1990a; Russo, 1997).

A considerable number of both cold- and warm-water algal species reach their distributional limits within the Portuguese coast (Ardré, 1971). In the lower eulittoral, northern shores are dominated by large macrophytes, such as *Himanthalia elongata* (Linnaeus) S.F. Gray, and the red algae *Chondrus crispus* Stackhouse and *Mastocarpus stellatus* (Stackhouse). Towards the south, these species are replaced by *Cystoseira tamariscifolia* (Hudson) and other red algae become dominant, especially *Plocamium cartilagineum* (Linnaeus) (Ardré, 1970, 1971). Despite these differences, no attempts have been made to couple such information with the patterns of distribution of the associated fauna. Recent biogeographical studies in the Portuguese coast addressed solely the distribution and abundance of conspicuous animals (see Boaventura *et al.*, 2002). In contrast, smaller organisms, including those inhabiting seaweeds, have been poorly studied. The information available on these *taxa* often comes from unpublished academic theses, and in most cases is of limited geographic scope.

The purpose of this study was to: (1) provide a description of the patterns of distribution of algal dwelling crustaceans (Amphipoda, Isopoda and Tanaidacea) along the Portuguese rocky coast and (2) make a preliminary attempt to test the relationship between patterns of distribution of crustacean epifauna and conspicuous macroalgal species.

2.1.3 Material and methods

Study area

The study area encompassed the whole continental Portuguese coast and was divided in three regions (North, Centre and South), corresponding to the main stretches of rocky coastline (Figure 2.1.1). Within each region, six shores with similar geomorphology and wave exposure were selected. Samples of the dominant macroalgae were collected from each shore.

Sampling procedures

Algal species were selected according to their geographical distribution. *M. stellatus* and *C. crispus* are abundant in the north of Portugal, becoming rare or absent towards the south. *Bifurcaria bifurcata* R. Ross is characteristic of northern and central shores. *P. cartilagineum* and *C. tamariscifolia* are abundant in the centre and south. *Corallina* spp. (*C. elongata* J. Ellis and Solander and *C. officinalis* Linnaeus) and *Codium tomentosum* Stackhouse are common along the entire study area. For further details see Figure 2.1.2.

Algae were collected either individually (*Cystoseira*, *Codium* and *Bifurcaria*) or by scraping 20 x 20 cm quadrats of monospecific stands (*Corallina*, *Chondrus*, *Mastocarpus*, *Plocamium*). Samples were preserved in formalin (10%). Extraction of animal species was made by washing the algae in flow water through a set of sieves (5 mm to 250 µm mesh). The fraction retained in the 250 µm sieve was sorted under the binocular miscroscope (10x magnification). In addition, the

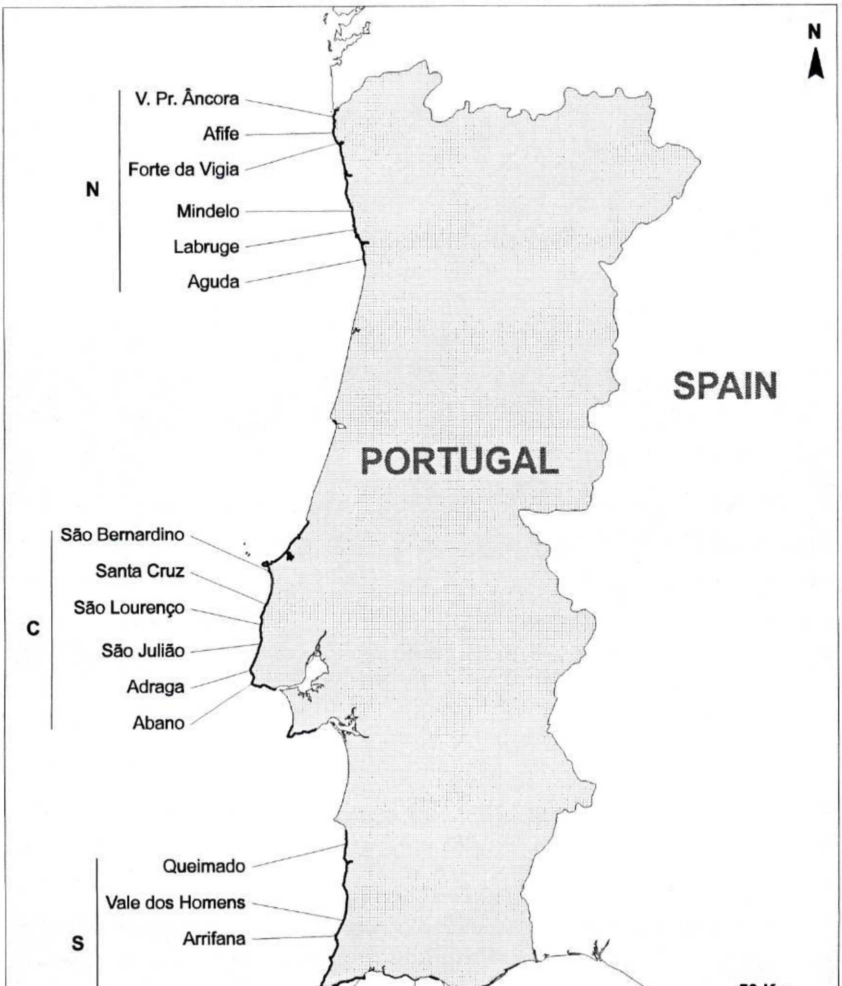

Figure 2.1.1 Location of the studied shores in the Portuguese coast. The main stretches of rocky coastline are depicted in black. sampled location. N: 1 – Vila Praia de Âncora, 2 – Afife, 3-Forte da Vigia, 4 – Mindelo, 5 – Labruge and 6 – Aguda; C: 7 – São Bernardino, 8 – Santa Cruz, 9 – São Lourenc¸o, 10 – São Julião, 11 – Adraga and 12 – Abano; S: 13 – Queimado, 14 – Vale dos Homens, 15 – Arrifana, 16 – Porto de Mós, 17 – Castelo and 18 – Olhos d'Água.

algae were also inspected under a binocular microscope to pick any remaining organisms. All animals were counted and identified to the

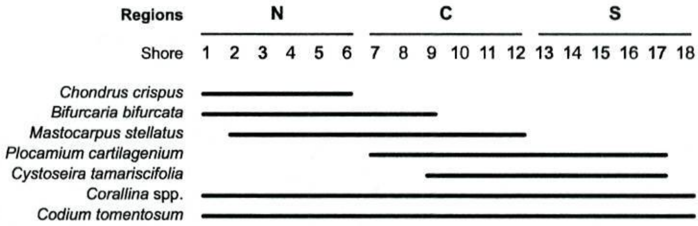

Figure 2.1.2 Shores where the algae species were sampled. For locations names see Figure 1.

lowest possible *taxon*. Due to the different structure of the selected algal species, the density of animals was expressed as number of individuals per volume of algae. After removal of macroinvertebrates the algae were dried for 2 h. They were then inserted into a graduated cylinder with a fixed amount of water, and the volume of algae was estimated as the difference between the initial and final volume.

Data analysis

Multivariate analyses were carried out with the PRIMER package (Clarke and Warwick, 1994). Non-parametric multidimensional scaling (nMDS) ordination of samples (alga/site) was performed using Bray-Curtis similarity coefficient. Transformation of animal abundances into presence-absence was chosen in order to minimise data variability. To determine a possible correlation between epifaunal assemblages and algal species a Mantel test (Sokal and Rohlf, 1995) was carried out using distance matrices for sites based on presence-absence of animal and algal species. One-way ANOSIM analyses to test for differences in epifaunal assemblages of algal species were made separately for each region to overcome the problem related to the lack of orthogonality of the two factors involved (regions and algal species). One-way ANOSIM analyses were also employed to test for differences in species composition between the three regions. In order to avoid confounding effects between regions and algae, only species which span along the entire coast were used (*Corallina* spp. and *C. tomentosum*). To achieve an overall Type I error rate of $\alpha = 0.05$ in multiple tests, a Bonferroni correction was used (Quinn and Keough, 2002).

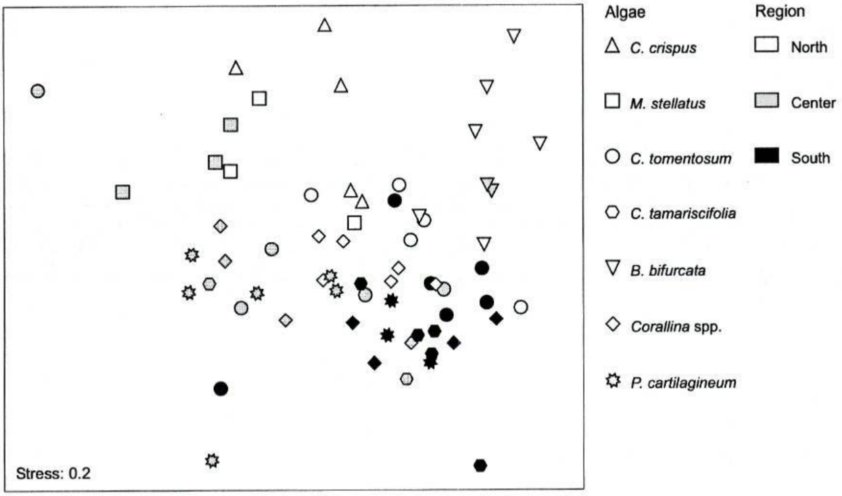

Figure 2.1.3 nMDS ordination of the samples (algae/site). Regions are depicted by different grades of shade, and algal species by different shapes.

2.1.4 Results

A total of 57 *taxa* were identified (34 amphipods, 19 isopods and four tanaids). Most *taxa* occurred with more than one algal species (32% of the *taxa* were observed at least in five algae). Seven species were seaweed-specific (five were found in *Corallina* and two in *Cystoseira*). From these, only *Biancolina algicola* Della Valle (found in *Cystoseira*) occurred consistently in more than one site. The nMDS ordination (Figure 2.1.3) revealed a significant interspersion of samples. No clear pattern between regions or algal species was observed. Furthermore, the stress value (0.2) suggests that too much reliance should not be placed on the detail of the plot (Clarke and Warwick, 1994).

Differences in macroinvertebrate assemblages were found between regions (ANOSIM $r = 0.209$; $p < 0.05$). Multiple tests revealed significant differences between all regions. A clear latitudinal gradient of substitution was shown plotting macroinvertebrate species against sampled sites. Figure 2.1.4 depicts this gradient in more detail. Low similarity within regions was found (32– 45%), denoting a high heterogeneity between replicate shores. The *taxa* with higher contribution to the dissimilarity between regions were found after SIMPER analysis: *Jassa* spp., *Idotea*

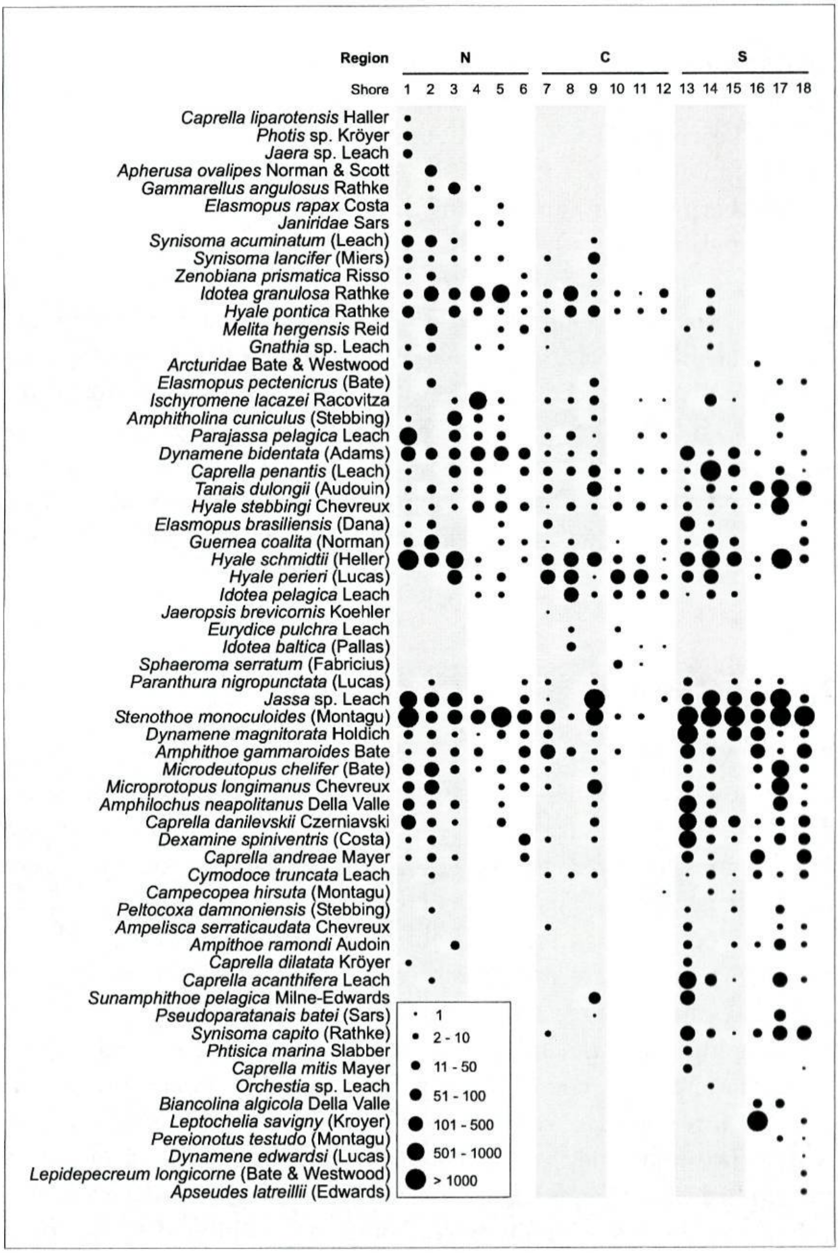

Figure 2.1.4 Graphical representation of macroinvertebrate abundance *vs.* sampled location. Abundances are expressed as number of individuals per 1000 cm^3 of algae. For locations names see Figure 1.

pelagica Leach and *Dynamene bidentata* (Adams) for North vs. Centre; *Idotea granulosa* Rathke, *Dexamine spiniventris* (Costa) and *Synisoma capito* (Rathke) for North vs. South; *Dexamine spiniventris* (Costa), *I. pelagica* Leach and *Jassa* spp. for Centre vs. South. Although most species were found along the entire coast, several were present exclusively in the northern or southern regions. In most cases, these species were represented by one or few individuals found in one type of seaweed at a single shore and did not contribute in a consistent way to the differences between sub-regions. ANOSIM analyses did not reveal any significant differences in epifaunal assemblages between algal species for the southern and central regions (ANOSIM $r = 0.048$, $p > 0.05$ and $r = 0.306$, $p > 0.05$ respectively). For the northern region differences were found between *B. bifurcata, Corallina* spp. and the remaining algae (ANOSIM $r = 0.445$, $p < 0.05$). The Mantel test revealed a low, but statistically significant, correlation between algae and epifauna ($r = 0.2429$; $p < 0.05$).

2.1.5 Discussion

Broad geographical differences in crustacean epifauna diversity were found along the continental Portuguese coast. A statistically significant difference in crustacean assemblage composition was found between the three regions. The species gradient supports the idea that the Portuguese coast acts as a region of contact between warm-water (from north Africa and the Mediterranean Sea) and cold-water species (from the North Sea and the Arctic) as described in earlier works (Ardré , 1970, 1971).

Four species were recorded for the first time in the Portuguese coast: two amphipods, *Caprella mitis* Mayer and *B. algicola*, one isopod, *S. capito*, and one tanaid, *Leptochelia savignyi* (Kroyer). Previously, the first three species were only recorded in the Mediterranean Sea. Not surprisingly, southern distribution limits were also detected in the studied area: *Amphitolina cuniculus* (Stebbing), *I. pelagica* and *I. granulosa*. The two idoteids were thought to be limited to northern Spain (Arrontes and Anadón, 1990b), but their range extends as far as southern Portugal.

Apparently, the observed geographical differences in epifaunal crustaceans were not related with differences in dominant algal species. These observations differ from those described by Arrontes and Anadón (1990a) for northern Spain, who found that several isopod species responded to geographical changes in algal composition. Interestingly, the three idoteid species were closely associated with algae that displayed geographical changes in abundance. This is certainly not the case in the Portuguese coast. *Idotea granulosa* and *I. pelagica* were commonly found in *Corallina* (which ranges from north to south) and in both northern (*Chondrus* and *Mastocarpus*) and southern (*Cystoseira* and *Plocamium*) algal species.

Most *taxa* displayed no preference for a particular alga, occurring in association with different macroalgae species at different geographical locations. Only *B. algicola* was found consistently in *Cystoseira* at two different sites. The lack of a strict host specialisation by epifauna has been reported by several authors (Russo, 1990; Parker *et al.*, 2001).

Algal architecture might play a more important role in determining epifaunal diversity and abundance (e.g. Crisp and Mwaiseje, 1989; Chemello and Milazzo, 2002; Kelaher, 2003). In the present study, finely branched macroalgae (*Cystoseira*, *Plocamium* and *Corallina*) exhibited a more diversified and abundant epifauna, when compared with the other five species, which have a less complex architecture. *Mastocarpus* and *Chondrus*, the only algae with blade-like structure, presented the lowest diversity values. These findings prompt for a more detailed analysis with a sampling strategy aimed towards algal complexity rather than algal species. In the present study, many non-dominant, but common, algal species were left out. Yet, when contiguous to the dominant plants, they may also account for a large proportion of the epifauna, especially when highly mobile organisms are considered (Gunnill, 1982).

Some of the species recorded in this study are probably transient in the lower shore. This is the case of *Phtisica marina* Slabber, *Synisoma acuminatum* (Leach), *Idotea baltica* (Pallas) and *Campecopea hirsuta* (Montagu), which are known to occur along the entire Portuguese coast, but appeared sporadically on some samples. The first three are mainly sublittoral species, whilst the latter is typically found in the upper midshore among barnacles and in *Lichina pygmaea* (Lightfoot) Agardh (Arrontes and Anadón, 1990b, for the isopod species). Other species are also abundant in non-algal substrates. In the present study *I. pelagica* was more common in the centre and southern Portuguese coast, but in fact it is one of the most abundant species found among mussels in the northern shores (A. M. Santos, unp. data). Removal of such species from the data did not alter the final outcome of the analysis.

Analysis of temporal and small-scale spatial variability was not addressed in the present study due to logistic constraints given the large sampling area. However, both sources of variation are known to be important (Kelaher *et al.*, 2001). Futhermore, some species may exploit distinct habitats in different phases of their life-cycle. For example, Arrontes and Anadón (1990a) found that many isopod species displayed marked seasonal variation in algal occurrence, with macroalgae providing a habitat for juvenile stages, while adults occurred elsewhere. Other traits, such as feeding behaviour, vagility or response to predators, may also contribute to the high variation in epifaunal abundance and composition observed among different algal species (Williams and Seed, 1992) or even different thalli of the same or similar species (Gunnill, 1982; Kelaher *et al.*, 2001). Therefore, replication at these small-scale levels is mandatory to distinguish wandering organisms from true host-plant specialists, which are more likely to be affected by changes in the distribution of their host.

The present study found that epifaunal crustacean assemblages display marked geographical differences along the Portuguese coast. Northern and southern limits of distribution were detected for several of the 57 *taxa* identified. In addition, four new species were recorded outside their previously known distribution range. Biogeographical patterns of epifauna seem not to be related with geographical changes in dominant algal species. Instead, physical factors, such as temperature, water currents and wave exposure, or biological factors, such as algal architecture, might play a more important role as determinants of epifaunal distribution and should be investigated in detail.

2.1.6 Acknowledgements

F. P. Lima and P. A. Ribeiro were funded by Fundação para a Ciência e Tecnologia (FCT) grants ref. SFRH/BD/8730/2002 and ref. SFRH/BD/8232/2002, respectively. We also would like to thank the contribution of two anonymous referees and Prof. Vitor Quintino for their helpful comments on the manuscript.

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Section 2.2

First record of *Halidrys siliquosa* (Linnaeus) Lyngbye in the Portuguese coast

2.2.1 Abstract

The occurrence of the pod weed, *Halidrys siliquosa*, is recorded for the first time in the Portuguese coast. Several specimens of this brown algae were observed attached to the rocky surface in tide pools at 41°44'10"N 8°52'34"W, extending southward its known geographical distribution.

2.2.2 Main text

Halidrys siliquosa (Linnaeus) Lyngbye is the only species of this genus that can be found on the European coast. It is a perennial macroalgae (Cabioc'h *et al.*, 1992; Buschbaum *et al.*, 2006) with a life span of at least three years (Moss and Lacey, 1963). Data from northern England showed that this species displays reproductive seasonality: in the first year only vegetative growing occurs; reproductive organs develop during the late summer and autumn and gamete discharge occurs from winter to early spring (Moss and Lacey, 1963).

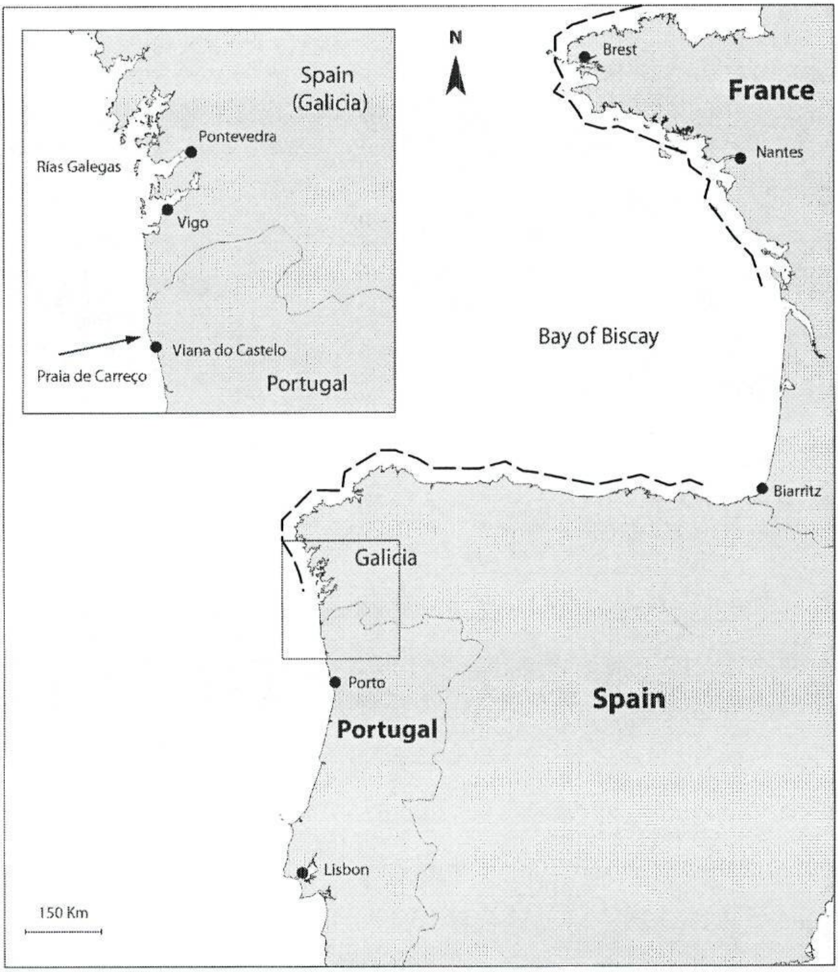

Figure 2.2.1 *Halidris siliquosa*: Distribution range of in South-western Europe. Historical distribution is depicted by the dashed line. Inset figure represents a magnification of northern Portugal and southern Galicia. The new reported boundary is signalled with an arrow.

Halidrys siliquosa is a common species in the intertidal zone from the north of the Scandinavian Peninsula (Luning, 1990) to Brittany, in north-west France (Crisp and Fischer-Piétte, 1959) (Figure 2.2.1). Towards the south its density decreases progressively and this species is completely absent on the French Basque coast. Like many northern species, colonization of shores in this warmer region fails, even under

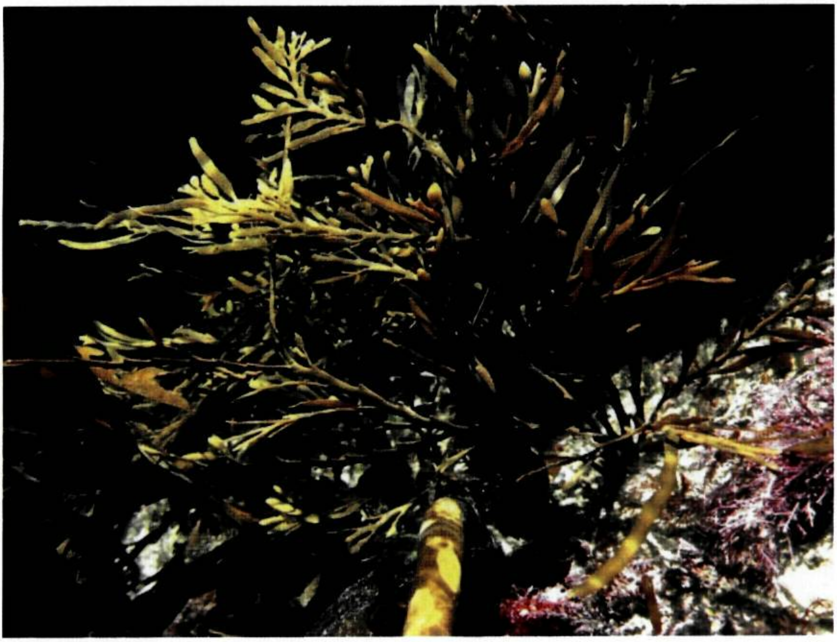

Figure 2.2.2 *Halidris siliquosa* in a tide pool in the Praia de Carreço, Northern Portugal.

a continuous supply of stranded fertile plants arriving from the north (Crisp and Fischer-Piétte, 1959). Throughout the northern Spanish coast, this species displays a scattered distribution (for a review, see Margalet and Navarro, 1990). Its historical southern range limit is located at the Galician province, in the Rìas Baixas region. Several authors confirmed the existence of *H. siliquosa* in this area, although most of the references are of isolated or stranded specimens(for example Hamel, 1928; Miranda, 1934; Fischer-Piétte, 1955; 1963). However, at least in the northern Rías of Coruña, Muros, Arosa and Pontevedra, some subtidal populations have been recorded (Bárbara and Cremades, 1996) in locations sheltered by the sinuous coastline and under strong upwelling influence (Otero-Schmitt and Pérez-Cirera, 2002). The southernmost individuals ever observed were found inside the Ría of Pontevedra (Miranda, 1934).

Halidrys siliquosa has a wide vertical range from pools at high water spring tides (HWST) to below the sublittoral fringe. On the most sheltered locations it can be found in the sublittoral and in rock pools below low water neap tides (LWNT), while on exposed locations it frequently occurs in deep pools in the eulittoral (Moss and Lacey, 1963).

Even though Portuguese intertidal communities have been extensively surveyed during the last decades (Fischer-Piétte, 1958; 1963; Ardré, 1970; Santos, 1994; 2000; Boaventura *et al.*, 2002; Araújo *et al.*, 2005; Araújo *et al.*, 2006; Pereira *et al.*, 2006), *Halidrys siliquosa* was never observed attached to substrata. Some stranded specimens were found during the 1930s (Rodrigues, 1963; Ardré, 1970), but apparently populations never established successfully in northern Portugal. Subtidal surveys in this area also revealed the absence of this species.

In the summer of 2006 several individuals were observed for the first time in Portugal, at Praia de Carreço (41º44'10"N 8º52'34"W), near Viana do Castelo. Specimens were firmly attached to the rock surface, in several deep pools in the lower eulittoral (Figure 2.2.2). While some algae were collected and preserved in herbarium for reference, other specimens were left *in situ* and the reproductive cycle was reassessed in the autumn. None of the observed individuals showed signs of reproductive development. This observation does not necessarily mean that this species is unable to reproduce at this location. Populations in the southern portion of the range frequently reproduce later in the year compared to northern populations (Lewis, 1986). Since Ardré (1957) observed fruiting *Halidrys siliquosa* in the north-western Spanish coast during February, this newly established population should be monitored at least until the end of winter.

These results showed a clear shift of the previous known southern boundary of *Halidrys siliquosa* distribution. Given that during the last decades an increase in temperature has been documented for this area (Lemos and Pires, 2004; Lemos and Sansó, 2006; Lima *et al.*, 2006), the present shift is inconsistent with general predictions of species migrations under warming climate conditions, which anticipate poleward shifts rather southern expansions (Hughes, 2000; Walther *et al.*, 2002) . These findings put emphasis on the importance of taking into account for the synchrony between climatic oscillations and species' population dynamics (Zacherl *et al.*, 2003) as well as accurate records of species distribution. There is also the possibility that in a warming world stronger equatorial winds could led to intensified upwelling causing counter-intuitive occurrence of coldwater low shore and subtidal species. Together with other species whose distributional limits are in a shifting process (see Lima *et al.*, 2006), *H. siliquosa* is ideal for a continuous study, which will definitely help to build more accurate predictive models on how species ranges are likely to shift in response to global climate change.

2.2.3 Acknowledgements

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Section 2.3

Detection of boundaries in one-dimensional unevenly distributed ecological data using split moving window gradient analysis (SMWGA)

2.3.1 Abstract

An improved version of the split moving window (SMW) algorithm is described. This new version, called split moving window gradient analysis (SMWGA), was developed to locate the position of one or more boundaries along a linearised series of unevenly distributed multidimensional data. The efficiency of the method was assessed using several artificially simulated data, including different scenarios with boundaries that varied in number, position and sharpness. Other important variables, like the heterogeneity of the gradient, noise in the data and the number of samples were also considered. The SMWGA method was also applied to real data, using abundances of 24 rocky intertidal species along both sides of the English Channel. Results showed that the SMWGA was able to detect the boundaries in most scenarios, and in real data, using unrestricted randomization significance tests. Its accuracy was highly dependent on data resolution, and sample size was the most influential variable. Positive and negative autocorrelation were found in practically all scenarios. Because of this, multivariate

autocorrelograms should be used to estimate autocorrelation prior to any interpretation of the SMWGA results.

2.3.2 Introduction

Over the last decades, ecologists began to consider spatial heterogeneity as a key for understanding nature's complexity and new theoretical models and methodological procedures were developed (Wagner and Fortin, 2005). Hence, new research has sought to explicitly understand, measure and model spatial patterns, instead of ignoring or trying to remove them from ecological studies (Liebhold and Gurevitch, 2002). Ecological boundary detection is usually the first step in the study of spatial heterogeneity. Boundaries can be defined as locations where the rate of change among the majority of variables is greatest (Burrough, 1986, Fortin *et al.*, 2000) Furthermore, boundaries are not static and have the potential to vary both spatially and temporally (Fagan *et al.*, 2003). Therefore, attention has turned from their simple description to the investigation of their functional importance (see Cadenasso *et al.*, 2003).

Community changes often coincide with regions of abrupt environmental clines which can condition the occurrence of some species (Fortin and Dale, 2005). This means that temporal changes on boundary locations may be used as indicators of environmental change (Wiliams-Linera, 1990; Fortin *et al.*, 2000). The detection of boundary shifts may thus be useful to track impacts of global warming (Fortin, 1994, Loehle, 2000), which is expected to cause abrupt and sudden ecological changes (IPCC, 2001).

Human observers often identify transition zones by using intuitive assignments, especially when data are univariate. However, identifying boundaries when dealing with compositional or multivariate datasets is not straightforward (Mac Nally, 2005). Therefore, it is clearly preferable to identify discontinuities based on objective, quantitative methods (Fortin and Edwards, 2001; Fagan *et al.*, 2003; Mac Nally, 2005). Traditionally, cluster analysis or ordination techniques have been used for this purpose, but interpretation was still subjective because the number of different groups (individuals, assemblages) had to be decided *a posteriori* (Panis and Verheyen, 1995). Modern hardware and software (e.g., Geographic Informations Systems – GIS), coupled with easy access to remote sensed data, boosted the development of spatial analysis in ecology, as revealed by the plethora of statistical techniques currently available (Dale *et al.*, 2002; Fortin and Dale, 2005). Detection of ecotones can be made on one-dimensional field data gathered along transects or on two-dimensional data collected across a grid, which will condition the methods to be used (Fortin *et al.*, 2000). Methods to analyse one-dimensional data have been neglected since the arrival of GIS based analysis, but given that they were the first to be developed the number of available techniques is still considerable (for a review see Cornelius and Reynolds, 1991).

One of the most used edge detection algorithms is based on the split moving window (SMW) method (Jacquez *et al.*, 2000; Dale *et al.*, 2002). Although initially designed for the analysis of geological data (Webster, 1973), this method was later introduced into ecology by Ludwig and Cornelius (1987). By making use of a kernel (i.e. a window of n cells), SMW computes rates of change in adjacent samples along gradient-oriented transects. These values are assigned to the centre of the kernel and the boundary placed in the location (or locations) with the highest variance. This approach was widely applied in soil science and vegetation ecology, where transects have a long-standing tradition (Jacquez *et al.*, 2000). However, the major drawback of SMW is that it requires evenly distributed sampling sites (Fagan *et al.*, 2003). Although this is straightforward for remote sensed data, the large sample size required, intense sampling effort, and cost attached to fieldwork makes it nearly impossible to sample field data in this way (Fortin, 1994). Even when human and financial resources are not limitative, some problematic cases remain.

Most long-term studies cannot make use of SMW without 'standardization' of data, which usually includes subsampling and loss of information, because they include ancient datasets in which data were in most cases irregularly sampled in space or time. Additionally, the nature of the studied subject may not allow regular sampling. For example, large scale surveys on intertidal rocky assemblages are typically restricted to rocky shores located between variable stretches of sandy beaches. Not surprisingly, only a few marine and coastal studies have

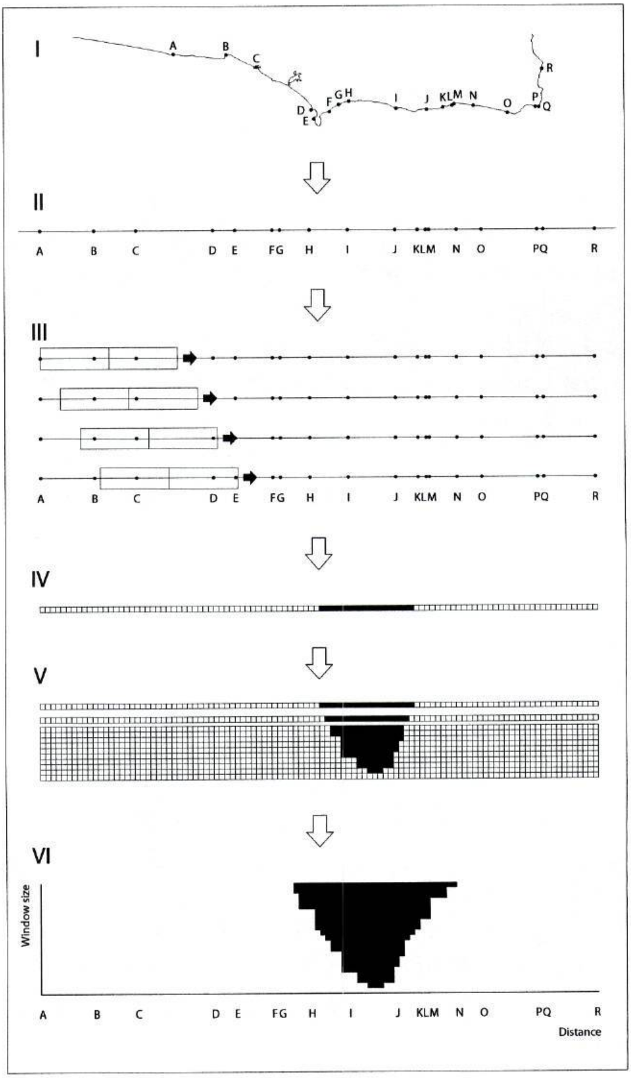

Figure 2.3.1 Schematic representation of the method. (I) Hypothetical transect along a coastline; (II) Transect linearization; (III) Split window moving along the transect; (IV) white (non-significant) and black (significant) results obtained with a particular window size; (V) results from several windows are combined; (VI) final result with an inverted triangle whose inferior vertex points to the boundary location.

used SMW analyses. Among these, most employ SMW only as a tool to analyse temporal series of climate data, following other approaches to interpret biological data (Beaugrand, 2003; Beaugrand and Reid, 2003). Some authors tried to solve the problem of data heterogeneity by using classes of distances instead of the real values (e.g., Panis and Verheyen, 1995).

In this work, an improvement of the SMW method described by Cornelius and Reynolds (1991) is presented. The method, hereafter named SMWGA (Split Moving Window Gradient Analysis), is appropriate to locate boundaries or discontinuities in one-dimensional unevenly distributed multivariate data sets. The efficiency of the method was assessed using several artificially simulated data sets, including different scenarios with boundaries that varied in number, position and sharpness. Other important variables, like the heterogeneity of the gradient, noise in the data and the number of samples were also considered. Finally, to analyse the efficiency of SMWGA under a real scenario, a data set with the abundances of 24 rocky intertidal species along both sides of the English Channel (Crisp and Southward, 1958) was used.

2.3.3 Material and methods

2.3.3.1 Split Moving Window procedure

The first step in SMWGA analysis is to gather multivariate data (species abundance, environmental factors, etc.) along a transect, such as a coastline (Figure 2.3.1 I). In SMWGA the transect does not have to be rectilinear but should always be a well defined path. Distances between consecutive locations along the path are then computed and the transect is transformed into a rectilinear segment with unevenly scattered sampling locations (Figure 2.3.1 II).

In the next step, a window of a given size is placed at the beginning of the series (Figure 2.3.1 III). The window is split in two halves and a dissimilarity measure is computed using the sampling locations falling inside each window half. The dissimilarity is assigned to the window's midpoint and the window is then moved one step forward. This process is repeated until the window reaches the end of the series. The result is an array of dissimilarities, one for each window's midpoint, which may or may not coincide with the actual position of sampling sites along the linearised path.

To determine the statistical significance of scale-dependent discontinuities, a permutation method is used (see below). Midpoints with significant dissimilarities ($p < 0.05$) are coded as one and the remaining ones are set to zero. Thus, in the end of a run for a given window size, a binary array of zeroes (non-significant dissimilarities) and ones (statistically significant dissimilarities) is obtained (Figure 2.3.1 IV). The process is then repeated for increasing window sizes and by combining the resulting binary arrays (Figure 2.3.1 V) it is possible to create a two-dimensional graphic depicting significant differences between sampled locations at different scales. The expected end result when a boundary exists is an inverted triangle with the lower vertex pointing to the putative boundary location (Figure 2.3.1 VI).

Several differences exist between the SMW algorithm described by Cornelius and Reynolds (1991) and SMWGA, namely the method used to compute dissimilarities between window halves, window size, placement and movement along the transect and the assessment of statistical significance of dissimilarities between windows halves. In SMW, dissimilarity between the two halves of a given window is computed using squared-Euclidean-distance (SED) after averaging each variable for all sampling sites within each half window. This sort of pooling is adequate when there is an equal number of observations in each half window and when variables are measured in a continuous scale.

However, in many ecological studies, variables are counts of individuals, some kind of abundance scales or even presence/absence data. Consider, for example a set of four sites (A, B, C and D) described by ten species and having seven species in common. Site B has an exclusive species and so does site C and D. Suppose that a given window compares site A against B, C and D, because the latter three are close together. The dissimilarity between the two halves will be inflated because it will compare seven species (A) against 10 (pooled B, C and D), even though location A only differs from B, C or D in one species. To avoid this problem, in SMWGA the dissimilarity for a given window is computed by averaging dissimilarities between every possible pair of samples from different halves. This unweighted-average, commonly used in some cluster analysis (see Legendre and Legendre, 1998) was the only one implemented in SMWGA algorithm to produce a faster code, but it can be easily extended to accommodate any sort of weighting technique which accounts for different numbers of locations or within dissimilarities of each half window.

Other major differences between SMWGA and SMW methods are the size, placement and movement of the window along the transect. In the original SMW analysis, because locations are evenly distributed along the transect, data can be transformed into an ordered data set – a vector or array - discarding any real distances between locations. Therefore, there is a fixed number of possible window sizes and a fixed number of windows midpoints: for a transect with *N* locations and a window size of *Q* there will be *N*-*Q* possible midpoints and the maximum window size will be *N*-2 (Cornelius and Reynolds, 1991). In SMWGA, due to the unevenly distribution of locations along the transect, this is not applicable. Since comparisons between window halves may be asymmetrical (with a different number of locations within each window half), there are almost no restrictions to the placement of windows midpoints. Thus a window midpoint may be placed exactly at the beginning of a series, coinciding with the first real position of a site (whenever a site coincides with the window midpoint it is treated as belonging to the left-half of the window). This has the advantage of allowing large windows to scan the whole series instead of being restricted to the centre of the series. On the other hand, this lack of restrictions, which also applies to the choice of the step distance (the amount by which the midpoint is incremented while moving the window along the series) brings some subjectivity to the analysis, because there will be multiple (technically infinite) combinations of window sizes and steps to analyse.

Simulated data

Several artificial data sets were constructed using Monte-Carlo simulations to evaluate the efficiency of the GSMW method under different scenarios. The use of a true quantitative abundance scale (real counts, percentage cover, biomass) was discarded from the beginning because it would increase the complexity of the simulations, adding

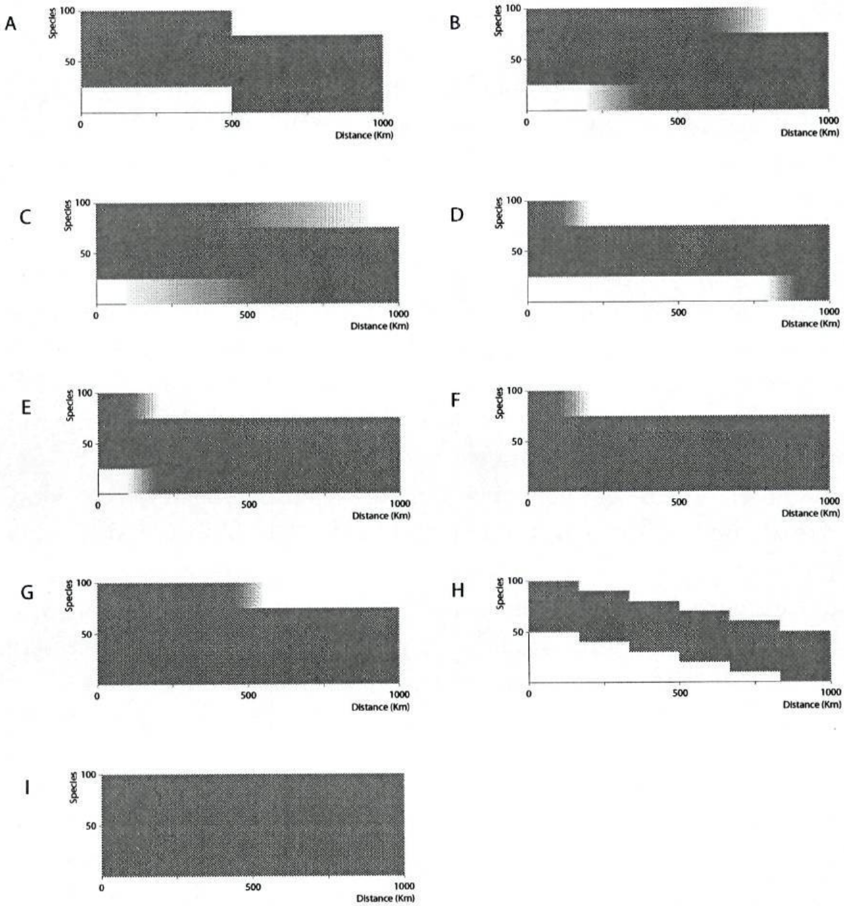

Figure 2.3.2 Visual representation of generated data sets. From A to E, boundaries were based on two groups of species, each decreasing from one side of the discontinuity. F and G simulated boundaries where the gradient was based on a single set of species. The last data set (I) was used as 'control', with none gradient present. H was made with a 'substitution gradient', without a boundary clearly defined. All the remaining cases had a single boundary, with the exception of D, with two. While in A-C and G the boundary was created on the centre of the transect (500 Km), in E-F it was generated near the beginning (100-200 Km).

another potential source of variability to the datasets. Instead, a semi-quantitative abundance scale with six levels of abundance was used. Simulations were based on the empirical distribution of these abundance levels for intertidal rocky-shore species, derived from an extensive data set of a 10-year survey encompassing part of the Western European and North African Atlantic coasts.

A total of 36 baseline scenarios was built, with the same basic configuration, consisting of 100 species and a variable number of locations distributed heterogeneously along a 1,000 Km transect. Eight gradient types were considered (Figure 2.3.2). One included two boundaries (Figure 2.3.2 D) while the remaining seven had a single boundary. Differences between the latter were based on the number of species in each side of the boundary, the boundary location in relation to the centre of the transect and the steepness of the species gradient around the boundary. Additionally, a ninth scenario was used as a control, in which no species gradient was created, although data variability was allowed (Figure 2.3.2 I).

The proposed method was devised to handle any situation where samples are unevenly distributed along a transect, thus including the case where sampling units are actually evenly distributed but, due to logistic constraints, are unevenly sampled. Nonetheless, its main purpose was to deal with cases where sampling is restricted to some kind of substrate or habitat covering only a small percentage of the whole transect. This is often the case in coastal surveys, where rocky and sandy habitats are interspersed (Crisp and Southward, 1958). However, density and distribution of suitable habitat along a transect may be important for the purpose of boundary detection. If the number of habitat regions in a large transect is small, samples will be more often clumped. Therefore, to assess the influence of habitat distribution heterogeneity (or sample 'aggregation') in SMWGA efficiency, four variants for each of the nine gradient scenarios were created, with habitat occupying 20, 40, 60, or 80% of the 1,000-Km transect.

Since survey data are typically characterized by having a 'noisy' structure which results from natural variation, misobservation due to species' cryptic habits, or measurement errors (Sagarin, 1999), artificially generated data were simulated with one of three possible levels of 'noise': 10%, 20% or 30%. This was achieved by randomly choosing non-zero values, after simulation of a dataset, and setting them to zero. Finally, because sampling in the real-world is generally limited by many logistic constraints, the number of samples effectively taken is usually only a small subset of the available sites in the transect. Hence, for each of the 36 baseline scenarios, sample data sets were created by randomly selecting 20, 40, 80 and 160 locations.

For each of the 432 combinations of these four parameters (gradient type, percentage of habitat, noise and number of samples), 100 replicates were simulated differing only in the placement of sample localities within the available sampling area. The comparison of boundary shifts in the results of these replicates allowed the investigation of SMWGA robustness to small-scale spatial variation of samples' location. To determine the effect of data quality on SMWGA efficiency, semi-quantitative datasets were converted to presence/absence data and analysed again.

Two window behaviours on transect endpoints were tested. The free mode allowed the window to be placed in such a way that the midpoint coincided with the first sampled point. In a similar way, the window slide ended only when the midpoint reached the last sample. This means that transect endpoints were always compared against a fraction of the data series on the first and last window positions. This behaviour can be very useful when boundaries are located in the beginning or the end of the gradient. The restricted mode did not allow the window to partially slide off the transect. Thus, the transect fraction covered by the window was inversely proportional to the window size, the bigger windows having less space to slide on. This behaviour is similar to the one described for the original SMW by Cornelius and Reynolds (1991).

Real data

Rocky shores from Britain and Ireland have been studied for many decades, and some of the best long-term data sets on distributions of marine species are available for this region (Crisp and Southward, 1958; Crisp, 1964; Southward, 1967, 1980, 1991; Southward *et al.*, 1995; Hawkins *et al.*, 2003; Simkanin *et al.*, 2005; Mieszkowska *et al.*, 2006). In particular, biogeographic boundaries are already known since the middle of the XIX century, when Forbes (1858) first described them. Posterior studies have confirmed the presence of a contact region between cold and warm-waters, coinciding with a sharp faunal and floral discontinuity on both sides of the Channel (Crisp and Southward, 1958). These boundaries are located midway along the Channel and coincide with the topographical limits separating the two Channel basins: the

Isle of Wight, on the English side, and the Cotentin Peninsula, on the French coast.

The intertidal zone of the English and French sides of the Channel was extensively surveyed between 1950 and 1957 by D. Crisp and A. Southward (1958). These authors sampled not only open-coast but also sheltered locations inside river mouths, having also visited the Ile d'Ouessant, the Channel Islands and the Isles of Scilly. Some transformations were made so as to obtain linear data sets: locations inside river mouths or from islands, with the exception of the Isle of Wight, were removed, and the remaining 162 places were divided in two groups (English and French) which were independently analysed.

The two data sets comprising 24 species (variables) in 89 English and 73 French locations were used. Whilst the abundance of some species was measured using quadrats haphazardly placed on the substrate, for other species it was assessed using the ACFOR semi-logarithmic abundance scale developed by Crisp and Southward (1958). Thus, all abundances were converted to this scale prior to analysis. Distances between sampled places were computed following the coastline contour and minimum straight distance was employed between both sides of river mouths.

2.3.3.2 GSMW implementation

SMWGA was written in C++ and is available as source code upon request. It is a text-based program which runs in a console and takes its parameters from the command line. It has several options, including the use of Bray-Curtis or Euclidean Distances and transformation of data prior to analysis. SMWGA may be run in batch mode to compute statistics for several windows' half-sizes within a given range.

2.3.4 Results

Simulated data

In terms of graphical output, the SMWGA was sufficiently robust to detect the boundaries in most of the artificial scenarios generated with discontinuities when the unrestricted randomization technique

Table 2.3.1 Percentage of boundaries correctly detected in the nine scenarios for different combinations of data type, noise and sample sizes. Results are for a transect with 40% of suitable habitat. Values marked with * indicate the percentage of discontinuities that were wrongly detected.

Presence/Absence												
Noise	10				20				30			
Sample Size	160	80	40	20	160	80	40	20	160	80	40	20
A	1	1	1	1	1	1	1	0.94	1	1	0.98	0.88
B	1	1	1	1	1	1	0.94	1	1	1	1	0.81
C	1	1	1	0.89	1	1	0.95	0.95	1	1	1	1
D	1	1	0.97	0.86	1	1	0.86	0.65	1	1	0.59	0.62
E	1	1	1	1	1	1	1	1	1	1	1	1
F	1	1	1	1	1	1	1	0.93	1	1	1	1
G	1	1	1	0.99	1	1	0.99	1	1	1	1	0.87
H	1*	1*	1*	1*	1*	1*	1*	1*	1*	1*	1*	1*
I	0	0	0	0.02*	0	0	0	0	0	0	0.03*	0

Abundance scale												
Noise	10				20				30			
Sample size	160	80	40	20	160	80	40	20	160	80	40	20
A	1	1	1	1	1	1	1	0.99	1	1	0.99	0.96
B	1	1	1	0.96	1	0.96	1	0.78	1	1	1	1
C	1	1	1	1	1	1	1	0.69	1	1	1	0.78
D	1	1	1	0.37	1	1	0.56	0	1	0.87	0	0
E	1	1	1	0.95	1	1	1	1	1	1	1	1
F	1	1	1	0.91	1	1	1	0.85	1	1	0.73	0.59
G	1	1	0.78	0.72	1	0.95	0.84	0.69	1	1	0.81	0.37
H	1*	1*	1*	1*	1*	1*	1*	1*	1*	1*	1*	1*
I	0	0	0.01*	0	0	0	0	0	0	0	0	0

was used for significance testing. A summary table (Table 2.3.1) depicts the results for 40% of habitat and the 'free' window behaviour, corresponding to 21,600 replicates. The remaining results (151,200 replicates, corresponding to 20%, 60% and 80% of habitat and the restricted window behaviour) are not shown. Detection patterns were

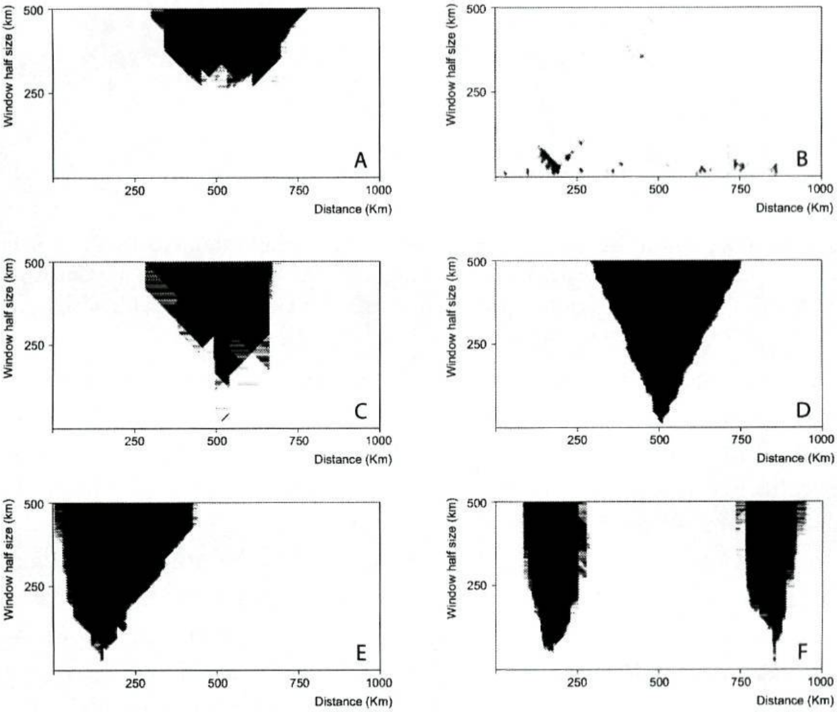

Figure 2.3.3 Results of SMWGA runs for different scenarios. A – 'ramp' scenario with a wrongly detected central boundary; B – control scenario with typical random pattern of significances; C – scenario with central discontinuity, 20% of noise, 20 samples and presence/absence data; D – same as C but with 30% noise and 160 samples; E – scenario with lateral boundary, 10% of noise and 40 samples, presence/absence data; F – scenario with two discontinuities, 10% of noise, 80 samples, abundance data.

very similar for the four percentages of habitat modelled. The behaviour of the window (free or restricted) had also little influence in the outcome of the analyses, except for the scenarios where the discontinuity was located near one of the sides of the transect (scenarios D, E and F) and in the 'ramp' scenario (H).

Detection of boundaries at lateral portions of the gradient was less efficient when the restricted window behaviour was used, since larger windows only produced outputs in the central region and the number of possible permutations was very small for statistical testing. In the 'ramp' scenario, results for the free window behaviour always depicted a

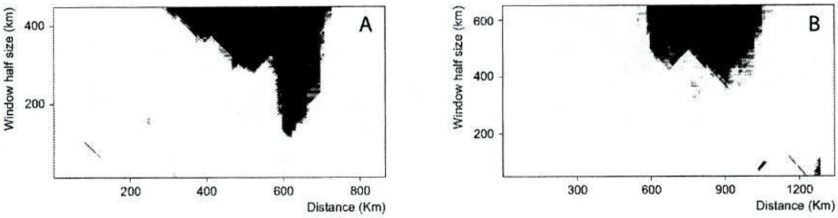

Figure 2.3.4 SMWGA results for the English Channel intertidal rocky shore data (Crisp and Southward,1958). A - United Kingdom (from left to right, Cape Cornwall to North Foreland); B – France (from left to right, Le Conquet to Pas-de-Calais).

central broad boundary, or a bump, although only at larger window sizes (Figure 2.3.3 A). In fact, at larger scales and when the window midpoint was placed at the centre of the gradient, not only the surrounding locations but also the endpoint samples were compared. Because the latter were notably divergent in species composition, dissimilarities were always significant at central midpoints. On the other hand, when small windows were used, there were no significant dissimilarities because the gradient of species substitution was regular throughout the window range. This was the only case where the restricted behaviour performed better than the free behaviour. Since for large window sizes there were few possible windows midpoints (all restricted to the centre of the transect), no significant discontinuities were detected, which was the expected correct result.

The analyses for the control scenario (no gradient) always resulted in a distinctive 'noisy' pattern, recognizable by a variable number of significant differences scattered all over the graphic (Figure 2.3.3 B). Overall, results suggest that data sets with boundaries can be easily distinguishable from randomly structured data because in the latter there is no coherence among the significance patterns emerging from different window sizes. Only in very few cases this random pattern could have been interpreted as a true boundary (mainly in presence/absence data, see Table 2.3.1).

In the remaining scenarios, the number of samples effectively taken was the variable with most influence on the efficiency of the method. In fact, quality and accuracy of the results were deeply related to the number of sampled locations, and as long as a high number of samples was used, the SMWGA was practically immune to variations in any of the other factors tested (Figure 2.3.3 C-D). For the 1,000 Km modelled gradient, it was clear that at least 40 samples should be taken, although more accurate results were achieved with 80 locations or more. When a sufficient number of samples was used, the method was able to identify the boundary in the correct place, not only where it was located at the centre, but also when it was at the periphery of the transect (Figure 2.3.3 E-F). On the other hand, for sample sizes of 20 locations, results were more variable and strongly influenced by the remaining factors, resulting in a complete failure to detect a boundary in many cases.

As expected, the efficiency of the method was also inversely proportional to the amount of 'noise' introduced in the data. For large sample sizes this was seldom a problem, but for sample sizes equal or smaller than 40, boundary detection decreased with 'noise'. Yet, the method was still able to correctly detect boundaries in data series with 30% of 'noise' and sample sizes of 20, except for the more complex scenario with two boundaries (Figure 2.3.3 D).

Overall, SMWGA efficiency was very similar when using qualitative or quantitative data. However, in most cases, presence/absence data produced slightly sharper results probably due to the higher abruptness in species gradients and lower data variability. The method was also quite robust to small-scale variation in sample location, especially when a reasonable number (> 40) of samples was used. For example, with a sample size of 80 locations, boundary identification had an accuracy of a few tens of kilometres, never exceeding 5 % of the whole transect range (1,000 Km). With a sample size of 20 locations, it was not possible to measure variation between results, since they were rarely clear enough to objectively define a boundary.

Significant spatial autocorrelation was observed in all scenarios except for the control (Figure 2.3.3 I). For the 'ramp' scenario (Figure 2.3.3 H) and scenarios with a central boundary (Figure 2.3.3 A, B, C and G) negative spatial autocorrelation was usually found for lags above 350-400 Km, and positive spatial autocorrelation was found for lags up to 200-250 Km. For scenarios with a peripheral boundary or two boundaries (Figure 2.3.3 D, E and F) negative spatial autocorrelation was detected at lags above 650-750 Km and positive spatial autocorrelation was found at lags up to 150-200 Km.

The presence of autocorrelation prompted for the use of restricted randomization tests, because positively autocorrelated data violate the assumption of independence of observations. However, restricted randomization tests seldom produced better results than unrestricted randomization tests. In many cases they were equally effective, producing similar graphical outputs, but in other cases they simply failed to detect the expected discontinuities. There was no apparent pattern for these failures, and even in cases were unrestricted randomization produced sharper and unambiguous graphs the restricted randomization failed completely.

Real data

Results for Crisp and Southward's (1958) data are depicted in Figure 2.3.4. On the English side, a clear discontinuity was detected 615 Km from the transect's western endpoint (eastern half of the Isle of Wight) by windows greater than 100 Km. On the French side, two discontinuities were identified, 424 Km and 659 Km from the transect's western endpoint, flanking the Cotentin Peninsula. While detection of the eastern boundary started at a scale of 400 Km, the western one was only distinguished at scales larger than 450 Km. These two boundaries merged at scales above 500 Km. Autocorrelation was present on both datasets. For the English side, positive spatial autocorrelation was found below 200-250 Km and negative spatial autocorrelation was detected for scales above 350-400 Km. For the French data set, positive autocorrelation was found below 250-300 Km and positive autocorrelation was detected at the 700-800 Km lag and then only above 950 Km.

Other boundary features were observed, some of which differing among the two tested transects. For example, the minimum scale at which significant differences were observed was much smaller in the English side. Since the accuracy of the boundary detection is highly dependent on data resolution (Fortin, 1997), the difference between the two transects may have been caused by the smaller average distance between sampled locations in the English (9.94 Km ± 8.08) than in the French (18.12 Km ± 14.45) side of the Channel. Furthermore, the two resulting graphs suggested a much more localized boundary in the English side of the Channel when compared to the broader transitional zone in the French coast. In the latter, there was more overlap between the assemblages from each side of the transect, resulting in an intermediate region (extending over approximately 130 Km) which differs from its surroundings at least at smaller-scales.

2.3.5 Discussion

One of the advantages of the SMWGA method described in the current work is the ability to work with unevenly distributed data, which brings the potential to analyse data from numerous new fields of study. This approach is particularly useful when studying locations that are irregularly distributed among non-informative space, like forest patches scattered over human-altered landscapes or rocky shores dispersed over large stretches of sandy coastline. In a similar way, it might also be suitable for dealing with long-term data, often heterogeneous due to the presence of gaps in the data series, whether variables are physical (Mann *et al.*, 1998, McGowan *et al.*, 1998, Mekis and Hogg, 1999, Oerlemans, 2005) or biological (Jassby and Powell, 1990; Southward *et al.*, 1995; Hawkins *et al.*, 2003).

Another major advantage of the method is that it allows the comparison of data coming from several independent surveys made in the same general area, even when the samples are not precisely replicated in number or in location. As shown empirically by comparing the results for different sets of samples (replicates) from the same scenario, the SMWGA method always correctly detected the boundary location with only very small errors. This ability is very important since one of the most striking problems in long-term monitoring is the non-coincidence of locations among available surveys (Thomas, 1996) or the incapacity to resample some locations because the exact place of the previous sample is unknown or even non-existent (Reichert and Buchholz, 2006). Prior to the GPS era, information from historical surveys consisted mainly of textual descriptions, sometimes old photos (Johansson *et al.*, 1998; Mieszkowska *et al.*, 2006) and thus relocating the precise area to sample is often difficult (Simkanin *et al.*, 2005). Therefore, SMWGA is ideal to compare long-term modifications in species distribution and abundance along one-dimensional gradients in response to climate change, since it can put side by side and analyse data sets which otherwise would be incomparable. This brings the possibility to take full advantage of many historical data sets that were simply ignored or analysed subjectively (Simkanin *et al.*, 2005; Mieszkowska *et al.*, 2006).

The SMWGA has several limitations, some of which were patent in the simulations with artificial data. The major constraint, aside from autocorrelation, was related with the quality of the acquired data. For smaller sample sizes, the combination of noise in the data with specific types of gradients (especially those with faint boundaries) was usually behind the poorest results and effectively contributed for most of the detection failures. Therefore, sampling should always be carefully planned. The main condition to obtain valuable results is the inclusion of a sufficient number of samples in the analyses, a simple rule which is valid for any boundary detection method (Fortin, 1997). Furthermore, since different patterns emerge at different scales of investigation, an appropriate scale of measurement should be chosen considering the goal of the study (Fortin *et al.*, 2000). Thus, when it is possible to make a raw prediction of the boundary (or boundaries) location, sampling should not be restricted to the boundary itself, but also encompass adjacent areas (Fagan *et al.*, 2003).

Autocorrelation was a common feature of most of the artificially generated datasets. Interestingly, levels of autocorrelation for Crisp and Southward's (1958) data were similar to the values observed for the simulated data, reinforcing the reliability of the simulator. These results are important because, as reiterated by some authors (see Fortin and Dale, 2005 for a review), they support the idea that spatial autocorrelation is a prevalent phenomenon in ecological data, although often ignored in many spatial analysis studies (in particular those dealing with one-dimensional transect data).

With the advances in the area of spatial analysis, acknowledgement of autocorrelation (either at spatial or temporal levels) and its implications has increased dramatically in recent years (Rangel *et al.*, 2006). Positive spatial autocorrelation is a property inherent to most ecological data, arising from causal interaction between nearby sample locations (Fortin and Jacquez, 2000) and it is of major concern since it invalidates the assumption of independence of observations required by many statistical tests. In the present work, results were often better when unrestricted randomization was used to detect significant dissimilarities.

Results suggest that the usage of this kind of restricted randomization test (one-dimensional toroidal shift) may not be appropriate for unevenly distributed data. The problem is that although it preserves positive small-scale autocorrelation in the data, it destroys the underlying distribution of informative and non-informative space. During the toroidal shift process, a given sampling site will be placed at all available positions in a data series, even when in reality some of these are actually unsuitable habitat zones. To avoid this problem, a modified version of the toroidal shift could be used, restricting it to the series of sample locations but ignoring inter-location distances. This would preserve the distribution of informative and non-informative space, but would partially destroy small-space autocorrelation: neighbours in a series would always be neighbours, but the distance between them would vary. This latter version of the method was also tested on a limited subsample of the artificial scenarios with no significant increase in efficiency.

There are other methods to deal with positively autocorrelated data, namely the adjustment of the effective sampling size, subsampling, restricted randomization conditioned by the degree of positive autocorrelation or 'model and Monte Carlo' methods (Fortin and Jacquez, 2000; Fortin and Dale, 2005). While the first two methods are 'quick fixes' and should be used only when there is no other alternative, the latter are probably more powerful but are also much more complex and time demanding, and thus were not implemented in the software.

Although the usage of unrestricted randomization for hypothesis testing - when in presence of spatial autocorrelated data - may seem inappropriate, this might not be the case, especially for data that displays both positive and negative spatial autocorrelation. This is a typical from data series including species gradients and boundaries, where negative autocorrelation arises at larger scales (Legendre and Fortin, 1989). According to Fortin and Dale (2005), in such circumstances strong positive small-scale autocorrelation may not compromise statistical tests if there is some sort of cyclic behaviour that also produces negative autocorrelation at larger scales. If positive small-scale autocorrelation is present, one may be tempted to correct for its effects by modifying the nominal value of α to reduce the expected Type I error rate inflation. However, if negative autocorrelation exists at larger scales, the final result will be a significant and unwanted deflation of Type I error, bringing with it consequences such as inflation of Type II error and decrease in statistical power. Because of this, they concluded that restricted or unrestricted (by that order) randomization tests are preferable, as long as they are applied carefully and with awareness of the possible problems.

Cornelius and Reynolds (1991) did not mention autocorrelation when they described the SMW algorithm, and subsequent works using this technique also ignored this important feature (e.g., Panis and Verheyen, 1995; Beaugrand, 2003; Beaugrand and Reid, 2003). The method, which used a variant of the unrestricted randomization test, was shown to be reliable using both simulated and real data. However, in cases where only small-scale autocorrelation is present, statistically significant discontinuities after an unrestricted randomization test are meaningless. Therefore, it is desirable, if not mandatory, to obtain autocorrelograms to assess the type (or types) of autocorrelation present in the data, prior to any interpretation of the SMW or SMWGA results.

A different method to detect boundary locations in both even and unevenly distributed ecological data was recently proposed by Mac Nally (2005). This method uses a Bayesian approach to assign probabilities to boundary locations for a whole set of possible boundaries within a given transect or series. The main disadvantage of this approach is that it is computationally intensive. Furthermore, if extended to cases where more than one boundary is present, the number of models (i.e., possible boundary locations) to search and test raises rapidly. Therefore, in such situation, solving a problem may only be achieved by using the computational power of large clusters of computers and parallelized programs. On the contrary, SMWGA requires much less computing power. The current method works well with data sets displaying more than one boundary. The increase in the number of boundaries does not correspond to any increase in computing time, since the steps of the algorithm are independent of the number of boundaries, and no additional calculations are needed. However, if there are several boundaries within a transect and species' gradients overlap to a greater extent, there might be a decrease in the sharpness of the results, with boundaries less evident in the significance plot. To increase the detection accuracy in such subtle discontinuities it might be necessary to resample some extensions of the transect using a higher density of sampling points.

2.3.6 Conclusions

The extension of the split moving window (SMW) method (Cornelius and Reynolds, 1991) here described, can be used to locate the position of one or more boundaries along a linear series of unevenly distributed multidimensional data. Results are easily interpretable due to its simplistic and empirical nature. The fact that the principles of the method are easily understandable means that in some circumstances, when only low-quality data are unavailable, it is still possible to reach some valid conclusions (Legendre and Legendre, 1998).

This method requires data to be ordered in one dimension. Distances between locations are computed and a virtual window, divided in two halves, is placed in the beginning of the data series. A multivariate dissimilarity index is computed between the two halves of the window and its value is assigned to the window midpoint. Statistical significance of discontinuities is computed using restricted (toroidal shift) or unrestricted randomization of data. The window moves along the data series, registering locations where there are significant differences. Consecutive window sizes are used to obtain results for the whole scale range.

Tests using a high number of simulated data sets and two transects on the English Channel rocky intertidal communities showed the robustness of the method, which was able to correctly identify a great variety of boundary types. It was shown that its accuracy was highly dependent on data resolution. Because autocorrelation is a ubiquitous feature of ecological data series, usage of multivariate autocorrelograms to estimate autocorrelation is mandatory prior to any interpretation of the SMWGA results.

The main feature of the improved method is the ability to work with unevenly distributed data, which can be particularly useful for studying ecological communities from patchy habitats like the rocky shore environment. It is also appropriate to deal and compare data from several surveys made in the same general area but with small-scale differences in sample locations, which is very useful in the assessment of climate change influence on species' distribution.

2.3.7 Aknowledgements

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Chapter 3

Processes driving temporal changes

Section 3.1

Recent changes in the distribution of a marine gastropod, *Patella rustica* Linnaeus, 1758, and their relationship to unusual climatic events

3.1.1 Abstract

Aim

Recent colonization of northern Portuguese shores by *Patella rustica* Linnaeus, 1758, led to the bridging of a historical gap in the distribution known since the 1900s. Long-term oceanographic data collected over the last half-century were examined in order to detect possible mechanisms for the observed change in its distribution.

Location

This study was carried out along the entire Portuguese coastline, from 41°50' N to 37°06' N. Time-series of hydrographical variables (sea surface temperature and salinity) were derived for the Atlantic coast of the Iberian Peninsula.

Methods

Abundance and size-frequency distributions of the newly observed limpet populations were compared with those from well-established populations in southern Portugal. Anomalies were computed for sea surface temperature (1950-2000) and sea surface salinity (1958-2001) data, covering the whole Atlantic coast of the Iberian Peninsula. An upwelling index (1967-2005) was derived for a single location within the distributional gap of *P. rustica*. Split moving window analysis was performed to detect significant discontinuities in hydrographical data sets.

Results

Patella rustica has gradually been expanding in northern Iberia, and in the late 1990s the historical gap in distribution in northern Portugal was bridged. Size-frequency distribution differed between historical and recent populations, the latter lacking small-sized individuals. At the same time, several anomalous oceanographic events occurred off the Portuguese coast and were probably related to this expansion.

Main conclusions

Although sea surface temperature might be a major determinant of the reproductive success of *P. rustica* and hence its dispersal potential, it is more likely that a coincidence of several factors occurring in the late 1990s provided exceptional conditions that allowed the geographical expansion of this species.

3.1.2 Introduction

Recent ecological literature reflects concerns with anthropogenic global climate change (Southward *et al.*, 1995; Stenseth *et al.*, 2002; Walther *et al.*, 2002; Parmesan and Yohe, 2003; Root *et al.*, 2003) and has provided insights into the causes of species range limits and shifts in response to changing climatic conditions (Sagarin, 1999; Sagarin and Gaines, 2002b; Zacherl *et al.*, 2003). Keeping records of alterations in the environment and creating predictive models that enable the detection of variations in climate is one of today's primary aims in ecology (Lewis, 1999; Hawkins *et al.*, 2003; Hiscock *et al.*, 2004).

Changes in the distribution and abundance of several marine species on the eastern coasts of the Atlantic and Pacific oceans have been particularly well documented over the last decades. Consistent responses to climate change have been described at different trophic levels for both sessile and pelagic assemblages (Southward *et al.*, 1995; Holbrook *et al.*, 1997; Sagarin, 1999; Wethey, 2002; Beaugrand and Reid, 2003; Borges *et al.*, 2003; Hawkins *et al.*, 2003; Zacherl *et al.*, 2003; Genner *et al.*, 2004; Hiscock *et al.*, 2004; Paine and Trimble, 2004). In contrast to pelagic systems, intertidal communities are ideal for studying climate-driven community changes because the constituent species are typically long-lived, less influenced by short-term factors and respond more readily to multi-decadal periods of environmental variability (Barry, 1995; Southward *et al.*, 1995). In addition, their ranges are roughly one-dimensional and easily defined as the coastal endpoints. Therefore, conspicuous, easily identified, slow moving or sedentary rocky shore species are some of the best candidates to monitor climate changes (Lewis, 1996; 1999; Sagarin and Gaines, 2002a; Hiscock *et al.*, 2004).

Because alterations of the environment affect a series of physiological factors that act on population-level processes, it is thought to be more important to understand the mecha-nisms that influence population dynamics and the synchrony between climatic oscillations and species life cycles, instead of studying only the physiological limitations of individuals (Holbrook *et al.*, 1997; Zacherl *et al.*, 2003; Hagberg *et al.*, 2004). Thus, quantitative approaches like studies of the populations dynamics of newly established populations are encouraged (Kolar and Lodge, 2001), and may indicate which processes determine the success or failure of a particular shift or invasion (Zacherl *et al.*, 2003; Genner *et al.*, 2004), allowing more successful prediction of the patterns of invasive species.

The Portuguese coast is particularly well suited for the study of the putative effect of climate warming on species distribution for several reasons. First, the clear north-south orientation of the coastline is the most appropriate for this type of analysis (Rivadeneira and Fernández, 2005). Second, it is characterized by particular hydrographical features, with a cooler northern region affected by both upwelling and rainfall leading to a higher volume of river run-off and a much warmer southern region with a strong Mediterranean influence (Sanchez and Relvas, 2003; Santos *et al.*, 2004; Peliz *et al.*, 2005). Third, this is a contact region between warm-and cold-water species, where both northern and southern boundaries of several organisms can be found (Fischer-Piétte, 1959; Fischer-Piétte and Gaillard, 1959; Fischer-Piétte, 1963; Ardré, 1970; Santos, 2000). Finally, shifts in species distribution have been described since the 1950s, not only for this particular stretch of coastline but also for the Iberian Peninsula (Fischer-Piétte and Forest, 1951; Fischer-Piétte, 1957; Fischer-Piétte and Kirsch, 1957; Fischer-Piétte and Prenant, 1957; Ardré, 1971; Santos, 2000; Pereira *et al.*, 2006).

The geographical distribution of *Patella rustica* Linnaeus, 1758, ranges from the Mediterranean to the Atlantic coast of the Iberian Peninsula and northern Africa, including the Macaronesian Islands (Ridgway *et al.*, 1998). In the Atlantic, its southern limit is speculated to occur further south than Mauritania, whilst its northern limit is located at the French Basque Country (Fischer-Piétte, 1955; Crisp and Fischer-Piétte, 1959). Within this range there is a well-documented gap. Hidalgo (1917) placed it between the locations of Nazaré (Portugal, 39°36'16" N, 9°05'08" W) in the south, and La Coruña (NW Spain, 43°22'54" N, 8°26'23" W) in the north. Although the work of Nobre (1940) provides no information regarding the northern boundary of this species, he identified São Pedro de Moel (39°45'34" N, 9°01'58" W) as the northern limit of *P. rustica* in Portugal.

The works of Fischer-Piétte (1955) and Fischer-Piétte & Gaillard (1959) still remain the most comprehensive accounts of the distribution and abundance of patellid limpets on the Atlantic coast of the Iberian Peninsula. According to these authors, during the 1950s *P. rustica* was still largely absent from northern Portugal (surprisingly, one individual was found at Vila do Conde, 41°21'05" N, 8°45'21" W). From its northern geographical boundary in Biarritz (south-west France) toward La Coruña, densities were described as progressively decreasing. However, they observed new populations in Galicia (north-west Spain), with limpets occurring in low densities only at very exposed locations. After a detailed review of Hidalgo's (1917) work, Fischer-Piétte & Gaillard (1959) concluded that they were observing an on-going expansion of *P. rustica* in the northern part of the distributional gap.

More recent data, based on multiple surveys carried out between 1993 and 1998 over the entire Portuguese coast (Santos, 2000), confirmed the southern boundary of the distributional gap in central Portugal (São

Martinho do Porto, 39º30'43" N, 9º08'33" W). In 1996, S. J. Hawkins (pers. obs.) spotted a single *P. rustica* at Moledo do Minho. Despite continuous sampling in the area since 1993, it was only in the winter of 2002 that several individuals (> 20) were recorded at Homem do Leme (Porto), within the historical gap. A subsequent survey revealed that the species was already present at very low densities in several shores north of Porto.

This study describes the recent bridging of the 280 km distributional gap of *P. rustica* in northern Portugal. Density and size-frequency distribution of the newly observed populations were compared with those from well-established southern populations, and long-term hydrographical data were used both to demonstrate the gap area as one with anomalous oceanographic conditions and to formulate alternative hypotheses to explain the recent change in the geographical distribution of this species. Plausible hypotheses, like changes in upwelling regimes, sea surface temperature or coastal current patterns are discussed, and a testable explanatory model is suggested.

3.1.3 Material and methods

On the Atlantic coasts of Europe and North Africa, *P. rustica* is normally found in the upper eulittoral zone (usually above mean high water neap) of exposed rocky shores. Although other limpet species (*Patella vulgata* Linnaeus, 1758 and *Patella depressa* Pennant, 1777) also occur in this zone, *P. rustica* is easily identified by the characteristic black spots that ornament its shell. This feature can be observed even in small (c. 5 mm) animals, so juvenile identification does not pose any problems. In addition, *P. rustica* has a strong preference for vertical walls or very steep surfaces and, at least on the Portuguese coast, is seldom found outside this habitat.

During February 2003, density and size-frequency surveys of *P. rustica* where carried out in two different regions. The first encompassed recently colonized locations within the distributional gap of *P. rustica* in northern Portugal, whilst the second included historically inhabited areas in central and southern Portugal. In each region, six shores were visited (Figure 3.1.1). Within the gap area, the southern half consists mainly of

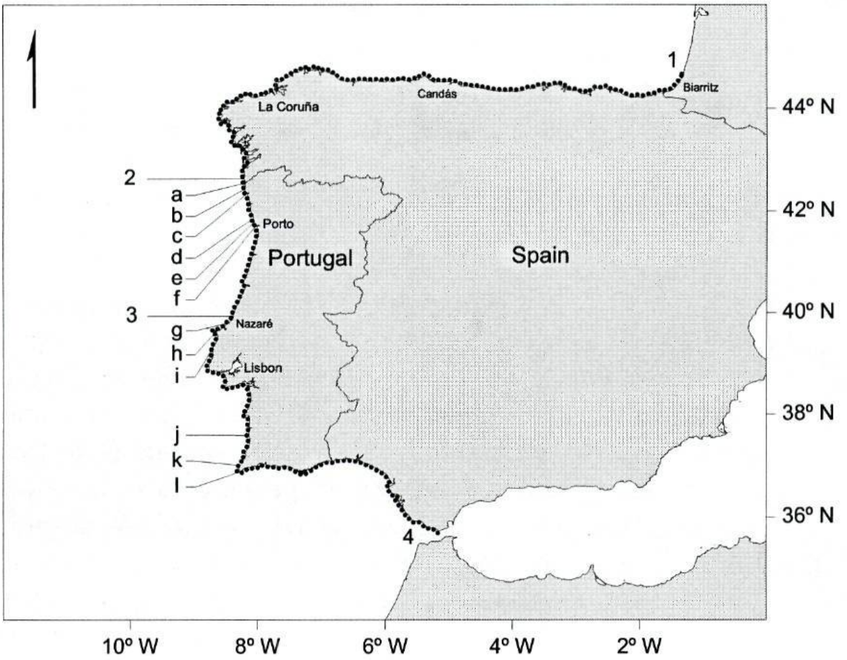

Figure 3.1.1 Study area. 1, Biarritz (northern limit of *P. rustica* distribution). The coastline between 2 (Baiona) and 3 (Sa˜o Martinho do Porto) is the historical gap in northern Portugal. 4, Strait of Gibraltar. Locations visited: (a) Moledo do Minho, (b) Montedor, (c) Forte da Vigia, (d) Mindelo, (e) Cabo do Mundo, (f) Homem do Leme, (g) Sa˜o Martinho do Porto, (h) Baleal, (i) Santa Cruz, (j) Amoreira, (k) Castelejo and (l) Beliche. Hydrographical coastal sampled points are represented as black circles. Inset figure shows known distribution of *P. rustica* prior to recent expansion.

large stretches of sandy shores, interspersed with a few rocky shores that do not provide suitable habitat for *P. rustica* (no rocky substrate above mean tide level). An initial survey was done over the entire area, but the species was only found in the northern half of the gap, which is mainly rocky. Since the recent colonization of northern Portugal could be an on-going process rather than a single event, sampling was repeated in February 2005 for the northern shores.

On the southern shores, the density of limpets was estimated using several haphazardly placed 50 × 50 cm quadrats. Due to the high density of limpets, and to avoid bias toward larger size classes, size-frequency data were collected by measuring all limpets within each quadrat. The maximum length of each limpet was measured with digital callipers and rounded to the nearest millimetre. Because low-water spring tides occur in the early morning (07:00 - 09:00), sampling time was roughly limited to 3 h on each shore. At northern locations, in order to obtain comparable values of density, a 3-h survey was also undertaken. However, because densities were very low, all individuals observed were counted and measured. Length- frequency histograms were built for each sample using 2 mm size classes.

To test for non-independence between size structure and location a chi-square test was used. Limpets were divided into three length classes: < 13 mm, 13-28 mm and > 28 mm. The choice of the interval to represent non-reproductive (juvenile) stages was problematic because size at sexual maturity is unknown for *P. rustica*. The upper limit of 12 mm was based on the assumption that it would be similar to the value already known for *P. depressa* (Guerra and Gaudêncio, 1986, P.A. Ribeiro, unpub. data),which displays a largely overlapping Atlantic distribution.

Sea surface temperature (SST) along the Atlantic coast of the Iberian Peninsula, from January 1950 to December 2000, was derived from *in situ* raw data obtained from the International Comprehensive Ocean-Atmosphere Data Set (ICOADS, Woodruff *et al.*, 1988). To avoid bias due to different daytime measurements, only data from 12:00 were used. Point data were imported into the GRASS Geographical Information System (GRASS Development Team, 2006) and transformed into raster maps with a spatial resolution of 4 × 4 km using a surface interpolation method. Each cell was derived from the 12 nearest data points using the distance squared weighting algorithm (Jarvis and Stuart, 2001).

Sea surface salinity (SSS) data, with an average resolution of 0.5° latitude × 0.5° longitude cells, were extracted from the SODA-POP v1.2 model data set, available at the National Virtual Ocean Data System live server webpage (http:// ferret.pmel.noaa.gov/NVODS/servlets/dataset) and were imported into GRASS GIS. Data were available for the period between January 1958 and December 2001.

The resulting set of 612 (51 years × 12 months) SST and 528 (44 years × 12 months) SSS maps was stored in GRASS GIS as monthly layers and sampled along the Iberian coastline at regularly spaced points, 10 km distant from each other and 2 km offshore. The resulting data for each physical parameter were combined to build a table with each row denoting a geographical location and each column a month-year combination. Monthly standardized anomalies were computed by subtracting from each value the monthly mean across all years and dividing it by the monthly standard deviation. To identify significant hydrographical time-series discontinuities on the recently colonized area, split moving window (SMW) boundary analysis (Ludwig and Cornelius, 1987; Cornelius and Reynolds, 1991) was carried out for SSS and SST anomalies from the area between 39°30' N and 41°54' N. This technique has been successfully applied to time-series of both biological and physical variables (Beaugrand, 2003; Beaugrand and Reid, 2003; Beaugrand, 2004). Because the SMW outcome may vary as a function of window size, three window sizes were used (12, 24 and 48 months). Only results simultaneously detected by the three windows were considered.

A monthly based upwelling index for the location of 41°00' N, 10°00' W (off Porto) and from January 1967 to March 2005 was provided by the Pacific Fisheries Environmental Laboratory (PFEL; http://las.pfel.noaa.gov/las/main.pl). A 4-month running mean was computed to remove small-scale variation.

3.1.4 Results

In 2003, recently established northern populations consisted of sparsely distributed and isolated individuals (Table 1). Although the 3-h sampling sessions were enough to cover the entire rocky surface of the appropriate high shore at each location, a maximum of 148 limpets was found at Homem do Leme and two shores appeared to completely lack this species, as not one individual was found. A sharp gradient of abundance, with number of individuals decreasing from south to north, was observed. In contrast, on southern shores densities were always higher than 60 individuals per m^2.

By 2005, all six shores on the northern Portuguese coast had been colonized by *P. rustica*. The total number of limpets in each locality increased several fold after 2003. However, a clear gradient of abundance, with number of individuals decreasing toward the north, could still be observed.

Length-frequency histograms showed a marked difference between

Table 3.1.1 Density (limpets m^{-2}) and modal class with minimum and maximum sizes (mm) of *P. rustica* sampled at each location during 2003 and 2005 surveys. - indicates the absence of this species in that site and year. Real counts are shown in parentheses. Locations not visited are indicated with n. a.

		2003		2005	
Site	Geographic location	Density	Modal class (min-max)	Density	Modal class (min-max)
Moledo do Minho	41°50’41”N 8°52’07”W	(0)	-	(109)	19 (12-30)
Montedor	41°44’30”N 8°52’37”W	(7)	24 (17-26)	(71)	21 (12-32)
Forte da Vigia	41°41’55”N 8°51’22”W	(0)	-	(92)	22 (13-31)
Mindelo	41°18’37”N 8°44’32”W	(46)	29 (17-43)	(246)	29 (16-42)
Cabo do Mundo	41°13’17”N 8°42’56”W	(87)	24 (13-37)	(109)	22 (14-34)
Homem do Leme	41°09’22”N 8°40’58”W	(148)	22 (13-37)	(279)	25 (12-39)
São Martinho do Porto	39°30’39”N 9°08’36”W	83 (250)	23 (5-30)	n.a.	n.a.
Baleal	39°22’29”N 9°20’21”W	98 (295)	20 (5-34)	n.a.	n.a.
Santa Cruz	39°08’02”N 9°23’00”W	70 (211)	17 (7-25)	n.a.	n.a.
Amoreira	37°20’57’ N 8°50’47”W	65 (196)	20 (8-31)	n.a.	n.a.
Castelejo	37°06’01”N 8°56’43”W	86 (259)	22 (8-42)	n.a.	n.a.
Beliche	37°01’30”N 8°57’48”W	98 (295)	23 (7-34)	n.a.	n.a.

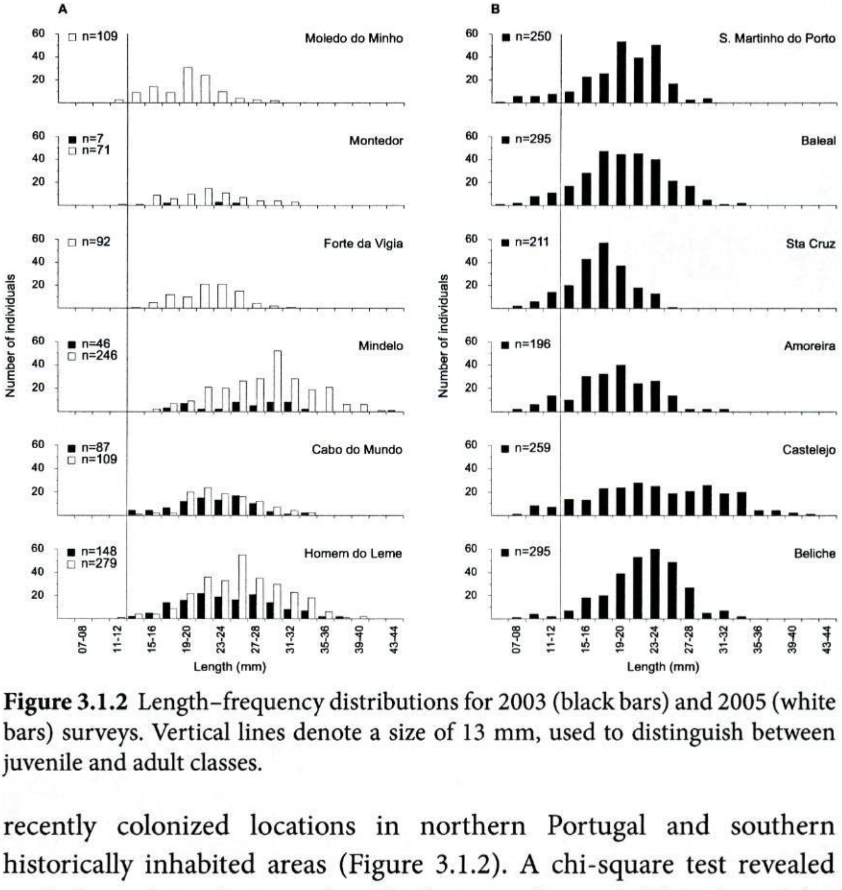

Figure 3.1.2 Length–frequency distributions for 2003 (black bars) and 2005 (white bars) surveys. Vertical lines denote a size of 13 mm, used to distinguish between juvenile and adult classes.

recently colonized locations in northern Portugal and southern historically inhabited areas (Figure 3.1.2). A chi-square test revealed no independence between length classes and sampled locations (χ^2 = 105.00, *d.f.* = 30, $p < 0.05$), meaning that the population structure was significantly different between sites. All northern populations had fewer small individuals than expected. In 2003 they were composed solely of adults and in 2005 only 0.75% of the observed limpets belonged to the smaller size class. By contrast, populations in the historic portion of the range had a considerably higher frequency of juveniles (7.65%). In 2005, two different patterns in population structure were observed in the newly colonized sites: whilst populations settled before 2003 had a high proportion of adults of more than 28 mm (35.64%), in those populations established in subsequent years this percentage was only 4.41%.

ICOADS monthly mean SST showed a consistent annual pattern

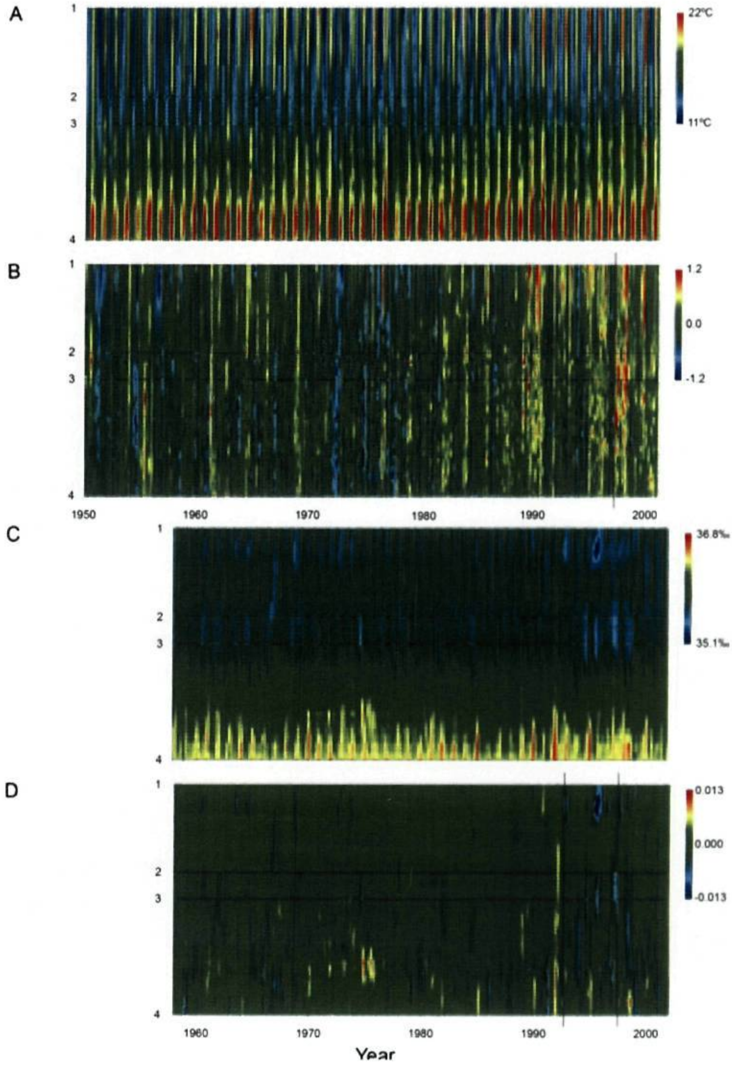

Figure 3.1.3 Monthly mean SST (a), SST normalized anomalies (b), SSS (c) and SSS anomalies (d) along the Atlantic coast of the Iberian Peninsula. Horizontal lines (2, 3) limit the historical gap in northern Portugal (see Figure 3.1.1 for locations). Vertical lines correspond to significant SMW results.

throughout the 51-year time-series, with evident seasonality. During winter and spring, a temperature gradient is established along the Iberian coast, from cold waters in Biarritz (south-west France) to the

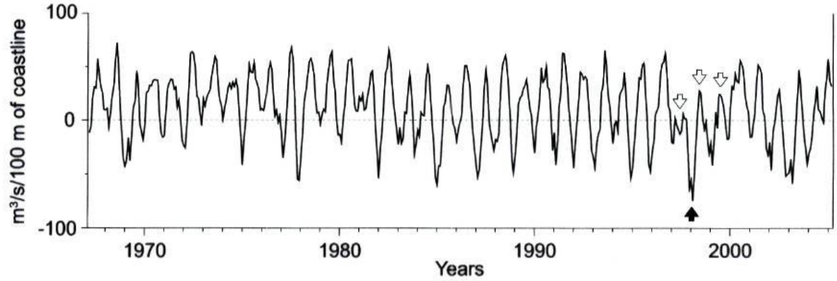

Figure 3.1.4 Four-month running mean computed on upwelling index (m^3 s^{-1} per 100 m of coastline) for the location of 41°00' N 10°00' W, between January 1967 and March 2005. The black arrow denotes the 1997/98 winter anomaly and white arrows indicate summer minimums from 1997 to 1999.

warmer zone in the Strait of Gibraltar (Figure 3.1.3 A). However, between summer and autumn the situation is not so linear. Although there is no change in the southern half of the gradient (3-4, Figure 3.1.3 A), the northern half experiences an inversion of the winter/spring pattern as surface waters become warmer (1-2, Figure 3.1.3 A). As a result, both extremes of the Iberian coast are warmer than northern Portugal (2-3, Figure 3.1.3 A). This colder region between these extremes matched the area from which *P. rustica* was traditionally absent.

SST anomalies were predominantly higher since 1990, with particularly warm sea water temperatures in the autumn, winter and spring during 1997 and 1998. Negative anomalies were almost absent for the last 15 years of the time-series. On the area between 39°30' and 41°54' N, SMW gradient analysis revealed one significant discontinuity in mid-1997 (Figure 3.1.3 B). This anomaly corresponds to the abrupt transition between one period of relative normality and another characterized by an unusual increase in SST.

POP-SODA sea surface salinity data also showed strong annual seasonality. Usually, SSS increases in warmer seasons and decreases during winter and spring (Figure 3.1.3 C). Even though salinity is generally inversely proportional to latitude, on the northern Portuguese coast it is lower than the surrounding areas, reaching values only comparable to those observed in the Bay of Biscay. For the area between 39°30' N and 41°54' N, SMW gradient analysis revealed two significant discontinuities (Figure 3.1.3 D): one in the autumn of 1992 and another in the summer/autumn of 1997. The first anomaly corresponds to a situation where a high-salinity phase that took place in the spring of 1992 ended abruptly and the second denotes a step transition from a period of anomalous low salinity (during the spring of 1997) to a state of relative normality.

Upwelling off the northern Portuguese coast typically occurs from late spring to late autumn (Lemos and Pires, 2004; Peliz *et al.*, 2005). Although this pattern was relatively constant between 1967 and 2005, several anomalous episodes were identified (Figure 3.1.4). The summer upwelling indexes of 1997, 1998 and 1999 were the lowest ever, reaching a historical minimum in 1997. Moreover, the lowest winter upwelling value over the entire time-series was recorded in 1998.

3.1.5 Discussion

The present results show unequivocally that *P. rustica* has recently colonized the northern Portuguese coast, leading to the bridging of a historical gap in distribution known since the early 1900s. From 2003 onward, there was an increase in the number of colonized locations, and most notably in the number of individuals present at each location. The estimation of the minimum time of colonization based solely on length-frequency data would require knowledge of the growth rates of *P. rustica.* However, this parameter has not yet been assessed and results from growth studies of other *Patella* species are discrepant. For example, Guerra & Gaudêncio (1986) suggest a possible longevity of no more than 4 years for *Patella ulyssiponensis* Gmelin, 1791, *P. depressa* and *P. vulgata* on the Portuguese coast, based on length-frequency analysis. Since these species reach a maximum size of 3-4 cm in the region, growth rates must be relatively high, especially during the early stages of benthic life. In contrast, at higher latitudes (the UK and France) estimated growth rates fall into the range of 1-5 mm year for *P. vulgata* and *P. depressa*, with a maximum life span of 5-16 years, depending on habitat conditions (Fischer-Piétte, 1941; Bowman, 1981).

Taking a conservative estimate of 4-6 years for the maximum longevity of *P. rustica*, and given that the largest individuals were observed in some of the northern shores, data from the present work suggest that colonization of the northern Portuguese coast by this species started in the late 1990s. Additionally, the lack of small size classes, when compared with the size-frequency distributions of well-established southern populations (where breeding and recruitment are thought to be more regular and successful) may indicate that populations of *P. rustica* in northern Portugal resulted from sporadic settlement events (Lewis, 1986; Zacherl *et al.*, 2003).

High growth rates of early life stages can explain, in part, the absence of limpets on two northern shores (Moledo do Minho and Forte da Vigia) during the 2003 surveys and their subsequent occurrence in 2005. Yet, a 2-year period seems not to be enough to explain the presence of the largest limpets. It is possible that juvenile limpets use different nursery habitats on northern shores, thus being difficult to observe during their initial life stages. Because in the midshore zone extensive sampling of the mussel/barnacle mosaic and rock pools in the scope of environmental monitoring studies never revealed a single *P. rustica*, whilst other species of *Patella* were abundant, it is more likely that cryptic habits, like sheltering in crevices in the upper shore, may have rendered these individuals almost impossible to spot.

Finding the factors that maintained the distributional gap until the late 1990s is a first step to understanding the causes of the recent colonization of *P. rustica* in northern Portugal. As previously stated, between 39°30' and 41°54' N, the Portuguese coast displays oceanographic features distinct from the surrounding areas. Considering that the breeding period begins in July and spawning occurs between August and November/ December (Ibanez *et al.*, 1986), low temperatures during this phase of the life cycle could have inhibited juvenile development, particularly because immature molluscs are very sensitive to severe conditions during settlement and early life stages (Lewis, 1986). Coincidently, an increase in average SST was observed on the Portuguese coast during recent decades (Lemos and Pires, 2004; Peliz *et al.*, 2005). Moreover, recent sea surface warming during autumn/early winter, as shown by the analysis of SST anomalies, might have provided temperatures within the limited range suitable for metamorphosis and fast growth, allowing limpets to attain a sufficient size to survive the coming winter. Northern Portuguese populations of *P. rustica* are characterized by low densities and predominance of large individuals, which is typical of populations that fail to reproduce successfully and hence have infrequent recruitment success owing to thermal stress at the northern boundary of their range, because of low temperatures (Lewis *et al.*, 1982; Lewis, 1986; Zacherl *et al.*, 2003).

Apparently, intolerance to low salinity alone is not a plausible explanation for the maintenance of such a long-term gap, since SSS in this area within the historical gap is similar to that observed in the Bay of Biscay, where *P. rustica* has been recorded since the early 1900s. Flow fields often observed in association with biogeographical boundaries have the potential to constrain a species' geographical range, even when suitable habitat is available elsewhere (Gaylord and Gaines, 2000). Therefore, another explanation for the maintenance of the gap would be a deficient larval input resulting from adverse sea currents. Although it was not possible to obtain detailed data on surface currents, it is known that over the continental shelf current intensity and direction are closely related to upwelling intensity and to the development of the Western Iberia Buoyant Plume (WIBP). During negative upwelling periods (downwelling), the predominant southward offshore currents decrease in intensity and inshore poleward circulation rises in strength (Figueiras *et al.*, 2002; Peliz *et al.*, 2002; Sanchez and Relvas, 2003). The WIBP consists of a low-salinity surface water layer fed by the winter-intensified run-off of several rivers on the northwest coast of Portugal and Spain (Santos *et al.*, 2004). The development of the WIBP results in isolation of inner-shelf waters and strong poleward transport (Peliz *et al.*, 2002; Peliz *et al.*, 2005). In years with strong buoyant discharge and weak upwelling, northward coastal transport is enhanced. On the contrary, strong upwelling, reduced river run-off or both, will have the opposite effect (Santos *et al.*, 2004).

Assuming the reproductive period suggested by Ibanez *et al.* (1986), larval release and dispersal will occur when equator-ward currents are at their maximum, because in late summer/autumn upwelling is usually strong and river run-off is at its minimum due to the drier summer season. Surprisingly, even though in the last decades hydrographical conditions remained stable, favouring larval drift from Galicia, there is no evidence of successful colonization. It is possible that southern Galician populations are not reproductive and subsist only through repopulation by larvae that arrive from north-west Spain every autumn.

In this case, larval drift coupled with larval life span may have limited dispersal toward the south. On the other hand, sporadic observation of isolated individuals within the historical gap (see section 3.1.2) may indicate that settlement has indeed taken place but is intermittent, or somehow that individuals did not survive to reach adult stages. Although not easily identifiable, this phenomenon is probably more frequent than assumed (Sax and Brown, 2000; Zacherl *et al.*, 2003), and is a more likely explanation for the maintenance of the gap under conditions that favour larval transport from Galicia.

Lower SSS values on the northern Portuguese coast from 1995 onward indicate an increase of the WIBP. In addition, from 1997 to 1999 upwelling was consistently low. These two phenomena combined could have favoured larval transport from central and southern Portugal toward the north. Taking into account that during this period positive SST anomalies could have reduced the thermal pressure on early life stages, it is plausible to assume a scenario where a combination of several oceanographic variables allowed southern larvae to drift northward, settle and survive in such numbers that populations started to develop. The observed decrease in number of individuals toward the north, which was consistent in 2003 and 2005 surveys, also supports the hypothesis that colonization occurred in that direction. The multi-factor explanation is more plausible than supposing that just one factor was responsible for the observed changes. In many cases, species range limits are determined by the interaction of several factors, including ocean currents, upwelling, salinity, fetch, sea temperature, as well as the type of planktonic development (Crisp and Southward, 1958; Menge, 2000; Zacharias and Roff, 2001; Rivadeneira and Fernández, 2005). By overlapping SST, SSS and upwelling time series it was possible to find a common time window, from the beginning of 1997 to the end of 1998, when it is more likely that the expansion has taken place. Moreover, 1997 was an exceptionally mild year over Europe, with a winter season characterized by high temperatures and intense rainfall (Dong *et al.*, 2000), and 1998 was the warmest year of the last millennium in the Northern Hemisphere (IPCC, 2001).

As proposed by Lewis (1986), occasional successful settlement may result in a sudden increase in numbers, which then persist conspicuously for several years. In the present case, however, several independent settlement episodes have to be considered, since between 2003 and 2005 the number of individuals increased several fold in colonized sites, and new populations were found. Two explanations are possible and not mutually exclusive: one or more new colonization episodes occurred with larvae that originated from historical locations, or reproduction of the newly established populations was successful, providing larvae that not only settled on the same shores but also expanded to the vicinity. Once critical population size was established self-recruitment would be possible.

The recent colonization described is most likely the corollary of the expansion process observed in Galicia during the 1950s by Fischer-Piétte & Gaillard (1959), which was also coincident with a warmer period in north-west Europe (see Hawkins *et al.*, 2003 for a review). However, the lack of detailed oceanographic data sets for that time frame in northern Spain makes it impossible to objectively correlate their findings with changes in the environment.

A detailed knowledge of the population dynamics of this species, particularly in this geographical region, is essential for a better understanding of the colonization process. Determining the exact extent of the reproductive period, as well as the growth rate and life span of *P. rustica*, will reduce the uncertainties related to the time of colonization. The multifactor hypothesis presented here describes a sequence of climatic and hydrographical events that ultimately led to the colonization of northern shores. It implicitly assumes that this colonization occurred from the south. Provided that there is a reasonable degree of genetic differentiation between northern and southern populations, this hypothesis can be tested using highly variable molecular markers. Thus, studies on population genetics should help to identify the source of newly established populations of *P. rustica* in northern Portugal and also to determine possible past expansion and/or retraction events in this region.

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Section 3.2

Do long-term changes in intertidal algae assemblages in the northeast Atlantic reflect warming?

3.2.1 Abstract

Well-documented changes in species abundances and distributions coinciding with global warming have been increasing during recent years. A trend of raising sea-surface temperature has also been observed along the Portuguese coast and is likely to be affecting intertidal species' ranges. The present study aimed at evaluating the direction and intensity of distribution changes of macroalgae in the area. The last 50-year trend of coastal air and sea temperature was reassessed, providing an accurate estimate of the warming process. Information on species' range shifts was obtained by comparing data from recent resurveys with historical records of algal distributions collected during the 1950s and 1960s. Although a prevalence of northward migrations was anticipated, this work showed a marked difference in the average direction of changes between cold- and warm-water species. Cold-water species, when considered together, showed no particular shifting trend, since the number of species that shifted north or south was the same. Contrarily, all warm-water species expanded their range northwards.

Therefore, generalizations about poleward range shifts due to increasing temperature should be made with caution.

3.2.2 Introduction

The distribution of species within and across ecosystems is ultimately determined by the environment (IPCC, 2001; Clarke, 2003). There have been significant responses in the Earth's biota to recent warming (Parmesan, 1996; Hughes, 2000). Perhaps the most pervasive change documented in biological systems is the shift in species' geographical ranges (Parmesan and Yohe, 2003; Rivadeneira and Fernández, 2005). The forthcoming climatic changes, which are expected to increase in strength, will act even more strongly on these limits (IPCC, 2001). The poleward movement in latitude or upperward in altitude has been observed, in different geographic regions, for many species' ranges (Parmesan, 1996; Parmesan *et al.*, 1999; Hughes, 2000; Stenseth *et al.*, 2002; Walther *et al.*, 2002; Parmesan and Yohe, 2003; Root *et al.*, 2003; Franco *et al.*, 2006; Hickling *et al.*, 2006), and marine organisms are no exception (Barry *et al.*, 1995; Southward *et al.*, 1995; Holbrook *et al.*, 1997; Sagarin *et al.*, 1999; Sims *et al.*, 2001; Zacherl *et al.*, 2003; Genner *et al.*, 2004; Southward *et al.*, 2004; Perry *et al.*, 2005).

Intertidal communities are attractive for studying climate-driven community changes because their ecologies are well-known (Simkanin *et al.*, 2005; Helmuth *et al.*, 2006) and, in addition they are exposed to temperature and weather extremes, living close to their thermal tolerance (Tomanek and Helmuth, 2002). In the North-East Atlantic there are extensive long-term records available to judge responses to climate change (see Southward *et al.*, 2004; Helmuth *et al.*, 2006 for review). It has long been known that the Portuguese coast is at an interface between warm- and cold-water faunas and floras (Santos, 2000; Boaventura *et al.*, 2002; Pereira *et al.*, 2006). Differences in species composition along this latitudinal gradient have been extensively studied since the middle of the 20th century, and both northern and southern limits of distribution of many species have been reported (Fischer-Piétte, 1963; Ardré, 1970). Additionally, there is a considerable number of species which display latitudinal abundance clines within this area (Ardré, 1970; Santos, 2000;

Boaventura *et al.*, 2002), although the upwelling regime of the Iberian Peninsula can influence patterns on mesoscales and may contribute to settle boundaries (Lima *et al.*, 2006).

Similar to the trends in air temperature (Klein Tank *et al.*, 2002), sea temperature off west Portugal has been showing a steady year-round increase from 1941 onwards, averaging more than 0.01°C per year in coastal waters (Lemos and Pires, 2004; Lemos and Sansó, 2006). Furthermore, shifts in species distribution have been described for the Iberian Peninsula since the 1950s (Fischer-Piétte, 1955, 1956, 1957a, b). Surveys suggest that significant changes have occurred in recent years, with some cold-water species disappearing from large stretches of coastline, whilst warm-water species are colonising new areas (Lima *et al.*, 2006).

To test the generality of the responses the past 50 year trend of coastal air and sea temperature was reassessed to provide an accurate description of the warming process. In face of the current climate warming, a prevalence of northward migration of both cold- and warm-water species was predicted (Hickling *et al.*, 2006).

The present work focused on the highly diverse group of macroalgal species inhabiting the Portuguese rocky coast. The most comprehensive and detailed study of algal biogeography along this region was made by Ardré (1970, 1971) during the 1950s and 1960s. More than 20 sites were exhaustively surveyed by this author. The total number of *taxa* identified and mapped largely exceeded 350 species, varieties and forms, from the largest Phaeophyceae to the smallest filamentous algae. The direction and intensity of macroalgae distributional changes along the Portuguese coast was examined by contrasting historical records of more than 120 conspicuous species with data from recent surveys. Moreover, Ardré (1971) empirically identified a distinct biogeographic boundary in central Portugal, near the Tagus estuary, by overlapping the distributions of species with range limits within this area. We tested the hypothesis that this boundary would be shifted northwards with current warming.

3.2.3 Material and methods

Temperature trends

Sea surface temperature (SST) along the Portuguese coast, between January 1950 to December 2000, was derived from *in situ* raw data obtained from the International Comprehensive Ocean-Atmosphere Data Set (ICOADS, Woodruff *et al.*, 1988). To avoid bias due to different daytime measurements, only data from 12:00 were used. Point data were imported into GRASS Geographical Information System (GRASS Development Team, 2006) and transformed into raster maps with a spatial resolution of 4 km using a surface interpolation method. Each cell was derived from the 12 nearest data points using the distance squared weighting algorithm (Jarvis and Stuart, 2001). Near-surface air temperature (NSAT) monthly averaged data from 1950 to 2000 covering European land surface at 10 minute resolution was obtained from the CRU TS 1.2 dataset, available from the Tyndall Centre for Climate Change Research (Mitchell *et al.*, 2002; Mitchell *et al.*, 2004).

The resulting set of 612 (51 years × 12 months) SST and 612 NSAT maps was stored in GRASS GIS as monthly layers and sampled along the Portuguese coastline at regularly spaced (10 km) points (Figure 3.2.1). The resulting data for each parameter were combined to build a table with each row denoting a geographical location and each column a month/year combination. Warming trends were determined for eight stations spaced along the coast and expressed as the slope of a simple linear regression between temperature and time.

Analysis of species abundances

It is commonly accepted that environmental conditions are major determinants shaping species ranges (Gaston, 2000; Walther *et al.*, 2002; Clarke, 2003). In this perspective, species abundances will be inversely proportional to the strength of adverse factors (Sorte and Hofmann, 2004), which are weaker in the middle of the range and stronger near the distribution limits (but see Sagarin and Gaines, 2002a, b). Changes in climate (such as long periods of rising temperature) might reduce the fitness of some populations, in particular those in peripheral regions, causing fluctuations in abundance or even extinctions (e.g. Southward *et al.*, 1995; Lewis, 1999).

To verify whether the current warming could be affecting species abundance and therefore altering the location of the main biogeographic boundary in the Portuguese coast, the first step was to identify objectively its historical location using Ardré's original data. Although two versions of the data were published (in 1970 and in 1971), we used the latter because information on the abundance was given in a semi-quantitative scale (absent, observed, rare, common, very common). A modified version of the Split Moving Window (SMW) method (Webster, 1973; Cornelius and Reynolds, 1991) was developed for this purpose. It requires information on species abundances for several locations along a transect. The coastline was "linearised" preserving real distances among sampling sites. A window with a specific size was placed in the beginning of the data series, splitting it in two equal halves and recording the locations inside each half. A multivariate measure of dissimilarity (Bray-Curtis) was taken between every possible pair of samples from different halves and the values of all comparisons were then averaged. The value obtained was assigned to the centre of the window, which then moved one step forward. This process was repeated until the window reached the end of data series. Statistical significance of dissimilarities for each window's midpoint was computed by permutation techniques. To avoid bias due to possible data autocorrelation, a one-dimensional equivalent of a toroidal shift was used (Fortin and Jacquez, 2000). Results from consecutive window sizes allowed the definition of regions where the highest number of significant results was observed along the data series. These identified zones where species substitution was greater, indicating the location of biogeographic boundaries.

After objectively locating the historical boundary, the same SMW methodology was applied to contemporary data. However, Ardré's sampling programme could not be precisely replicated. Although the majority of locations visited by Ardré were resurveyed between 2001 and 2006, not all could be revisited since some sites simply disappeared due to coastal development such as port construction (e.g. Peniche, Outão and Sines). To avoid possible bias in the SMW results caused by the mismatch between the number and position of locations in the two sets, the nearest rocky shores were reassessed during the 2001-2006 survey (Figure 3.2.1). Therefore, original site ordination was

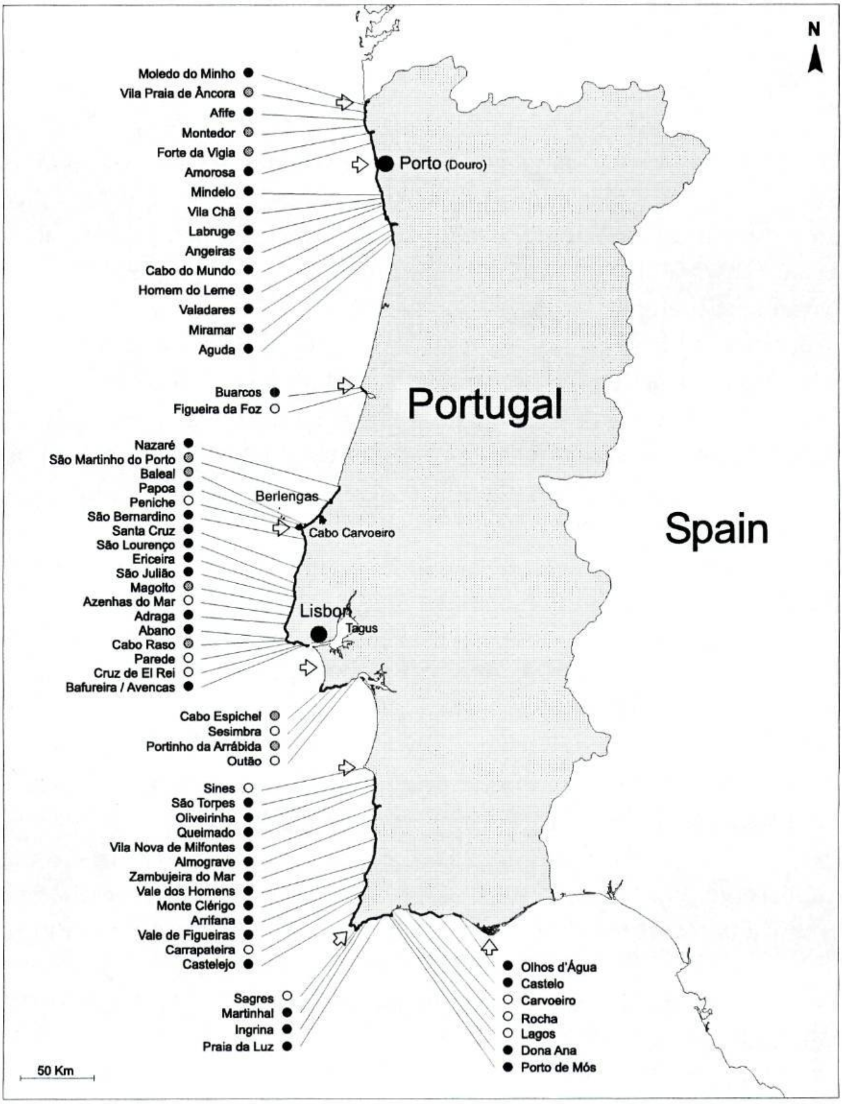

Figure 3.2.1 Study area with rocky coast depicted in bold. The two major cities (Lisbon and Porto) and the respective rivers (Tagus and Douro) are shown for reference. Climatic sampled locations are represented by white arrows. White circles represent locations visit only by Ardré (1970) in the 1950s and 1960s. Black circles correspond to locations only resurveyed in 2001-2006. Grey circles represent locations visited in both periods.

maintained and distances between locations were hardly affected. Ardré's semi-quantitative abundance scale was also adopted in order to obtain comparable values. After considering the time and taxonomic expertise that a full species study would require, it was determined only to resurvey easily identifiable and conspicuous species, thus reducing the algal checklist for comparison to 129 species.

Analysis of range shifts

From the 129 species used in the previous analysis, 39 were selected for the analysis of range shifts according to the location of their distributional boundaries. A first group consisted of species with an absolute range limit in the Portuguese coast (like *Himanthalia elongata* which cannot be found further south or *Sargassum flavifolium*, not found towards the north). Another group encompassed species which have their absolute range limit outside the Portuguese coast, but that displayed a distributional gap in this area. This unusual situation is caused by particular hydrographical features in the Eastern Atlantic Coast, such as cold upwelling areas in Western France, Northern Portugal and Morocco, and warm areas in the Bay of Biscay and Southern Portugal (OSPAR, 2000; Sanchez and Relvas, 2003; Lima *et al.*, 2006). For example, *Fucus vesiculosus* and *Bifurcaria bifurcata* have their southern boundary in Morocco, where the temperature is still cold enough to sustain populations, but cannot be found in the warmer southern Portugal. On the other hand, *Padina pavonica* and *Codium adhaerens* are abundant in Northern Spain and Southern France, but are absent from the colder region of Northern Portugal. Together, these two groups comprised 25 cold- and 13 warm-water species whose changes in their distributional limits in the Portuguese coast could be correlated with environmental warming. Additionally, the non-native species *Sargassum muticum*, which has been spreading from the north during the last decades, was also surveyed.

The classification of species in cold- or warmer-water groups was adopted following Ardré (1970, 1971), Luning (1990) and Guiry and Guiry (2006). For each one of the selected species, all available historical records of their range boundaries were used, even if the location was not visited by Ardré herself. Thus, the use of several complementary historical studies (Miranda, 1934; Palminha, 1951; Dizerbo, 1954b, a; Ardré, 1957; Fischer-Piétte, 1958; Rodrigues, 1963) improved the correct identification of historical boundaries. Any abundance details were discarded, since the only required information was the southernmost (cold-water species) or northernmost (warm-water species) locality where each seaweed was found.

Contemporary range limits were assessed by carefully surveying a considerable number of localities during the low spring tides between 2001 and 2006. More than 50 locations were selected covering the entire continental Portuguese rocky coast (Figure 3.2.1), thus providing accurate data on extant distribution limits. To objectively identify significant changes in distribution endpoints, the methodology proposed by Rivaderneira and Fernández (2005) was adopted. Coastline distances were linearised and distances between every pair of adjacent locations measured. These distances were used as null expectation since they reflect the level of sampling error for which changes can be assessed. Therefore, only shifts greater than the percentile 95 (38.6 Km) of the distance distribution were considered significant.

3.2.4 Results

Temperature trends

A consistent increase in sea temperature was observed throughout the entire Portuguese coast. The slopes of all the linear regressions were statistically significant except for Faro, which is the southernmost location. SST warming rates ranged from 0.0009 to 0.0015 °C month^{-1} and the average temperature increase in the eight localities over the 50-year period was 0.74 °C. With the exception of short cold pulses in the mid 1960s, 1970s and mid 1990s, SST rose continually with the main warming period occurring during the last decade (Figure 3.2.2 B). On the other hand, monthly NSAT revealed a higher variance over the time series and the increases in monthly temperature were not significant in any of the eight localities analysed (Table 3.2.1). In this case, a stronger predominance of the cooling phase was observed during 1960s-1970s. Nevertheless, the overall trend was similar to that recorded for the SST,

Table 3.2.1 Warming trends (expressed by the slope of OLS regression) of sea surface temperature (SST) and near surface air temperature (NSAT) at eight coastal locations along the Portuguese coast. Locations can be found in Figure 3.2.1. Data ranges from January 1950 to December 2000. Significant slopes are depicted in bold.

			SST		NSAT	
Location	Lat.	Long.	Slope (°C per month)	Probability	Slope (°C per month)	Probability
Moledo do Minho	41.8756° N	8.8803° W	**0.0012**	0.008	0.0016	0.075
Douro estuary	41.1482° N	8.6820° W	**0.0012**	0.009	0.0016	0.078
Figueira da Foz	40.1316° N	8.8719° W	**0.0014**	0.002	0.0014	0.131
Peniche	39.3645° N	9.4098° W	**0.0015**	0.000	0.0011	0.227
Tagus estuary	38.6601° N	9.2967° W	**0.0013**	0.001	0.0010	0.282
Sines	37.9379° N	8.8768° W	**0.0012**	0.004	0.0015	0.122
Sagres	36.9941° N	8.9489° W	**0.0013**	0.003	0.0012	0.123
Faro	36.9608° N	7.9254° W	0.0009	0.058	0.0016	0.110

Table 2. Number and direction of changes in range boundaries of selected species.

Direction of shift	Cold-water species	Warm-water species	Total
Northwards	7	8	15
Southwards	7	0	7
No significant change	12	5	17
Total	26	13	39

with a major period of warming in the late 1990s (Figure 3.2.2 A).

Species abundances

SMW analysis successfully detected significant boundaries in the three tested data sets (two historical and one contemporary). The first analysis, performed on Ardré's complete species list, revealed a clear boundary in central Portugal, in the Tagus estuary (Figure 3.2.2 C). The boundary was detected at window scales ranging from 300 and 400 Km. On the other hand, the second analysis, aimed at pointing the location of the historical boundary in the smaller subset of species, gave a different result. In this case, the boundary was detected near São Pedro de Moel, approximately 197 Km north of the Tagus mouth, at window scales of 50 - 300 Km. Hence, the location of the historical boundary varied with the dataset considered. The analysis of the contemporary data set identified a boundary roughly at the same position as for the sub sample of Ardré's data (Figure 3.2.2 C).

Range shifts

The analysis of range shifts revealed a significant rate of change among species, which differed from the random expectation of zero (one-sample t-test, $t = 5.520$, $d.f. = 36$, $p < 0.05$). Additionally, more than one half of the studied species (22 out of the 39) displayed a significant displacement in their range limit (*i.e.*, more than the 38.6 Km threshold - Table 3.2.2). The remaining 17 species exhibited no shifts at all (with the current range boundary coinciding with the historically reported location) or the shifted distance was smaller than the assessment error (Rivadeneira and Fernández, 2005). The complete list of shifting and non-shifting

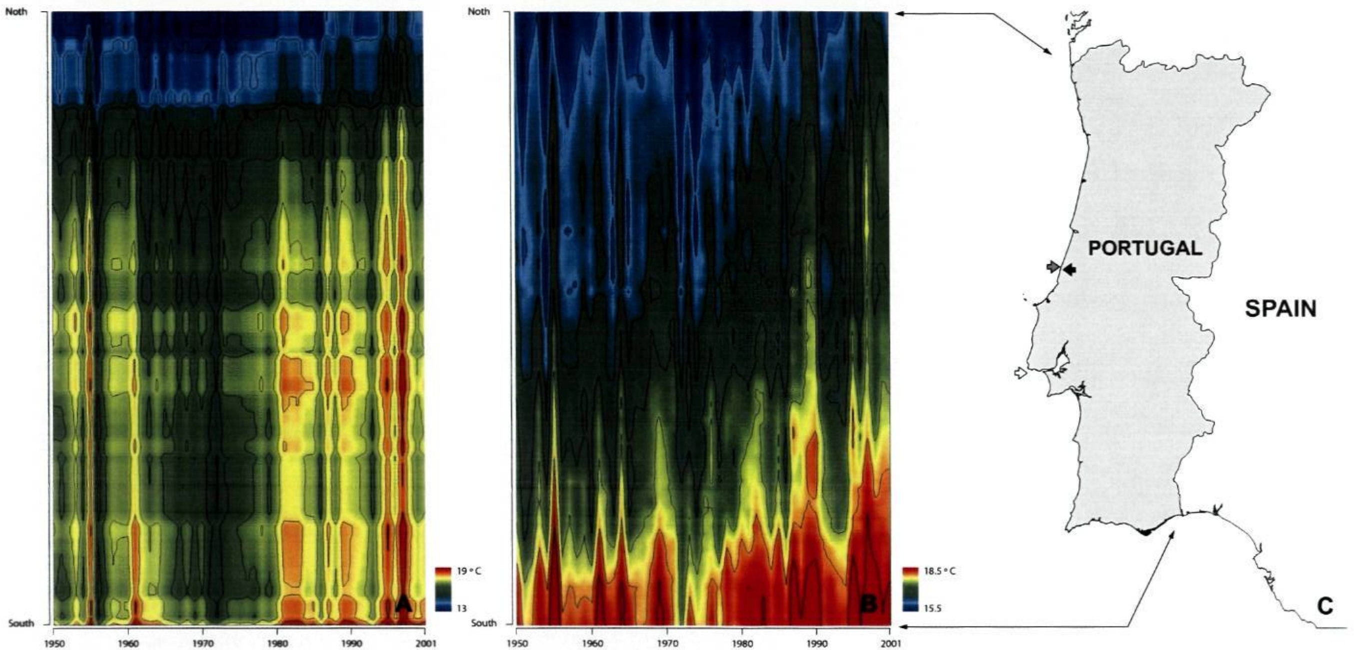

Figure 3.2.2 Yearly averaged NSAT (A) and SST (B) along the Portuguese coastline from 1950 to 2000. (C) Boundary location detected by SMW analysis. White arrow indicates the locality identified using Ardré's complete dataset. Black arrow stands for Ardré's smaller dataset and grey arrow indicates contemporary boundary location.

Table 3.2.3 Species for which shifts in range were assessed. n. a. stands for not applicable and n. s. for non significant.

			Historical range boundary	References	Current range boundary	Shift in Km
Cold-water species	Shifted northwards	*Chondrus crispus*	Sines	Ardré 1971	Cabo Raso	180
		Desmarestia ligulata	Portinho d' Arrábida	Ardré 1971	Avencas	70
		Dumontia contorta	Douro estuary	Ardré 1971	Amorosa	62
		Himanthalia elongata	S. Martinho do Porto	Ardré 1971; Fischer-Piétte 1958	Labruge	219
		Palmaria palmata	Tagus estuary	Ardré 1971	Valadares	358
		Pelvetia canaliculata	Berlengas Islands	Palminha 1958	Cabo do Mundo	245
		Phycodrys rubens	Moledo	Ardré 1971	species absent	n.a.
	Shifted southwards	*Ahnfeltia plicata*	Tagus estuary	Ardré 1971	Martinhal	330
		Bifurcaria bifurcata	Tagus estuary	Ardré 1971; Fischer-Piétte 1958	Monte Clérigo	257
		Desmarestia aculeata	Douro	Ardré 1971; Rodrigues 1963	Baleal	227
		Fucus vesiculosus	Vila Nova de Milfontes	Dizerbo 1954a	Ingrina	157
		Halidrys siliquosa	Pontevedra (Spain)	Miranda 1934; Ardré 1957	Montedor	90
		Mastocarpus stellatus	Sines	Ardré 1971	Monte Clérigo	121
		Sargassum muticum	n.a.	n.a.	Almograve	n.a.

Table 3.2.3 Continuation. WWS stands for warm-water species and SN for shifted northwards

Cold-water species	Non-significant shift	*Ascophyllum nodosum*	Forte da Vigia	Ardré 1971; Fischer-Piétte 1958	Forte da Vigia	n.s.
		Calliblepharis ciliata	Portinho d' Arrábida	Palminha 1958	Portinho d' Arrábida	n.s.
		Cystoseira baccata	Lagos	Ardré 1971	Dona Ana	n.s.
		Fucus spiralis	Sagres	Ardré 1971; Fischer-Piétte 1958	Martinhal	n.s.
		Laminaria hyperborea	Baleal	Ardré 1971	Baleal	n.s.
		Phyllophora crispa	Peniche	Ardré 1971	Peniche	n.s.
		Fucus serratus	Forte da Vigia	Ardré 1971; Fischer-Piétte 1958	Amorosa	n.s.
		Gelidium corneum	Algarve	Ardré 1971	Castelo	n.s.
		Lam inaria saccharina	Forte da Vigia	Ardré 1971; Fischer-Piétte 1958	Amorosa	n.s.
		Petalonia fascia	Sines	Ardré 1971	Vila Nova de Milfontes	n.s.
		Delesseria sanguinea	Montedor	Dizerbo 1954b	Vila Praia de Âncora	n.s.
		Dilsea carnosa	Douro estuary	Ardré 1971	Labruje	n.s.
WWS	SN	*Asparagopsis armata*	S. Martinho do Porto	Ardré 1971	Vila Praia de Âncora	287
		Codium adhaerens	Baleal	Ardré 1971	S. Martinho do Porto	59
		Halopithys incurva	Lagos	Ardré 1971	Bafureira	475

Table 3.2.3 Continued.

Warm-water species	Shifted northwards	*Hypnea musciformis*	Sagres	Ardré 1971	Portinho d' Arrábida	269
		Leathesia difformis	Peniche	Ardré 1971	Vila Praia de Âncora	320
		Padina pavonica	Sesimbra	Ardré 1971	Baleal	187
		Sargassum flavifolium	Sines	Ardré 1971	Moledo	593
		Valonia utricularis	Tagus estuary	Ardré 1971	S. Martinho do Porto	197
	Non-significant shift	*Cystoseira tamariscifolia*	Vila Praia de Âncora	Ardré 1971	Vila Praia de Âncora	n.s.
		Scytosiphon lomentaria	Peniche	Ardré 1971	Baleal	n.s.
		Halopteris filicina	Vila Praia de Âncora	Ardré 1971	Afife	n.s.
		Amphiroa sp.	Sines	Ardré 1971	Vila Nova de Milfontes	n.s.
		Caulacanthus ustulatus	Forte da Vigia	Ardré 1971	Moledo	n.s.

species can be found in Table 3.2.3. From the group of southern species showing significant shifts (62%), all were found northward in relation to their historical range limits. Apparently, these results were in agreement with the initial prediction of a northward dominance in migration events. On the other hand, the pattern observed in the cold-water species was quite different. In this case, 54% of the species exhibited significant shifts in their range limits, but the direction of such shifts was not consistent among all the species. Half of the species shifted northwards and the other half southwards. Globally, shifts in endpoints varied from 59 to 583 Km with a mean value of 235 Km. The distance travelled by northward shifting species did not differ from those shifting southward (*t*-test, $t = 0.872$, $d.f. = 13$, $p > 0.05$).

3.2.5 Discussion

The sea and air temperature are naturally highly variable over space and time. Due to the density and specific heat of seawater, the ocean is more resilient to changes in temperature than the atmosphere which shows higher short-scale variability (Levitus *et al.*, 2000). The absence of a significant trend for NSAT of coastal sites may have been caused by a longer cooling period during 1970-1980, which obscured the effects of a noticeable increase in the last decade. Rates of change in ocean temperature are similar to those already reported by Lemos and Pires (2004) and Lemos and Sansó (2006) for coastal Portuguese waters. Moreover, this warming rate also matches the increase in SST temperature observed in the Bay of Biscay and English Channel (Hawkins *et al.*, 2003; Southward *et al.*, 2004) in the North Sea (Genner *et al.*, 2004; Perry *et al.*, 2005) and in coastal North-Western Pacific (Sagarin *et al.*, 1999). In all of these locations significant changes in species distributions have been described.

There are only a few marine and coastal studies in which SMW analyses have been applied. Among these, most employ SMW only as a tool to analyse temporal series of climate, while using other approaches to interpret biological data (but see Beaugrand, 2003; Beaugrand and Reid, 2003). In the present study, the applicability of the analysis was tested by using a data set for which the boundary location was well known a priori. The match between the boundary position described by Ardré (1971) and the one derived from the SMW procedure provided confidence for the two subsequent analyses.

The differences between boundaries detected by SMW analyses for Ardré's (1971) full set and subsampled data were not unexpected. Ardré (1971) observed that the group of northern species whose southern limits were located in the Portuguese coast included mainly large and conspicuous brown algae such as *Himanthalia elongata*, *Ascophyllum nodosum* or *Pelvetia canaliculata*. On the contrary, the majority of the southern species which displayed northern limits in this area were small and cryptic red algae belonging to genus such as *Griffithsia*, *Polysiphonia* or *Coelotrix*. Since in the present resurvey small and inconspicuous species were discarded from the analysis, the mismatch between boundaries was anticipated. Ardré (1971) reported the region of Cabo Carvoeiro as a secondary but nevertheless important region of change if only large species were considered.

The analysis of contemporary data indicated the same location for the boundary, suggesting that the observed increase in sea-surface temperature has not caused a significant effect on the distribution of the studied species, when considered as a whole assemblage. It should be emphasised that this conclusion is only valid for this particular group of species, and since only macroalgae were resurveyed, results should not be considered out of their context. Another important aspect is that the maintenance of the boundary position does not necessarily mean that individual ranges remained unchanged. This result may arise from two different scenarios: when no changes occurred or when individual range limits and abundances vary but the overall changes are symmetrical. Providing that a change in one particular species has a correspondent and inverse change in another, the average region of change (boundary location) should remain unaltered. The SMW method is therefore unable to distinguish between these situations and caution must be taken in the interpretation of the results.

The study of individual shifts helped to address the question concerning the non-changing boundary. However this analysis was performed solely using distributional limits, meaning that any possible changes in abundance that might have contributed to the present boundary location were not taken into account. Apparently, the boundary did not move due to a combination of several factors, such as a low number of shifting species (only 23 in a totality of 129) and the existence of opposite shifts that ended up neutralizing each other.

The most evident feature, however, was the clear divergence between shifting patterns of northern and southern species. Cold-water species, when considered together, showed no particular shifting trend, because the number of species that shifted north or south was precisely the same. Contrarily, all warm-water species expanded their range northwards. Similar trends were already observed both by Helmuth *et al.* (2006) in Britain, where only two northern intertidal species showed contraction of their range, contrasting with eight range expansions of warm-water species, and by Parmesan and Yohe (2003) in a meta-analysis involving a wide number or range shifts in terrestrial species.

Several hypotheses can be put forward to explain the observed differences between the two groups of species. The simplest explanation is that their range shifts are no more than chance fluctuations not differing from the random expectation. This probably happened in the cold-water group, since the proportion of species shifting northwards, southwards, or not shifting did not differ from chance ($\chi^2 = 1.93$, d.f. = 2, $P > 0.05$). On the other hand, in the warm-water group those proportions cannot be easily explained by chance given that the observed changes were unidirectional (towards the north).

Differences in metabolism which determine growth rates and the time required to attain sexual maturity or even life span may also explain the observed patterns. It is known that warm-water species generally grow faster and reproduce earlier during their shorter life extent compared with cold-water congeners (Lewis, 1986). Thus, it is reasonable to expect that geographical responses to climate warming will be noticed earlier on warm-water species, since their life-cycle characteristics confer them a more opportunistic character. A different explanation could be due to a possible advantage that southern species experience in a warming world. These new environmental conditions allow them to expand their range, thus releasing them from competitor and predator pressures (Sax and Brown, 2000). Furthermore, native cold-water species still have to interact with co-evolved competitors, predators and diseases in addition to the invaders, which might decrease their fitness (Sax and Brown, 2000).

On the other hand, there are potential mechanisms which can be in the origin of some of the southward expansions of northern species. It is possible that stronger equatorial winds originated by the warming process lead to intensified upwelling causing counter-intuitive expansion of cold-water low-shore and subtidal species. Nonetheless, recent evidence suggests that upwelling has been decreasing in this area (Lemos and Pires, 2004).

A possible explanation for the observed differences between cold- and warm-water species is that the former are probably more resilient, tolerating more easily longer periods of adverse conditions. In these situations they may grow slower, ceasing their reproductive growth and offspring production, but might not go extinct. Moreover, if during the generally warming trend some cold pulses occur, even if only for short periods of time (as those observed along the Portuguese coast in SST during the middle 1960, 1970 and 1990), then the reproductive output of these species might be enough to maintain local populations and to allow them to expand towards the south. This situation was observed by Southward (1967;, 1975) and Southward *et al.* (1995), who reported southward range expansions of cold-water intertidal barnacles associated with cooling SST pulses, followed by warmer periods during which these populations were able to maintain their extended ranges.

It has been shown that the distributions of both terrestrial (e.g., Brooker, 2006) and marine organisms (e.g., Connell, 1961; Wethey, 2002) are conditioned not only by the physical environment but also by biological interactions, and that the responses to the environment can themselves be affected by biotic factors like competition and predation (Sanford, 1999; Sanford, 2002; Richardson and Schoeman, 2004). Hence, future studies should address the role and the relative importance of species interactions on the distributional changes here described.

These findings emphasise the importance of considering the synchrony between climatic oscillations and population dynamics (Zacherl *et al.*, 2003) and the need to understand single-species' responses, which when combined shape the patterns of community change (Genner *et al.*, 2004; Gilman, 2006). Additionally, results from the present work suggest that since single-species responses may be highly variable, generalizations about poleward shifts should not be taken lightly. To accurately identify and predict community structure changes under climate change scenarios, it is essential to gather and keep up to date accurate records of a high number of species distributions. The algal assemblages considered in this work, coupled with additional species whose distributional limits are in a shifting process (see Lima *et al.*, 2006), are ideal for a continuous study, which will definitely help to build more accurate predictive models on how species ranges are likely to shift in response to global climate change.

3.2.6 Aknowledgements

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Section 3.3

Transplant experiment on the retreat of the southern distribution limit of *Himanthalia elongata* (Linnaeus) S.F. Gray in the northeast Atlantic

3.3.1 Abstract

During the last decades, the southern distributional limit of the brown algae *Himanthalia elongata*, located in the Portuguese coast, has been retracting towards the north. It has moved approximately 350 Km in the last 150 years and over 200 Km in the last 40 years. These changes were coincident with a general warming of the sea surface temperature. The aim of this study was to assess the likelihood that the extinction of the southernmost populations of *Himanthalia elongata* has been caused by recent warming. The reproductive growth of specimens was used as a measure of species performance under experimental treatments. Individuals transplanted to southern shores within the region from where the species became extinct were compared with individuals from stable populations in northern Portugal. Results indicated that contemporary sea surface temperatures are not hampering reproductive growth. The findings that individuals were overgrow by sabellarian reefs or subjected to intense grazing at the southern locations suggest that biological interactions might have played a more significant role in the

retraction of *H. elongata* range than previously anticipated.

3.3.2 Introduction

Recent ecological literature reveals an increasing interest in the study of species' distributional limits, particularly in the background of current climate change. The acknowledgement that rapid environmental changes are expected to continue in this century makes it crucial to understand how species' distributions are likely to be affected by those alterations (Parmesan *et al.*, 2005). Long-term based studies indicate that some species are already responding to recent climate anomalies. The poleward movement in latitude or upward in altitude has been observed in different geographic regions and in most of the major taxonomic groups, including terrestrial (Parmesan, 1996; Hughes, 2000; Peñuelas and Filella, 2001; Stensen *et al.*, 2002; Walther *et al.*, 2002; Parmesan and Yohe, 2003; Root *et al.*, 2003; Hickling *et al.*, 2006) and marine organisms (Barry *et al.*, 1995; Southward *et al.*, 1995; Holbrook *et al.*, 1997; Hoegh-Guldberg, 1999; Sagarin *et al.*, 1999; Sims *et al.*, 2001; Stachowicz *et al.*, 2002; Zacherl *et al.*, 2003; Genner *et al.*, 2004; Southward *et al.*, 2004; Perry *et al.*, 2005; Harley *et al.*, 2006; Helmuth *et al.*, 2006). More than 80% of the species showing changes are shifting in the expected direction based on their known physiological constrains (Root *et al.*, 2003).

Intertidal communities have been used as sensitive indicators of environmental modifications (Barry, 1995; Southward *et al.*, 1995; Thompson *et al.*, 2002; Hawkins, 2003; Harley *et al.*, 2006). Likewise, recent surveys in the Portuguese coast indicate that significant changes in species' distributions have occurred during the last decades, with cold-water species disappearing from large stretches of coastline and warm-water species colonising new areas, expanding their range or narrowing distributional gaps (Lima *et al.* 2006; see also section 3.2). These changes were coincident with a general warming of the sea temperature in the area (Lemos and Pires, 2004; Lemos and Sansó, 2006).

One of the retracting species is the fucalean seaweed *Himanthalia elongata* (Linnaeus) S. F. Gray. This cold-water species can be found along the northeast Atlantic coast of Europe, from Scandinavia to northern

Portugal, including the Faeroes, Ireland and the U.K. (Luning, 1990; Guiry and Guiry, 2006). The southern distributional limit appears to be unstable and has been retracting northwards at least throughout the last 150 years. Obtaining data from the literature to track the southern range shifts of *H. elongata* proved to be a difficult task, since most data were in the form of herbarium records, museum reprints, technical reports or unpublished academic theses.

In an extensive review of the Phaeophycota of the Portuguese coast, Rodrigues (1963) examined the herbarium collections of F. Welwitch (University of Lisbon) and found that between 1845 and 1849 this species ranged as far south as the Tagus estuary (Figure 3.3.1). One hundred years later Palminha (1951) set the southern boundary of *H. elongata* at Cabo Raso, a few kilometers to the west. In the early 1960s, both Rodrigues (1963) and Ardré (1970) independently located the southern distributional limit at São Martinho do Porto. Since then, no more observations were published until the 1980s, when Santos and Melo (1983) recorded a single non-reproductive individual at Baleal (20 Km south of the previously established southern boundary). In the early 1980s, *H. elongata* was still present in Porto (A.M. Santos pers. obs.). Multiple surveys made between 1993 and 2001 (e.g. Santos, 1994; 2000), set the current southern boundary of the distribution at Labruge.

The aim of the present study was to assess the likelihood that the extinction of the southernmost populations of *Himanthalia elongata* may have been caused by recent warming.

H. elongata has a singular life-cycle and growth strategy (Creed, 1995; Stengel *et al.*, 1999). Unlike other members of the Fucales which are perennial, it is a biennial species which invests up to 98% of the total biomass in reproductive rather than vegetative tissue (Brenchley *et al.*, 1996). Vegetative growth starts in late winter, when first macro-recruits become visible as small button-like thalli on the rocky surface of the shore. During spring, thalli grow on small discs, which increase in diameter during the following months. In late autumn, when they reach 10-20 mm in diameter, reproductive growth begins (a small percentage continues to grow vegetatively). Discs start to develop receptacles, which increase rapidly in length during winter, forming bifurcated ribbon-shaped structures. In the summer the reproductive structures are normally more than 1.5 – 2.0 m in length. From June onwards, gametes

Figure 3.3.1 Study area. Individuals were transplanted from the northern locations of Montedor and Mindelo (black circles) to the shores of Buarcos and São Martinho do Porto (white circles). Past and present distributional limits are represented by grey circles, see the text for details. The rocky coastline is depicted in black.

are produced by mature receptacles, fertilization occurs and the new generation of germlings settle on the rock surface (Stengel *et al.*, 1999; Lagos and Cremades, 2004).

Since the species allocates the majority of its biomass to reproductive growth, this was used as a surrogate for the overall fitness of the organism. Specimens transplanted to shores in central Portugal (well beyond the current southern range limit of the species) were compared with individuals from stable populations in northern Portugal. To provide an accurate description of the warming process, patterns in sea surface temperature along the last 50 years were analyzed for the studied locations. These two sources of information were coupled to determine if the recent increase in temperature could be affecting algal fitness in the southern locations, leading to population extinction.

3.3.3 Material and methods

Transplant experiment

The study was carried out in four rocky shores from two separated regions in the Portuguese coast. Two shores, hereafter referred as 'northern' shores or 'controls', Mindelo (41°18'37"N 8°44'32"W) and Montedor (41°44'30"N 8°52'37"W), were selected from within the current distribution range of *Himanthalia elongata* in Portugal. The other two locations, Buarcos (41°10'10"N 8°54'20"W) and São Martinho do Porto (39°30'39"N 9°08'36"W), referred as 'southern' shores, are presently outside the species range, but had reasonably large populations of *H. elongata* until, at least the late 1960s (Rodrigues, 1963; Ardré, 1970) and most likely until 1980s (Santos and Melo, 1983). Since *H. elongata*'s reproductive growth starts during late autumn, the two northern shores were visited in early November 1999 during low tide and approximately 40 discs without visible reproductive organs were collected at each location to be subsequently transplanted. Algae were kept at the laboratory in seawater at 12-14°C. The experiment was set up simultaneously at the four shores in the following day.

In each shore, three zones roughly 20-40 m apart were selected. In each zone, six algae were attached to the rock using 10 × 10 cm quadrats of 8 mm plastic mesh fastened with stainless steel screws. The use of several 'zones' in each shore was mandatory to account for possible small-scale spatial variation. In the northern shores transplanted individuals could be easily placed among their conspecifics, since *H. elongata* is very abundant and often one of the dominant species in the lower shore. On the contrary, in the southern sites there was no way to know exactly where the species had occurred. Descriptions of the two southern sites by Rodrigues (1963) and Ardré (1971) were broad and shore heterogeneity made it impossible to select a single 'suitable' zone. Therefore, based on the knowledge of *H. elongata* occurrence in northern shores, specimens were placed on the lower shore, usually below the mussel (*Mytillus galloprovincialis*) and *Sabellaria alveolata* zones, in areas where red algae formed a distinct belt.

In the two northern shores, six untouched specimens were randomly selected from all possible individuals in each of the three zones to serve as controls for the effects of experimental manipulation (including the use of plastic mesh quadrats, storage and transportation). These individuals were signaled by a stainless screw fastened to the rock at their right side. Mortality and reproductive growth were assessed on a monthly basis by visiting the locations and measuring the specimens. Since the reproductive organs of *H. elongata* consist of two main branches, both were measured, and the average was taken as a measure of reproductive growth. The experiment was repeated in 2004/2005 to obtain independent measurements from a different year.

Climatic data

Sea surface temperature (SST) along the Portuguese coastline was derived from *in situ* raw data obtained from the International Comprehensive Ocean-Atmosphere Data Set (ICOADS, Woodruff *et al.*, 1988). To circumvent bias due to different daytime measurements, only data from 12:00 were used. Monthly point data from November 1949 to July 2000 were imported into GRASS Geographical Information System (GRASS Development Team, 2006) and transformed into raster maps with a spatial resolution of 4 × 4 km using a surface interpolation method. Each cell was derived from the twelve nearest data points using the Distance Squared Weighting algorithm (Jarvis and Stuart, 2001). The result was a set of monthly SST maps covering the entire study area. For each year, average, tmaximum and minimum monthly SST were computed based on the nine-month period from November to July, since this timeframe overlaps *H. elongata*'s reproductive season (Stengel *et al.*, 1999). SST maps were sampled at the four locations where the experiment was done (Montedor, Mindelo, Buarcos and São Martinho do Porto).

Statistical analyses

To determine the significance of the differences on receptacle growth between northern and southern sites, a five-way asymmetrical ANOVA was planned, due to the lack of controls for the transplant in the southern sites. Factors were 'region' (R), 'treatment' (T), 'sites' (S), 'zones' (Z) and 'years' (Y). The main factor 'region' was used to compare average reproductive growth in sites within current (northern) and historical (southern) range of *H. elongata* in Portugal. Factor 'treatment' was restricted to control (northern) shores and included manipulated *vs.* unmanipulated individuals, being the source of asymmetry in the ANOVA. Shores and zones were treated as random factors, given their nesting into 'regions' and 'shores', respectively. Factor 'year' was treated as random to make sure that results were independent of time of experiment.

The ANOVA was constructed so as to allow a priori statistical tests of hypotheses. First, the interaction between 'treatment' and 'shores' was tested for the northern 'region'. If non-significant, the effect of 'treatment' was tested subsequently. This was one of the most important tests because, if significant, it would show that the manipulation of algae (storage, transport and attachment) had some effect on the observed growth differences, and the analysis would stop. If the 'treatment' effect was not significant, a one degree of freedom comparison between the average growth on the northern and southern shores was computed.

Homogeneity of variances was assessed through the Cochran's test. Missing values were individually replaced by the average of the corresponding ANOVA cell and the degrees of freedom of the error term were corrected accordingly (Underwood, 1997).

3.3.4 Results

In both experiments most of the algae developed their receptacles after transplantation (Table 3.2.1). However, in the 1999/2000 experiment, development started in December, while in the 2004/2005 growth did not take place before January. A small percentage of individuals remained stationary in their button-like life stage and did not grow, which seems to be a normal phenomenon (Stengel *et al.*, 1999). Of the remaining algae, after an initial length increase, some were lost probably due to the sweeping effect caused by wave action, which enhanced friction

Table 3.3.1 Average receptacle growth in the four experimental locations at the end of the experiment.

	November 1999 - May 2000			November 2004 - March 2005		
	n	Average growth (cm)	Standard deviation	n	Average growth (cm)	Standard deviation
Moledo do Minho	22	89.3	34.5	23	27.2	6.1
Mindelo	22	38.7	18.3	23	26.1	6.6
Buarcos	11	70.1	38.5	10	25.7	5.8
São Martinho do Porto	-	-	-	3	27.4	6.5

between the plastic mesh and the thalli, cutting them loose.

Algal losses accumulated as the experiments progressed. The first experiment ended after eight months (in June) and the second after five months (in March), because by then only four (sometimes three) algae survived per combination of zone/shore. This was considered as the minimum number of replicates required to perform a sufficiently robust statistical analysis. In the 1999/2000 experiment, individuals transplanted to São Martinho do Porto showed signs of being under active grazing pressure (Figure 3.2.2). Here, receptacles did not grow significantly after being partially consumed, but the vegetative discs remained under the plastic meshes and some resisted until the end of the first experiment. In July, even after holding meshes were destroyed, some discs were still present and had reattached to the rocky surface. In Buarcos, although no grazing was observed, algae were overgrown by sabellarian reefs (*Sabelaria alveolata*) in early summer. This was also observed at S. Martinho do Porto, although by then receptacles had already been consumed and only the discs remained.

During the 2004/2005 experiment, intensive grazing was again observed at S. Martinho do Porto. However, this time a few individuals (three) survived until the end of the experiment and, although not formally tested, their growth was not much different from the remaining populations (Table 3.2.1). Grazing was also responsible for the loss of transplanted specimens in Buarcos, and after May the number of replicates was below the acceptable level, dictating the end of the

Table 3.3.2 ANOVA results for *H. elongata* reproductive organs growth for the years 1999 and 2000 for control (Moledo and Mindelo) and transplant locations (Buarcos and São Martinho do Porto). Significant slopes are depicted in bold.

	1999-2000					2004-2005					
Source of Variation	**DF**	**SS**	**MS**	**F**	**P**	**DF**	**SS**	**MS**	**F**	**P**	**Against**
Among All	14	9823.871	701.705	1.600	0.120	14	660.722	47.194	1.364	0.217	Error
Controls vs Buarcos	1	212.879	212.879	0.485	0.490	1	38.315	38.315	1.107	0.299	Error
Among Buarcos	2	2686.272	1343.136	3.063	0.058	2	47.722	23.861	0.690	0.508	Error
Among Controls	11	6924.720	629.520	1.435	0.194	11	574.685	52.244	1.510	0.167	Error
S	1	2723.551	2723.551	11.862	0.026*	1	1.565	1.565	0.018	0.899	Z(S)
T	1	769.868	769.868	2.141	0.382	1	14.815	14.815	0.113	0.794	S × T
Z(S)	4	918.394	229.599	0.524	0.719	4	341.481	85.370	2.467	0.061	Error
ST	1	359.525	359.525	0.668	0.460	1	131.120	131.120	6.120	0.069	Z(S) × T
Z(S) × T	4	2153.382	538.346	1.228	0.314	4	85.704	21.426	0.619	0.651	Error
Error	41	17980.772	438.555			39	1349.333	34.598			
Total	55	27804.643				56	2010.055				

Figure 3.3.2 Photographs of some transplanted specimen of *Himanthalia elongata* from the shore of São Martinho do Porto, showing signs of active grazing.

experiment. Due to the shorter duration of this experiment, it was not possible to observe any effects of sabellarian overgrowth.

Differences between start and end dates of the experiments in different years did not allow the results to be treated simultaneously in one ANOVA. Hence, factor 'year' was discarded and two ANOVAs were computed independently for each time. Furthermore, because in S. Martinho do Porto there was an insufficient number of replicates, this site had to be excluded from the analysis, introducing another source of asymmetry in the ANOVAs. Since only one southern site (Buarcos) remained available for comparison with the northern sites, the layout of the analyses was modified accordingly (Table 3.2.2).

In both ANOVAs (1999/2000 and 2004/2005) the interaction between 'shores' and 'treatments' (S × T) for northern sites was not significant. This allowed the interpretation of the tests for 'treatments' (T) and 'shores' (S). The first test (T not significant) showed that the experimental artifacts did not interfere with the observed growth patterns. Differences in growth were observed among northern shores only in 1999/2000 (S significant).These did not preclude further comparisons between northern and southern sites, because even if local differences existed, the main hypothesis was about differences in average growth between regions. No differences between 'northern' and 'southern' regions were detected in the two experiments ('northern shores' vs. 'Buarcos' not significant).

Receptacle growth did not differ between zones in each shore (Z(S) and 'among Buarcos' not significant in both experiments). This was

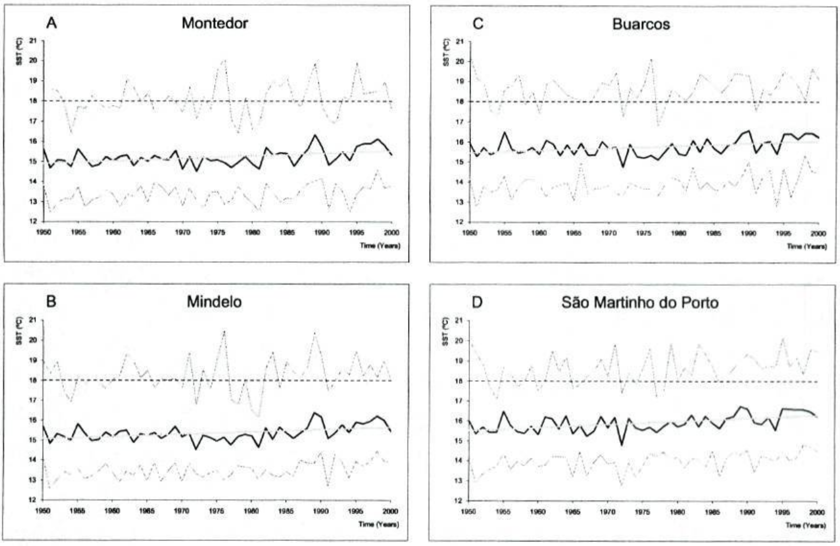

Figure 3.2.3 Sea surface temperature during *H. elongata*'s reproductive growing season (November-June) between 1950 and 2000. Each graph shows the mean (in bold) and the minimum and the maximum (thin grey lines) values for one of the four studied locations. The trend is shown by the grey thick line superimposed to the mean.

particularly important for southern shores where *H. elongata* was absent, meaning that growth was not affected by the areas where the experiment had been set. Since no information existed on the precise locations of *H. elongata* at those shores during the 1960s, differences in growth were expected if, by chance, transplants were set on zones with unfavourable microhabitats.

Minimum, mean and maximum monthly temperatures during each year for each location are depicted in Figure 3.2.3. The temperature trend analyses illustrated that a similar average increase in temperature was observed among the four studied locations (0.0129 ± 0.0019 ºC per year). During the 50 year period, the absolute increase raised the average SST in the two northern shores (Moledo do Minho and Mindelo) to levels similar to those recorded in the 1950s for the southern locations (Buarcos and São Martinho do Porto).

3.3.5 Discussion

Overall, the southern range of *H. elongata* retreated approximately 350 Km in the last 150 years and over 200 Km in the last 40 years. The speed at which this species disappeared from central Portugal is, nonetheless, misleading. In this region, especially from Nazaré to Porto, the coastline consists of large extensions of sandy shores, with only a small number of sites having suitable habitats for a lower intertidal rocky-shore species. Thus, whilst in the 1960s *H. elongata* occurred at S. Martinho do Porto and Buarcos in fairly large numbers (Ardré, 1970) these populations were virtually isolated from the main population groups in northern Portugal. When those two populations disappeared, the southern boundary shifted approximately 200 Km north. The exact time of this shift is not easy to determine given the lack of observations for this particular stretch of coastline from 1960 to the 1990s. The observation of a non-reproductive individual at Baleal in the early 1980s (Santos and Melo, 1983) suggests that the southernmost populations of S. Martinho do Porto and Buarcos were most likely present at the time, narrowing the probable time window of disappearance.

Increasing anthropogenic pressure over the coastline (e.g. pollution, erosion) and climate change were the two most probable candidate explanations for the observed decline of *Himanthalia elongata* in central Portugal (see Franco *et al.*, 2006). Whilst the former is especially effective at small scales, climate is one of the main determinants of species distributions at large scales (Pearson *et al.*, 2002; Pearson and Dawson, 2003).

The range retraction observed in the last decades could have been a consequence of the observed increase in SST off the Portuguese coast during the same period (Lemos and Pires, 2004; Lemos and Sansó, 2006). This hypothesis was supported by evidence indicating that the reproductive growth rate of *H. elongata* is increasingly inhibited by temperatures higher than 10-12 °C, failing completely at 17-18 °C (Stengel *et al.*, 1999). These threshold values should be considered with caution since they refer to experiments made with individuals from populations at higher latitudes (Ireland). Therefore, they might not apply directly to Portuguese populations where different temperature ecotypes may exist (Gerard and Du Bois, 1988; Breeman and Pakker, 1994; Wiencke *et al.*, 1994; Pakker *et al.*, 1996). Even so, the results of Stengel *et al.* (1999) support the hypothesis that reproductive growth is temperature-limited.

Other life-traits of *H. elongata*, such as biennial life-span, regular reproductive period and reduced dispersal ability (Stengel *et al.*, 1999; Lagos and Cremades, 2004) make this species a typical 'southern retreater', according to the classification of Hiscock *et al.* (2004). These include potentially sensitive species which should respond to environmental temperature increases by retracting their southern distributional ranges. It has been shown that many southern limits of Mediterranean and Atlantic species of algae are set by summer lethal temperatures (Yarish *et al.*, 1986).

The absence of significant differences among receptacle grow in the experimental sites suggests that the species can develop reproductive organs under present environmental conditions, even in the shores from where it disappeared. Thus, the present results suggest that current SST alone is not limiting *H. elongata* reproduction in the southern part of its distributional range. Yet, an extreme climatic event could have been responsible for the extinction of this species at the southern locations. Apart from eventual drifting of adult individuals, dispersal ability of *H. elongata* is known to be small, since germlings often attach to the rocky surface nearby their parent algae (Stengel *et al.*, 1999). Therefore, since the closest populations were 200 Km further north, dispersal limitations could have prevented a rapid recolonization of the southern shores. However, an inspection of SST trends (Figure 3.2.3) and anomalies (see Lima *et al.*, 2006) revealed no extreme temperature events, from the 1950s to the late 1990s, that could explain the extinction of this species in the southernmost part of its range.

Although results do not support the hypothesis of a retreating range driven by a harmful effect of the rising sea temperature, they should be interpreted with caution. While the seaweed's life-span is approximately two years (Kitching, 1981; Stengel *et al.*, 1999), the experiments lasted no more than a few months. Therefore, it is impossible to know if the temperature affected any other life stage (such as propagules or germelings) being directly responsible for the extinction of this species at its southern range. This aspect might be of great importance as temperature requirements/limitations can vary among life stages

(Wiencke *et al.*, 1994). SST long term analyses showed that globally, minimum, average and maximum monthly temperatures have been steadily increasing. The absolute increment during the 50 year period was roughly 0.5 ºC at all sites. The possible disruptive effects of this subtle change on earlier life stages or even on gamete maturation remain unknown.

Another hypothesis is that the retreat of the southern range of *H. elongata* was a consequence of the increasing anthropogenic pressure over the coast that could have resulted in habitat loss and/or severe modifications on the southern shores. Although this was not assessed directly in the present work, and apart the absence of *H. elongata*, no other noticeable changes in algal composition were observed during the experimental set up, when compared with the general description provided by Ardré (1971). In addition, human pressure seems not to be stronger in this region than in the remaining study area, and *H. elongata* populations still exist near Porto, despite intense harbor traffic, harvesting and sewage discharges.

On the other hand, the observed exclusion of *H. elongata* by sabellarian reefs during the 1999/2000 experiment can possibly be linked with human pressure over the coast. The reef building/destruction cycle is highly variable, but depends on availability of adequate sand particles (Gruet, 1986). Building of coastal defenses in central Portugal has increased over the last decades, which might have caused impacts on the sediment transport along the coast. Nonetheless, the hypothesis that these reefs are becoming more common and excluded *H. elongata* from the southernmost part of its range cannot be easily tested, since no historical data exist regarding the abundance of sabellarian reefs in the area.

Even though few studies have reported significant grazing on *H. elongata* (but see McGrath, 1992), the present results showed that at the southern locations the transplanted individuals were intensively grazed and therefore were unable to reach the final stages of reproduction. The fact that none of the northern specimens showed signs of being consumed might indicate that the putative grazer (or grazers) was confined to the area where the seaweed became extinct. This implies that grazing pressure was less intense in the past. Therefore, one can speculate that the organism currently excluding the seaweed from the southern region is a warm-water emigrant species, whose recent arrival was related with sea warming. This would simultaneously explain why grazing pressure was only unleashed in the last decades and why it has apparently been 'advancing' northwards (in Buarcos, grazing was only observed in 2004/2005). Similar phenomena have also been reported for other regions. For example, in the NW Atlantic, *Zostera marina* transplants were reported to be significantly affected by the activities of an introduced crab species (*Carcinus maenas*). Even without consuming the plants, crabs cut their shoots, causing a significant impact on the transplanted populations (Davis *et al.*, 1998). Alternatively, it is possible that grazing itself was triggered by the temperature increase. It is known that the strength of biological interactions may vary with latitude (Leonard, 2000) and with temperature (Sanford, 1999; Sanford, 2002). Thus, the two species may have coexisted sympatrically, at least in part of their range, but the algae were only excluded from the area where temperature crossed a given threshold (which stimulated the grazer's behavior).

Even assuming that the observed increase in temperature is limiting one or more life cycle stages, it is very likely that grazing is playing a major role in *H. elongata*'s survival at southern sites. It not only hinders reproductive growth, but more importantly, prevents any hypothesis of regeneration. *H. elongata* has one unique apical, non-regenerating meristem per bifurcation, meaning that reproductive structures with damaged tips are unable to resume growth. In this situation, specimens might be able to slightly increase their length, but by stretching already existent cells, not by cell division (Moss, 1969).

Concluding, it is unlikely that the recent sea-surface warming was the direct cause of the extinction of *H. elongata* in central Portugal. Biological interactions such as herbivory and/or competition for space and the limited dispersal capability of this species, can better explain the observed range shift. Nonetheless, the importance of temperature over the species' entire life cycle remains to be studied (see Adahl *et al.*, 2006). Additionally, the relative importance of biotic interactions in determining the southern limit should be tested with adequate field experiments, either by removing space competitors using fences or by preventing grazing over both vegetative and reproductive forms. These improvements in the knowledge of the mechanisms underlying species-mediated responses to climate change would be crucial to create more realistic models on species responses to climate change.

3.3.6 Acknowledgements

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Chapter 4

Species modelling

Section 4.1

Modelling past and present geographical distribution of the marine gastropod *Patella rustica* as a tool for exploring responses to environmental changes

4.1.1 Abstract

A climate envelope approach was used to model the distribution of the intertidal gastropod *Patella rustica*, to test the robustness of forecast responses to climate change. The model inc orporated likely mechanisms limiting the abundance and northern range limit of this species in the NE Atlantic. The model was built using classification and regression tree analysis (CART) which was trained with historical distribution data from the mid 1950s and a set of corresponding climatic and oceanographic variables. Results indicated air and sea temperature, in particular those acting during the reproductive and settlement periods, as the main determinants of the Atlantic distribution of *P. rustica*. The model was subsequently fed with contemporary climatic data and its output was compared with the extant distribution of *P. rustica*, assessed during a 2001-2002 survey. Model evaluation was used to assess the 'robustness' of inferred mechanisms instead of to estimate its predictive accuracy. The model correctly hindcasted the recent collapse of the distributional gap in northern Portugal as well as an increase in abundance at locations

within its range. The predicted northwards expansion of the northern range limit has not occurred as a targeted survey encompassing the whole French coast up to Brest showed no signs of the presence of this species. Barriers to dispersal are the likely mechanism controlling the northern limit of the distribution of this intertidal species.

4.1.2 Introduction

The application of species distribution models has increased considerably in the last two decades, mainly driven by the need to predict the potential impacts of climate change on the distribution of organisms (Guisan and Thuiller, 2005). From the vast array of methods currently available, single-species bioclimatic envelope models (BEMs) have been most widely used (Heikkinen *et al.*, 2006). Yet, given their correlative nature, the validity of such approaches has been progressively questioned (see Araújo and Guisan, 2006). The problem is twofold. First, BEMs seldom account for the effects of biotic interactions, adaptive change and dispersal (Pearson and Dawson, 2003). This results in highly biased models that tend to produce inaccurate scenarios (Davies *et al.*, 1998; Hampe, 2004). Second, independent validation of models is often not possible, because the events being predicted have not yet occurred or are poorly known (Araújo and Guisan, 2006). Non-independent validation (resubstitution, data splitting) usually ends up in unrealistically optimistic estimates of their predictive ability (Araújo *et al.*, 2005).

Despite being highly deterministic, BEMs have some advantages over the more complex rule-based mechanistic models (see Guisan and Zimmermann, 2000), provided that they are used in the appropriate context (Araújo *et al.*, 2005), that the choice of the model is well-grounded (Hijmans and Graham, 2006) and that results are interpreted with caution (Hodkinson, 1999). BEMs can present a fast and useful tool for the identification of key relationships between species and the factors controlling their distribution (Huntley *et al.*, 2004), especially at large scales (e.g. continental and global) where the importance of climatic forcing is thought to be higher (Pearson *et al.*, 2002; Pearson and Dawson, 2003). When range-limiting physiological factors for a given species are poorly known, these methods may represent the best possible approach (Crumpacker *et al.*, 2001).

In the marine environment, BEMs have been sparsely applied to model species distributions (but see De'ath and Fabricius, 2000; Clark *et al.*, 2003; Friedlaender *et al.*, 2006; Kaschner *et al.*, 2006). This is unfortunate because there are many well documented cases of recent changes (either expansions or retractions) of species' ranges which are thought to be a direct consequence of global warming (for a review, see Helmuth *et al.*, 2006b). Rocky intertidal communities, in particular, are well-suited for studying climate-driven community changes (Herbert *et al.*, 2003; Simkanin *et al.*, 2005) because their ecologies are well-known (Southward *et al.*, 1995) from decades of experimental studying of recruitment dynamics and biological interactions (see Raffaelli and Hawkins, 1996; Bertness *et al.*, 2001 for reviews). Moreover, their inhabitants are often exposed to temperature and weather extremes, living close to their thermal tolerance (Wolcott, 1973; Tomanek and Helmuth, 2002). Also, intertidal organisms can be easily surveyed since they are generally conspicuous, slow moving or sedentary, and their ranges are roughly one-dimensional, conveniently defined by the coastal endpoints (Sagarin and Gaines, 2002). Thus, the seashore provides both a trackable testing ground for scientific debate on the utility and applicability of BEMs to model and predict species distributions under climate change and a wealth of insight into the probable complexity of the phenomena being modelled (see Helmuth *et al.*, 2006b).

In this work, a single-species bioclimatic envelope approach was used to gain further insights into the factors driving the distribution of a marine gastropod, *Patella rustica* Linnaeus 1758, in the northeast Atlantic. In a recent paper, Lima *et al.* (2006) described the collapse of an historical distributional gap, in northern Portugal, which occurred in the late 1990s and coincided with a combination of unusual climatic and hydrographic events that were particularly pronounced between 1997 and 1999. In this period, a significant warming of sea-surface temperature (SST) during autumn/early winter was observed in addition to the general increase in average SST off the Portuguese coast (Lemos and Pires, 2004; Peliz *et al.*, 2005; Lemos and Sansó, 2006). This, combined with a strong river runoff and weak upwelling (Dong *et al.*, 2000; Santos *et al.*, 2004), may have facilitated the bridging of the gap.

The present work focused only on the northern part of *P. rustica* distribution in the Atlantic, mainly because empirical evidence showed that recent changes have already occurred in this area, and a northwards expansion was expected. *P. rustica* ranges from the Mediterranean to the Atlantic coast of the Iberian Peninsula and Northern Africa, including the Macaronesian Islands (Ridgway *et al.*, 1998). In the Atlantic, its southern limit is speculated to occur further south than Mauritania (Christiaens, 1973). However, apart from this reference, no reliable data exists which could have been used for modeling purposes. Thanks to the exhaustive work of Fischer-Piétte and coauthors (Crisp and Fischer-Piétte, 1959; Fischer-Piette and Gaillard, 1959) the distribution of *P. rustica* along the Atlantic European coast is well known from the late 1950s. This data was used together with several climatic and oceanographic variables to build a bioclimatic envelope model. The model was subsequently evaluated by feeding it with climatic and oceanographic data from the 1990s, when the distributional gap was bridged, hindcasting the present-day distribution of the species. The output was then compared with the extant distribution of *P. rustica* surveyed in 2001-2002. Thus, the model was implemented to 'understand' the likely mechanisms governing the distribution of this limpet rather than to 'predict' its future distribution and model evaluation was used to assess the 'robustness' of inferred mechanisms instead of to estimate its predictive accuracy (Araújo and Guisan, 2006). More importantly, evaluation was done with an independent data set (apart from spatial and temporal autocorrelation), which is highly recommended but rarely used in BEMs (Araújo *et al.*, 2005).

4.1.3 Material and methods

Biological data

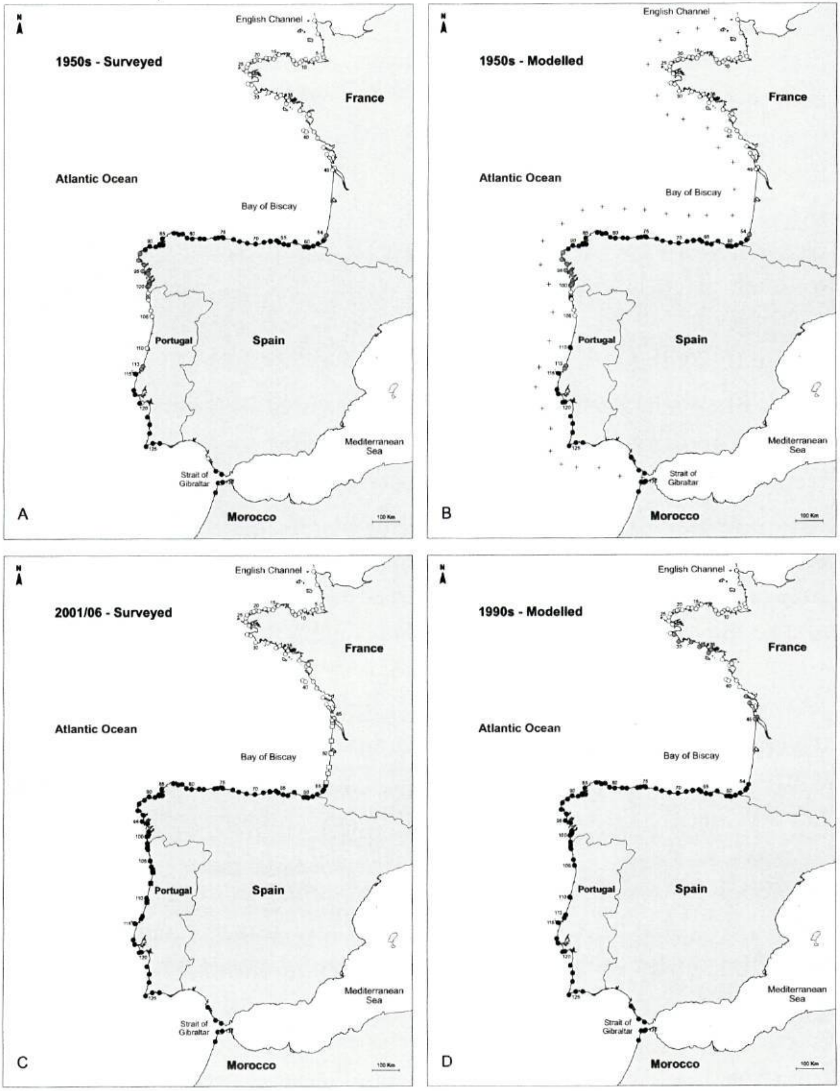
Data on the distribution and abundance of *Patella rustica* along the European coastline (from the English Channel to Morocco) were gathered for the 1950s from the comprehensive works of Fischer-Piétte (1953, 1955, 1958, 1963), Crisp and Southward (1958), Crisp and Fischer-Piétte (1959) and Fischer-Piétte and Gaillard (1959). Since in each work density of limpets was expressed in different abundance scales, the number of abundance categories was reduced to three:

absent, rare and abundant. This caused some information loss (in some cases true densities were available), but avoided wrong categorization and provided comparable data for the Atlantic range of *P. rustica*. Contemporary abundances were recorded by thoroughly resurveying historical localities between 2001 and 2002 and from Biarritz towards the north in 2006 (see Figure 4.1.1). Density of limpets was estimated using several haphazardly placed 50 x 50 quadrats, and then converted to the three-class abundance scale.

Environmental data

Two climatic data sets were assembled and used in the model. Because climatic and oceanographic factors such as temperature and salinity are highly variable over the years (Levitus *et al.*, 2000), a time window large enough to encompass a significant amount of variability but simultaneously representative of the sampling years and correlated with changes in distribution of *P. rustica* was selected (Lima *et al.*, 2006).The first set included data from the 1950s (January 1950 – December 1959) and the second one incorporated data from the decade of 1990 (January 1991 – December 2000). The environmental conditions were described using six main climatic and oceanographic variables: near surface air temperature (NSAT), cloud cover (CC), precipitation (PP), sea surface temperature (SST), sea surface salinity (SSS) and wave action (WA).

NSAT, CC and PP monthly averaged data covering European land surface at a 10 minute resolution was obtained from the CRU TS 1.2 dataset, available from the Tyndall Centre for Climate Change Research and Climate Research Unit (http://www.cru.uea.ac.uk/, Mitchell *et al.*, 2002; Mitchell *et al.*, 2004). Sea surface temperature (SST) along the North-Eastern Atlantic coast, was derived from *in situ* raw data obtained from the International Comprehensive Ocean–Atmosphere Data Set (ICOADS, http://icoads.noaa.gov/, Woodruff *et al.*, 1988). To avoid bias due to different daytime measurements, only data from 12:00 GMT were used. Point data were imported into GRASS Geographical Information System (GRASS Development Team, 2006) and transformed into monthly raster maps with a spatial resolution of 4 km using a surface interpolation method. Each cell was derived from the 12 nearest data points using the distance squared weighting algorithm (Jarvis and



1950s - Surveyed

1950s - Modelled

2001/06 - Surveyed

1990s - Modelled

Figure 4.1.1 Abundance of *P. rustica* along the studied area. Circles represent rocky shore locations and boxes represent seawall constructions. White stands for absent, grey represents rare and black means abundant. A- Historical abundance. B-Abundance modelled for the 1950s. Offshore points represent the sites for which wave climatology are available. C- Contemporary abundance. D-Model output for 1990s. 1-Cap de la Hague, 2-Cap de Carteret, 3-Granville, 4-Carolles, 5-Pte. Grouin, 6-Rotheneuf, 7-Dinard, 8-Cap Fréhel, 9-Cap d'Erquy, 10-Pt. Pléneuf, 11-Pte. Roselier, 12-Pte. Pordic, 13-St. Quay – Portri, 14-Trestrignel, 15-Pte. Bihit,

Fig 4.1.1 (Continuation):16-Pte. Locquirec, 17-Pte. Primel, 18-Pte. Bloscon, 19-Greve Poulfoén, 20-Pontusval, 21-Guissény, 22-Greve Vougot, 23-Greve Lilia, 24-Trémazan, 25-Melon, 26-Le Conquet, 27-Camaret, 28-Pte. Raz, 29-Pte. Lervily, 30-St. Guénolé, 31-Trévignon, 32-Pte. Pen Men, 33-Port-Louis, 34-Quiberon, 35-Pte. Kerbihan, 36-Pte. Croisie, 37-St. Michel Chef Chef, 38-Pte. St. Gildas, 39-Yeu, Pte. But, 40-Yeu, Pte. Tranche, 41-Croix de Vie, 42-Les Sables d'Olone, 43-Phare Balenes, 44-Phare Chassiron, 45-Royan, 46-Courdouan, 47-L'Amelie, 48-Montalivet, 49-Lancanau, 50-Arcachon, 51-Mimizan, 52-Contis, 53-Vieux-Boucau, 54-Capbreton, 55-Boucau, 56-Biarritz, 57-Cabo Higuer, 58-San Sebastian, 59-Zarauz, 60-Zumaya, 61-Deba, 62-Bermeo, 63-Barrica, 64-Urdiales, 65-Santoña, 66-Noja, 67-Magdalena, 68-Cabo Menor, 69-Ubiarco, 70-San Vicente de la Barquera, 71-Llanes, 72-Ribadesella, 73-Luces, 74-Perlora, 75-Candas, 76-Salinas, 77-San Juan, 78-Luarca, 79-Navia, 80-Cangas de Foz, 81-Ribadeo, 82-San Ciprian, 83-Vivero, 84-Espasante, 85-Cobas, 86-Carnoedo, 87-La Coruña, 88-Sta. Cristina, 89-Arteijo, 90-Malpica, 91-Lage, 92-Mugia, 93-Finisterre, 94-Muro, 95-Corrubedo, 96-Grove, 97-Punta Corbeiro dos Castros, 98-San Miguel de Oia, 99-Bayona, 100-Cabo Sillero, 101-La Guardia, 102-VP Âncora, 103-Montedor, 104-Viana Castelo, 105-Vila do Conde, 106-Leixões, 107-Aguda, 108-Espinho, 109-Aveiro, 110-Cabo Mondego, 111-Buarcos, 112-Leirosa, 113-Nazaré, 114-S. Martinho Porto, 115- Cabo Carvoeiro, 116-Peniche, 117-Azenhas do Mar, 118-Cascais, 119-Cabo Espichel, 120-Sesimbra, 121-Sines, 122-VN Milfontes, 123-Odeceixe, 124-Sagres, 125-Lagos, 126-Armação de Pêra, 127-Rota, 128-Trafalgar, 129-Punta Paloma, 130-Punta Malabata, 131-Tanger, 132-C. Spartel, 133-Arcila.

Table 4.1.1 Summary of the independent variables used in the CART modelling of *Patella rustica* distribution

Environmental variables	Acronim	Unit	Considered periods	Statistics
Sea surface temperature	SST	ºC	10-year, Winter, Summer, Reproduction	Mean, minimum, maximum
Near surface air temperature	NSAT	ºC	10-year, Winter, Summer, Reproduction	Mean, minimum, maximum
Cloud cover	CC	%	10-year	percentile 25, 50, 75
Precipitation	PP	%	10-year	percentile 25, 50, 75
Sea surface salinity	SSS	‰	10-year	percentile 25, 50, 75
Wave power	WP	kW	-	Mean

Stuart, 2001). Monthly averaged SSS data, with an average resolution of 0.5° lat × 0.5° long cells, were extracted from SODA-POP v1.2 model data set, available at the National Virtual Ocean Data System live server webpage (http://ferret.pmel.noaa.gov/NVODS/servlets/dataset) and were imported into GRASS GIS. Because data were only available from January 1958 onwards, the computed average for the decade of 1950s was based solely on two years.

The resulting set of 240 (20 years × 12 months) SST, NSAT, CC, PP and 164 SSS maps was stored in GRASS GIS as monthly layers and sampled along the studied coastline in the locations visited by D.J. Crisp, E. Fisher-Piétte and J. Gaillard during the 1950s (Fischer-Piétte, 1955; Crisp and Southward, 1958; Fischer-Piétte, 1958; Crisp and Fischer-Piétte, 1959; Fischer-Piétte and Gaillard, 1959; Fischer-Piétte, 1963). Sampled data for each parameter were combined to build a table with each row denoting a geographical location and each column a month-year combination. For SST and NSAT, the general 10-year mean and the average value of winter, summer and reproductive seasons were computed, as well as the mean value of the coldest and hottest month during those seasons. Reproductive season was assumed to be from September to November (according to Ibanez *et al.*, 1986; P. A. Ribeiro, unpub. data). For CC and PP, the 10-year average and the values of the percentiles 25, 50 and 75 were calculated. For SSS, only the long-term average value during each studied period was considered. An overview of the climatic variables can be found in Table 4.1.1.

On the Atlantic coasts of Europe and North Africa the presence of *P. rustica* is generally associated with steep surfaces found in the upper eulittoral of exposed rocky shores (Fischer-Piétte and Gaillard, 1959; Lima *et al.*, 2006). Thus, a quantitative measure of sea exposure was included in the model. Average wave power was used as surrogate for the exposure of sampled locations to the effects of wave action (WA). The EXA (EXposure estimates for fragmented Archipelagos) procedure as described by Ekebom (2003) was generally followed, apart from the need to obtain wave climatology parameters from prevailing winds since they were directly incorporated in the exposure model. Hence, that computational step was skipped. Wave climate data were downloaded from the European Environmental Agency database (http://www.eea.europa.eu). Data were only available for regularly spaced offshore

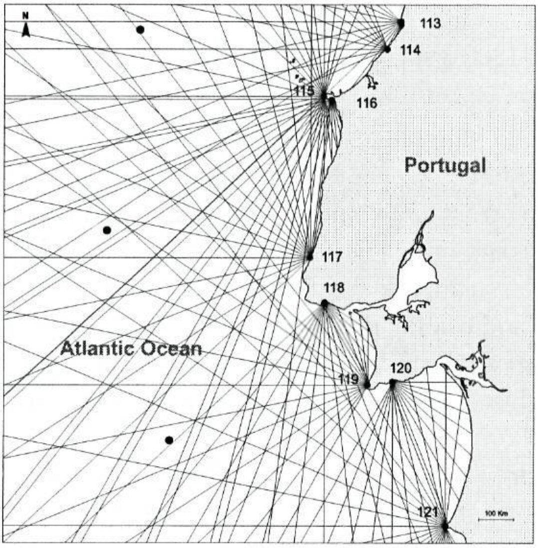


Figure 4.2.2 An illustration of the fetch lines plotted for several coastal locations. For site names, see Figure 4.1.1. Offshore points represent the sites for which wave climatology are available.

locations 50 to 100 km away from the coastline (Figure 4.1.2). Therefore, in every coastal location the wave parameters of the nearest offshore point were used. The fetch length was measured for each direction by a group of lines radiating from each coastal point with a 7.5° bearing step between them. Lines were trimmed when reaching the coastline. For each one of the remaining lines, wave parameters from the corresponding directional sector were selected and used to estimate the wave power observed in coastal location over that specific direction. Wave power (P) in kW was defined as $P = n \; E \; 1.56 \; T$, where $n = 0.5$, T = mean significant wave period (in seconds) and E (Energy in Joules) = $1/6 \, \rho \, g \, H$, where ρ = sea water density (1,020 Kg m^{-3}), g = acceleration due to gravity (9.8 m s^{-1}) and H = mean significant wave height in meters. For each coastal location, total wave power was computed as the sum of all converging partial estimates from the different directions, weighted by the percentage of time waves were observed in each direction. The online wave data was only available for the period between 1985 and 2001 and records were summarised in statistics relative to that 16-year period without the possibility to extract specific years or months, which forced the use of the whole data set. As a consequence, the parameter WA was considered static (i.e., not varying from the 1950s to 1990s), which may not be entirely true (see Davies and Johnson, 2006).

Modelling approach

Classification and Regression Trees - CART (Breiman *et al.*, 1984) are one of the currently available climate envelope approaches. Traditionally applied to fields such as medical diagnosis, meteorology, plant physiology, soil sciences and wildlife management, they have recently been used to successfully model terrestrial (e.g. Vayssières *et al.*, 2000; Edwards *et al.*, 2006; Fronzek *et al.*, 2006) and marine species distributions (De'ath and Fabricius, 2000; DeVantier *et al.*, 2006; Friedlaender *et al.*, 2006).

For the purposes of the current study, CART models were selected primarily because they are relatively immune to multicollinearity (Breiman *et al.*, 1984; Jackson and Bartolome, 2002; Karels *et al.*, 2004), and the data set incorporated 20 potentially correlated predictor variables. Other advantages included the possibility of output response variables with more than two levels, the robustness regarding possible outliers and non-normal distributions of variables (Breiman *et al.*, 1984) and the capacity to determine complex interactions among explanatory variables without the need to specify them a priori (Vayssières *et al.*, 2000; Rouget *et al.*, 2001). Additionally, these analyses are easy to interpretate (De'ath and Fabricius, 2000) since they provide an hierarchical view of the relationships between species and environmental variables, allowing the identification of those which are the most correlated with the presence of species (Vayssières *et al.*, 2000).

Homogeneity of groups was assessed by the Gini purity index (Breiman *et al.*, 1984). Since the maximal tree is usually overfitted to training data, a computational step to constrain the tree to its best size is required to avoid the problem of overfitting (Araújo and Guisan, 2006). Overfitted models tend to perform exceptionally well on the training data because they are adapted to the specific data set used to build them. Conversely, outside that particular data they will fail when trying to predict independent events because they are not able to parsimoniously identify the relations between independent and response variables. Thus, a balanced model including sufficient complexity to uncover subtle effects and interactions but not compromising predictive power should be chosen. A common approach in tree-based techniques is to freely allow the maximum growing process and then prune the over-branched tips of the tree (Breiman *et al.*, 1984; De'ath and Fabricius, 2000; Questier *et al.*, 2005). The initial tree was allowed to attain the maximum size and then pruned using the mode of 50 repeated 10-fold cross-validation (see Breiman *et al.*, 1984; De'ath and Fabricius, 2000 for details). For the cross-validation, the data set was divided in ten parts and each subset was removed in turn, being used as a test sample against predictions based on the remaining 90% of data. This technique is similar but more robust than jack-knifing, as it gives a better reflection of its performance on new data (Fielding and Bell, 1997). The average error rate was plotted in relation to the tree size and the best size for the tree was chosen as the smallest having an error rate within one SE of the minimum (De'ath and Fabricius, 2000).

The predictive power of the model was evaluated using the area under curve (AUC) obtained from the receiver operator characteristic (ROC) plot. AUC is a reliable measure of model performance because it is largely unaffected by the data prevalence, i.e. the proportion of study sites naturally occupied by the species (Manel *et al.*, 2001; McPherson *et al.*, 2004; Vaughan and Ormerod, 2005).

The model was evaluated by feeding it with climatic and oceanographic data from the 1990s, when the distributional gap was bridged, to hindcast the contemporary distribution of *P. rustica* along the NE Atlantic coast. The output was subsequently compared with the real distribution and abundance of *P. rustica* assessed in the 2001-2002 survey.

4.1.4 Results

A total of 122 locations for which data were available were revisited during the 2001-2002 survey, enabling abundance and distribution to be mapped (Figure 4.1.1 A and 4.1.1 C). In the 40-year period between the two surveys, the most remarkable changes were: (i) the bridging of the distributional gap in northern Portugal (Lima *et al.*, 2006); (ii) a global increase in abundance in NW Iberia (Galicia) and on some southern Portuguese shores; and (iii) no extension of the northern boundary of the range at Capbreton, although an increase in abundance was also observed in this region.

The final model, selected and pruned after cross-validation, could be represented as a five leaf tree explaining 94 % of data variance for the distribution during the 1950s (Figure 4.1.3). Scores of the area under curve (AUC) obtained from receiver operator characteristic (ROC) plots for test data were 0.93 for category class 0 (absent), 0.99 for category 1 (rare) and 0.92 for category 2 (abundant), which according to Swets (1988) and Zweig and Campbell (1993) indicates excellent classification accuracy. From the variety of climate data fed into the model, SST and NSAT were selected as determinant factors of the distribution of *P. rustica*. The first data partition, based solely in the observed value of the average NSAT of the coldest month during the reproductive period, explained nearly 38 % of data variation and was responsible for identifying the break which corresponds to the northern boundary of the distribution. The remaining cases were generally explained by the average SST of the coldest winter month, average NSAT and average SST. Nearly half of missclassifications occurred within the distributional gap in northern Portugal. In this area, the model erroneously predicted the presence of *P. rustica* at two locations where the species had not been observed (Cabo Mondego and Buarcos). It also predicted the existence of limpets at high densities at Vila do Conde, a location where Fischer-Piétte and Gaillard (1959) reported only a single individual during their 1950s survey. In addition, the model over-estimated the abundance in three locations in the southern part of the studied distribution (Sesimbra, Rota and Tangier). In one locality in northern Spain (Santander) the predicted abundance was misclassified as rare, while in reality it was abundant (Fischer-Piétte and Gaillard, 1959). Nevertheless, globally the model performed quite well, since the main distributional features such as the northern range limit, the existence of a distributional gap in Northern Portugal and the region of low abundance in North-Western Iberia were correctly modelled (Figure 4.1.1 B).

When the model was fed with environmental data from the 1991-2000 period, 87% of the observed abundances were correctly predicted. In particular, the model correctly hindcasted the bridging of the historical gap in northern Portugal and also the observed increase in densities at Galicia (NW Iberia) and at the current northern limit of the species range

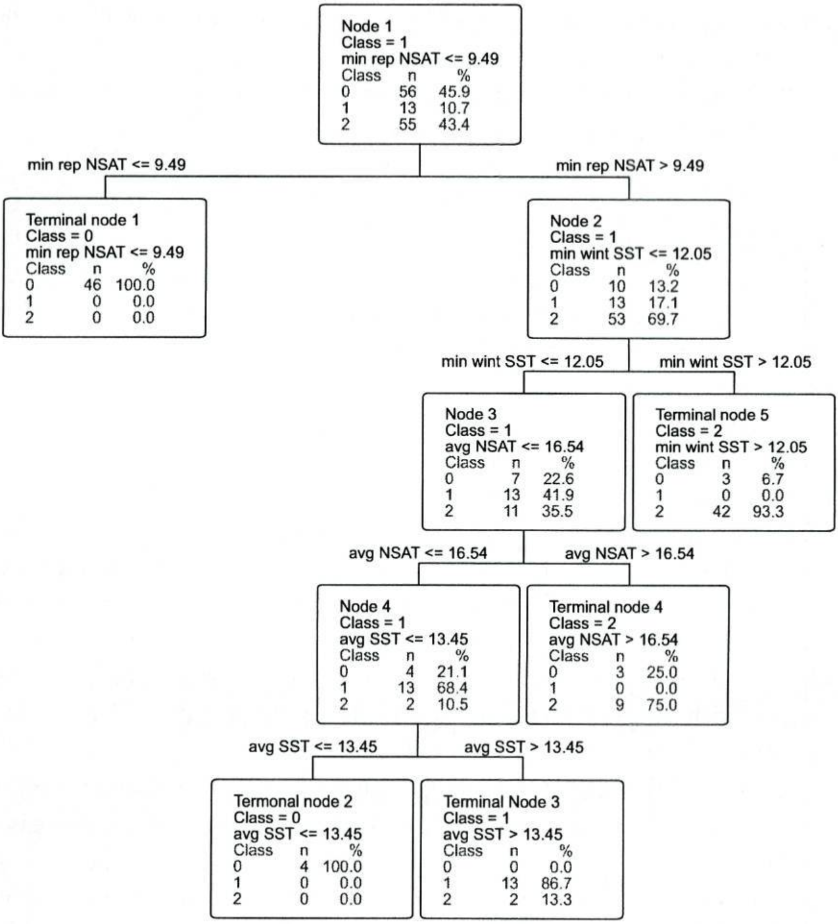


Figure 4.1.3 Decision tree of the CART model built using historical (1950s) survey data. At each partition, the value of the splitting variable is shown. Information featured in the nodes includes the node identification, the level of the predicted response and the value of the split variable associated with that node. Finally, the number and percentage of cases for each level of the predicted response is also displayed. Climatic variables refer to the period of 1950-1959. Min rep NSAT - mean NSAT value of the coldest month during reproductive season; min wint SST - mean SST value of the coldest month during winter; avg NSAT - mean NSAT value during the 10-year period; avg SST - mean SST value during the 10-year period.

(Capbreton). However, it failed in identifying the actual northern limit of the species range, since it predicted the species presence (although at low densities) in all locations between Capbreton and Ille d'Óléron and further north, between Pointe de Kerbihan and Pointe de Lervily. A new survey made in 2006, from Capbreton towards the Cotentin Peninsula (in the English Channel), revealed that the predicted northern expansion of the species range had not occurred.

4.1.5 Discussion

The CART model suggested that the distribution of *Patella rustica* during the 1950s was highly correlated with temperature. According to the model output, the distribution of this species in the European Atlantic coast could be accurately explained by air and sea temperature patterns, especially during the reproductive (autumn) and initial growth (winter) periods. The model correctly excluded *P. rustica* from locations where temperature was too low, such as most of the French Atlantic coast and in the historical distributional gap in northern Portugal, where upwelling has a dominant cooling effect on the sea temperature, at least during some periods of the year (Peliz *et al.*, 2002; Peliz *et al.*, 2005). On the other hand, regions characterized by a warmer climate such as the southern Portuguese coast and the Bay of Biscay were correctly modelled as having high densities of *P. rustica*.

The use of the climate envelope with contemporary environmental conditions, correctly predicted the bridging of the gap and the increase in densities in northern Spain. This suggests that some of the factors used in the model do determine, to some extent, the distribution of *P. rustica*, at least in this section of the range. Both events are probably connected, constituting an ongoing expansionary episode whose onset was already noticed by Fischer-Piétte and Gaillard (1959). However, the model failed to predict the correct northern range boundary in the Western French coast (Capbreton), extending the 'suitable habitat' for *P. rustica* as far north as Pointe de Lervily. This probably indicates that although both air and sea temperatures could be nowadays favourable to the presence of the species, some other factor, or even a conjugation of factors are probably hampering the expansion.

The recent expansion of *Patella rustica* observed in northern Portugal, which led to the collapse of a long-term distributional gap in the late 1990s, was coincident with sea surface anomalies recorded over the last decade off the Portuguese coast (Lima *et al.*, 2006). The current patterns observed off the Portuguese coast in the autumn/winter are part of a wider and well known system called 'Navidad' which affects the Atlantic European continental slope (Pingree and Cann, 1992). During winter, a warm water stream flows northward along the east coast of Portugal and Spain. It then splits into two streams, one flowing directly to northern France and the British Isles, and the other moving eastward, following the Spanish coastline, and turning north along the French coast. This stream is tightly correlated with the North Atlantic Oscillation Index (NAO). An extremely negative winter NAO Index was observed during 1996 and 1998, enhancing poleward flow and an anomalous winter warming along the coast of the Bay of Biscay (Pingree and Cann, 1992; Garcia-Soto, 2004). Therefore, since the observed changes in the distribution of *P. rustica* are likely to be related with increases in temperature (either from air or sea), a similar expansion was anticipated in southern France, where an analogous warming trend was observed (Koutsikopoulos *et al.*, 1998). Hence, it was interesting to notice the absence of such phenomenon. The only evidence of a tendency for expansion in the northern portion of the range was the huge increase in densities observed in the two northernmost locations (Boucau and Capbreton) when compared with the data from Fischer-Piétte and Gaillard (1959). However, this evidence is fairly weak, since in these locations the building of coastal defences largely expanded the area of suitable habitat, thus confounding the effect of any other factor, such as environmental changes due to sea or air temperature increase.

Several explanations can be advanced for the mismatch between the model hindcast for the 1990s and field observations. It is possible that *P. rustica* is already present in locations north of Capbreton, but at densities which hindered its detection even by experienced observers. This is very unlikely considering the effort of the fieldwork, with more than 50 locations visited between Capbreton and Royan. In addition to the few rocky shores, all artificial coastal defences were also surveyed.

It is also possible that certain variables not accounted in the model have a strong limiting influence on survival and/or expansion of this species. For example, recent work suggests that marine populations may be less open than originally thought (Bohonak, 1999, Cowen *et al.*, 2000, Levin, 2006) and that sea currents can potentially constitute non-transposable barriers to species with a dispersive larval stage, constraining their ranges even when there is suitable habitat beyond those barriers (Gaylord, 2000). The situation becomes even more complicated when effects of dispersal barriers are confunded with effects of physiological limitations imposed by steep clines in climatic factors such as sea temperature, since they usually co-occur in space (Zacherl *et al.*, 2003). The ocean circulation in the Bay of Biscay has been studied by numerous authors (Koutsikopoulos *et al.*, 1998, Bardey *et al.*, 1999, Puillat *et al.*, 2004, Planque *et al.*, 2006), who pointed out several hydrographical fronts, upwellings, eddies and low salinity plumes from the rivers Loire and Gironde as being responsible for strong discontinuities in oceanic and coastal waters. Thus, these factors may represent considerable dispersal barriers for *P. rustica*.

Another hypothesis could be related with the limited larval dispersal potential of *P. rustica*. Even assuming that oceanographic barriers are not obstructing larval transport, a limited dispersal ability coupled with the lack of suitable habitat may pose a serious problem to expansion, as previously reported by Crisp (1958) for the barnacle *Elminius modestus*. The 200 Km of coastline between Capbreton and Royan are mainly sandy and therefore do not allow larval settlement. The ability to transpose such a gap depends on the existence of a sufficiently long larval stage, able to survive during the transport towards the north, and even so, favourable currents must exist during larval drift. In the Bay of Biscay, the current flow over the continental slope was determined as having a characteristic northward velocity of 5 cm s^{-1} during the winter, and probably reversing during the summer (Aken, 2002). Spawning is thought to happen during the autumn (Ibanez *et al.*, 1986) but unfortunately very little is known regarding ocean circulation in this region during that season. However, and considering a travelling speed of 5 cm s^{-1}, larvae would need more that 45 days to transpose the sandy coastline, a prohibitive period for a species whose planktonic stage lasts approximately six days (P. A. Ribeiro, unpub. data). If this is the main factor limiting the species expansion, why has it not prevented the recent colonisation of several locations in Northern Portugal, bridging the historical 280 km gap? Coastal currents off the Portuguese coast display a stronger northward component during the reproductive period of *P. rustica*, with mean velocities of 15.1 ± 4.4 cm s^{-1} (Martins *et al.*, 2002).

In six days, this current may transport larvae for distances of up to 100 Km, which is enough to cover the largest sandy stretch of coastline.

Additionally, the construction of a high number of artificial sea defences to protect both the sandy shores and the main city harbours from wave action has most likely increased population connectivity of rocky shore species in the Portuguese coast. In fact, most sea defences are massive structures hosting typical rocky shore communities (F. P. Lima, unpubl. data), where for example it is possible to find intertidal algae (*Porphyra* spp., *Fucus spiralis*), polychaetes (*Sabellaria alveolata*) crustaceans (*Pachygrapsus marmoratus, Pollicipes pollicipes, Chtamalus montagui* and *C. stellatus*) and molluscs (*Mytilus galloprovincialis, Littorina neritoides, L. saxatilis, Patella depressa, P. vulgata* and *P. rustica*). These artificial reefs have shortened the largest sandy stretches to approximately 50 Km, allowing a much easier expansion. On the contrary, along the 200 Km rocky hiatus of the French coast, the construction of sea defences was done in a much more subtle way. With the exception of the two sea walls at Boucau and Capbreton, all constructions are substantially small in height and length, unable to accommodate more than a few ephemeral green algae (genus *Ulva* and *Enteromorpha*), a few mussels (*Mytilus* sp.), oysters, and in some rare occasions, no more than a handful of *P. depressa*. These structures clearly lack the typical habitat of exposed vertical walls required by *P. rustica*. Similarly, Gilman (2006) found that the most likely explanation for the determination of the northern range limit of the intertidal limpet *Collisella scabra* in California was an increase in the distance between populations at the range margin, reducing the chances of dispersing larvae to find suitable habitat for settlement, rather than any climatic constraint. Thus, it is possible that the limits of many marine species can remain unchanged even when peripheral habitat conditions become favourable (Crisp and Southward, 1958; Fields *et al.*, 1993).

It has been noted that range expansions, even from those species which eventually become successfully established, are frequently preceded by several failures (Sax and Brown, 2000). In addition, it was shown that species with a similar larval duration to *P. rustica* may take several years to become completely established over an area similar to the one for which the present expansion was anticipated (see Shanks *et al.*, 2003; Siegel *et al.*, 2003, for a review). Therefore, even with present favourable climatic conditions and assuming that some extraordinary events such as storm-strengthened anomalous currents allowed the species to overpass the sandy barrier, the elapsed time for such a large expansion to occur may still be insufficient. In this perspective, the hindcasted northern range expansion is not completely wrong (see Araújo *et al.*, 2005), and might become visible in the following years, providing that the sea and air warming phase of the last decades is maintained.

In the light of current results, the hypothesis proposed by Lima *et al.* (2006) that the changes in the geographical distribution of *P. rustica* observed in NW Iberia were largely related with a joint effect of increasing temperature and alteration in oceanic circulation patterns is reinforced. Therefore, the conceptual model here proposed has the ability to simultaneously explain several spatially independent phenomena, giving it a higher degree of confidence. Nonetheless, since other valid explanations could be advanced, future investigations are still needed in this area. Several recent studies indicate that some organisms have the ability to adapt to different conditions at diverse parts of their range (Sagarin *et al.*, 2006), and also that environmental variables might not be physiologically limiting at all range edges (Helmuth *et al.*, 2006b). Hence, it is even possible that the factors which were until recently limiting the expansion in northern Portugal could be distinct from those currently governing the northern boundary. Nonetheless, the existence of barriers to dispersal, resulting in limited or no connectivity remains the most parsimonious and thus the most probable scenario. This hypothesis can be tested using a bioclimatic approach coupled with a dispersal simulation model, encompassing information about oceanic currents and habitat availability. This approach would help to definitely solve the question of the relative importance of the temperature or transport in establishing limits in the distribution of *P. rustica*.

This study also strengthens the idea that intertidal organisms are clearly influenced by both air and water temperature. Although it has already been shown that various aspects of both terrestrial and aquatic climate drive the physiological performance of these species (Helmuth *et al.*, 2006a), the use of a non-linear modelling technique showed that these factors frequently alternate with one another and with non climate-related factors, in determining distributional limits (Helmuth *et al.*, 2006b).

Although the present results partially support previous suggestions that bioclimatic envelope models may be inadequate for making projections of future events, they also suggest that this approach can be of great utility in gaining further insights into the nature of the relationship between the distribution of the species and the environment (Araújo *et al.*, 2005). Therefore, although sometimes bioclimatic envelopes may appear too limited or deterministic, they certainly still have an important role in ecology by helping to effectively work on some explanatory hypothesis which can be subsequently tested.

4.1.6 Aknowledgements

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Chapter 5

General discussion

In this chapter, information from the different sections that constitute the thesis are taken together and analysed in the light of the state-of-the-art theories on species responses to climate change. The use of a wide range of taxonomic groups strengthens the present analysis. It is shown that, contrary to what is suggested in a great percentage of the currently available literature, biological responses to the warming climate are highly complex and variable.

5.1 Biogeographic patterns

The first solid effort to link species distribution with climate gradients along the Portuguese coast was made in the late 1960s by Ardré (1970). Unfortunately, in the following decades no broader scale studies focusing on intertidal communities along the entire region were published. Thus, it is nearly impossible to know if the distribution of many of these organisms in the Portuguese coast shifted, while a major cold spell was occurring in the North-East Atlantic (Southward, 1991; Southward *et* *al.*, 1995). More recently, a series of national and international research projects have been promoted, recognizing that the study of distributional patterns plays a fundamental role in understanding rocky intertidal communities (Boaventura *et al.*, 2002b), but in general their main output have not gone beyond the pure description of distributional patterns with only a few emphasis given to the environment (e.g., Santos, 2000; Boaventura *et al.*, 2002b; Araújo *et al.*, 2005c). There are some exceptions, however. For example, Monteiro *et al.* (2001; 2005) have shown that the breeding ecology of the intertidal pipefish *Nerophis lumbriciformis* is dependent of the sea water temperature, which is probably the main determinant of its distribution.

Most of the aforementioned projects have, however, the merit of contributing to regular monitoring of the rocky shores in this region. Without the accurate knowledge of which species existed and where they inhabit, it would be impossible to know, for example, if newly discovered *taxa* in this area represent real distributional changes or if those discoveries reveal nothing more than past misobservations. In a geographic region such as the Portuguese coast, due to the existence of several range limits, changes in species' distributions might represent responses to environmental change (Barry, 1995; Southward *et al.*, 1995; Thompson *et al.*, 2002; Hawkins *et al.*, 2003; Harley *et al.*, 2006). Hence, tracking possible expansions or retractions has extreme importance, as some of the current results highlight. The value of keeping accurate records on species distributions can be illustrated by the discovery of *Patella rustica* outside its traditional distributional area. Without the cumulative knowledge gathered from a suite of monitoring studies supervised by A.M. Santos, focused on the biogeography of the Northern Portuguese coast since the early 1990s (Santos, 1994; 2000), it would be otherwise impossible to detect the subtle change in distribution that characterised the beginning of the expansion. The second case regards the high number of Isopoda, Amphipoda and Tanaidacea, for which historical records of occurrence are scarce and spatially fragmented. The absence of generalized and accurate records makes it impossible to know if four species now observed for the first time in the Portuguese coast (*Caprella mitis*, *Biancolina algicola*, *Synisoma capito* and *Leptochelia savigny*) are in fact expanding their distribution. The third example is illustrated by the poor quality of historical data on mollusc distributions. Some recent results (Lima *et al.*, 2006) suggest that it could be interesting to make a long-term study comparing past and present mollusc distributions in the Portuguese coast. However, with the exception of a handful of species (like those belonging to the genus *Patella*) which were studied in the 1950s by Fischer-Piétte and collaborators (e.g., Fischer-Piétte and Gaillard, 1959), the only historical records available are from Nobre (1931a; 1931b; 1936; 1938; 1940). However, most of these records do not include detailed information on the locations were the species were observed or even the date of observation, making almost impossible to objectively compare them with current data.

The present work has provided an exceptional opportunity to update the records of distribution of more than two hundred algae and animal macrospecies that inhabit the rocky shores of the Portuguese coast. In addition, the wide range of substrates sampled in each location allowed the construction of a herbarium and a reference collection of macroinvertebrate fauna. While a portion of the sampled material have already been processed and the results published (e.g. Pereira *et al.*, 2006), other sets are still being analysed by taxonomic experts. The bulk of collected data can, therefore, be of extreme importance in the future, providing a baseline for which the expected changes in species distribution (IPCC, 2001) can be contrasted. The fact that for the first time a sampling programme has addressed the distribution of macroinvertebrate species at a country-wide scale might be especially valuable since the current results suggest that the distribution of epifauna does not seem to be related with geographical changes in the dominant algal species (Pereira *et al.*, 2006). Thus, admitting that physical factors, such as the sea temperature play the main role in determining the distribution of these organisms, it is even more probable that future climate warming will cause changes in their distribution.

5.2 Relation between the biogeographic changes and the warming climate

The intertidal communities of Northern Portugal have been repeatedly pointed out has having a singular species composition, distinct from the surrounding regions (Fischer-Piétte, 1959; van den Hoek and Donze, 1967; Ardré, 1970; 1971; Santos, 1994; 2000; Boaventura *et al.*, 2002b). These authors found that, at least considering some groups of organisms, the northern Portuguese coast and part of Galicia were more similar to northern France or to south-western Britain than to the adjacent regions of southern Portugal, or even north-eastern Spain.

The anomalous pattern became apparent through two peculiar species groups: some cold-water species, such as *Laminaria saccharina* and *Pelvetia canaliculata* were only abundant in Northern Portugal and Western Galicia and in the regions northwards from the Bay of Biscay. On the other hand, warm-water species such as the algae *Hypnea musciformis*, *Leathesia difformis*, *Valonia utricularis*, *Halopithys incurva*, *Codium adhaerens*, *Padina pavonica*, *Sargassum flavifolium*, *Asparagopsis armata*, *Scytosiphon lomentaria*, and the molluscs *Patella rustica* and *Siphonaria pectinata* were commonly found in Southern Portugal and throughout the Galician and Asturian provinces of Spain (Nobre, 1940; Fischer-Piétte and Gaillard, 1959; Ardré, 1970) or even further north (*Onchidiella celtica* occurs in South-Western Britain, Hayward and Ryland, 1995). However, all these species were absent from northern Portugal, which represented, therefore, an important gap in their distribution. Surprisingly, except from van den Hoek and Donze (1967), no solid hypothesis was ever advanced to explain the mechanisms underlying this pattern. The main factor (or factors) preventing these species from bridging this distributional gap remained largely unknown. Nonetheless, recent changes in their distribution might have provided some clues, helping to solve this problem.

From the warm-water species group traditionally absent from the Northern Portuguese coast, major changes in distributional ranges were firstly observed in two pulmonate gastropods (*Onchidella celtica* and *Siphonaria pectinata*). In the 1940s, their northern range limit was located at Peniche and Baleal - central Portugal (Nobre, 1940). In the early 1990s, both species could already be found within their former gap, in the rocky shores of Vila Chã and Angeiras - nothern Portugal (Santos, 1994). In 2000, *S. pectinata* expanded further north, reaching Viana do Castelo (Santos, 2000). Finally, within the scope of the current work in 2002, it was discovered that this species had already expanded its range along the entire northern Portuguese coast. Moreover, a large increase in abundance in all rocky shores up to the Spanish border was also noticeable. At that time, it was possible to observe not only a high number of adults but also eggs masses, juveniles and intermediate-sized individuals, meaning that populations were effectively reproducing. *Onchidella celtica*, on the contrary, was never observed further north than Cabo do Mundo, which still seems to be its northern range limit within the Portuguese coast.

The best studied expansion was, however, the colonization of the northern Portuguese coast by *Patella rustica* in the late 1990s (Lima *et al.*, 2006). The evidence that this process has been facilitated by the conjunction of a significant increase in temperature coupled with changes in upwelling and sea current patterns, originated two main hypotheses. The first states that this species has never been able to successfully establish in the region due to the inhibitory effect of dominant oceanographic patterns which seasonally cooled the coastline waters to levels only found in distant regions, towards the north (see section 3.1). Assuming that this was in fact the case, it could also explain why many other species have been prevented from colonizing the area. The second hypothesis stems from the first: if the temperature/current barrier had generalized effects with consequences for a whole set of species, then the weakening of that barrier and consequent changes in distribution should also be noticed in a wide range of species. Thus, the main question is: were these anticipated changes already observable in the field? Results have shown that apparently the answer was yes, although some difficulties have arisen. First, from the algal group above mentioned, only one species has colonized the entire gap (*Leathesia difformis*). The remaining changes varied from species to species: *Hypnea musciformis* expanded its distribution from Sagres (Ardré, 1970) to Portinho d'Arrabida, *Valonia utricularis* from the Tagus Estuary (Ardré, 1970) to São Martinho do Porto, *Halopithys incurva* from Lagos (Ardré, 1970) to Bafureira, *Codium adhaerens* from Baleal (Ardré, 1970) to São Martinho do Porto, *Padina pavonica* from Sesimbra (Ardré, 1970) to Baleal, *Sargassum flavifolium* (Ardré, 1970) from Sines to Moledo do Minho, and *Asparagopsis armata* was observed for the first time in Vila Praia de Âncora, in 2005.

The only species whose distributional limit suffered no significant changes was *Scytosiphon lomentaria*. Therefore, most of algal species showed partial expansions, contrasting with the molluscs *S. pectinata* and *P. rustica*.

Since it is known that each species responds in its own way to climate (e.g. Hodkinson, 1999), differences between expansion rates probably reflect distinct tolerances to temperature. It should be remembered that although the average temperature has been rising, there have been some interspersed cold episodes (see Figure 3.1.3) that organisms had to withstand. Thus, species better prepared to cope with cold spells would be expanding their range more successfully. Another probable explanation is related with different dispersal abilities. Most intertidal animals have sessile adult forms and as a result their free-living, planktonic larval stage is their main mode of dispersal (Levin and Bridges, 1995). Similarly, algae species are strongly dependent on the water transport to carry their propagules which usually settle in the vicinity of the source populations (Gaylord *et al.*, 2002; Bobadilla and Santelices, 2005). Long-distance dispersal seems to occur mainly via drifting of adult plants, which are transported accordingly to the prevailing currents (van den Hoek, 1987). Intertidal species with longer pelagic phases or with special adaptations (like flotation bladders in algae) will disperse better and will therefore colonize larger areas during the same period (Bohonak, 1999; Cowen *et al.*, 2000; Levin, 2006). Since the northern group of rocky shores is isolated from their southern counterparts by large stretches of sandy coast, dispersal ability certainly has a relevant role. Although the construction of a high number of sea defences in the region of Aguda, Aveiro and Figueira da Foz might have provided enough hard substrata which could have been used as a 'stepping stone', species still needed to overcome some large distances without suitable habitat. In this perspective, organisms better adapted to artificial substrata would have a greater likelihood of expanding their geographic distribution.

From the two algal species only found on northern Portugal, one has significantly retracted northwards (*Pelvetia canaliculata*), while the other (*Laminaria saccharina*) has undergone a slightly, non-significant southward expansion.

There were just a few warm-water species reaching absolute limits on the Portuguese coast, all of which are algae. Detailed analysis can be found in the section 3.2.5. *Valonia utricularis* was the only species who significantly expanded northwards (from the Tagus estuary to São

Martinho do Porto). The distribution area of the remaining species did not change.

Among the cold-water species that have their southern range limit within the study area, no congruent trends emerged from data. In 1960, the southern range limit of *Nucella lapillus* was reported at Sagres (Fischer-Piétte, 1960). During the early 1990s it was located at Praia da Luz (AM Santos, unpub. data), approximately 25 Km to the East. This limit remained stable in the following years (Santos *et al.*, 2000) and during the current surveys no significant changes were found. In the 1960s, the limits of *Patella vulgata* and *Littorina saxatilis* were both at Portimão (Fischer-Piétte, 1960). Nowadays, the range of *P. vulgata* has slightly retracted to Praia da Luz (3 Km to West) and the distributional limit of *L. saxatilis* is located at Olhos d'Água (a shift of approximately 30 Km towards the East). Thus, none of these three mollusc species showed a significant distributional change in relation to the 1960s.

The analysis of algal distributions, which can be seen in sections 2.2 and 3.2, has shown that although a high number of species exhibited a significant northward shift in their distributional limits, an equal number displayed changes in the opposite direction, and a third group has not significantly changed at all.

The present results are in agreement with the hypothesis that the 'atypical' communities in northern Portugal are somehow determined by a strong upwelling influence which in contrast to the general climatic pattern is responsible for a cooler area in that reagion (van den Hoek and Donze, 1967). Furthermore, the recent trend of increasing coastal sea temperature (probably both related with a regional decline in upwelling and with global warming) may explain why many distributional boundaries migrated northwards. It was interesting to observe that distinct groups such as algae and gastropods showed highly similar patterns in the observed changes of their ranges during the last decades. Of the warm-water species which did not existed in Northern Portugal, the majority has been expanding their distribution and thus bridging or narrowing distributional gaps (although at different rates). It seems that intertidal communities in this region are increasingly losing their 'northern' character, becoming progressively similar to the southern assemblages. These results are in agreement with the general hypothesis predicting a poleward movement of species in response to climate change (see General Introduction). Keeping this in mind, it is possible that the three crustacean species (*Caprella mitis, Biancolina algicola, Synisoma capito*) which were previously thought to be exclusively from the Mediterranean Sea and that were recently recorded for the first time in the Portuguese coast (Pereira *et al.*, 2006), are in fact southern emigrants whose changes in distribution are being driven by the recent increase in sea temperature. However, the lack of historical information makes this a purely speculative inference.

It should also be noticed that although seven cold-water species have retracted their distribution towards the north, an additional bulk of species has not shown a significant range displacement, contrary to what would be expected in response to the warming environment. This is particularly difficult to interpret since a finding of no-response cannot be used to determine the relative importance of the limiting factors operating at the range edge (Parmesan *et al.*, 2005). In addition, many other species have even showed the opposite tendency, expanded their range southwards. This was a consistent and recurrent result, seen among algae (see sections 2.2 and 3.2), molluscs (see above) and crustaceans (see section 2.1). Again, in this last group some uncertainty still persists concerning the existence of a true expansion, since historical data is very scarce.

Different hypotheses were advanced to explain the contrast between warm- and cold-water species range shifts (section 3.2). One hypothesis is based on the marked opportunistic character of southern species, generally with a shorter life span and higher reproductive outcome (Lewis, 1986). In addition, they have the advantage of being released from their current competitor and predator pressures when shifting northwards (Sax and Brown, 2000). This would allow these species to quickly change their geographical ranges, taking advantage of rapid alterations in the environment which, for example, modify or create new suitable habitat. Thus, changes in distribution would consequently be noticed earlier on warm-water species.

The second proposed explanation is based on the hypothetically greater resilience of northern species, which also seem to be stronger competitors when compared to their southern equivalents. For example, it was reported that *Patella vulgata* outcompetes *Patella depressa* (Boaventura *et al.*, 2002a); that *Semibalanus balanoides* outcompetes

Chthamalus stellatus and *Chthamalus montagui* (Svensson *et al.*, 2006); and that *Laminaria digitata* outcompetes *Laminaria saccharina* and *Saccorhiza polyschides* (S J Hawkins, pers. comm.). Therefore, cold-water species could be better suited to withstand adverse conditions, maximizing the advantage of short cold spells for maintaining (or even expanding) their geographical domains.

On the other hand, it could be possible that stronger equatorial winds originated by the warming process lead to intensified upwelling, as already reported for the North-East Pacific (Snyder *et al.*, 2003). That would cause counter-intuitive expansion of cold-water low-shore and subtidal species. Nonetheless, recent evidence suggests that upwelling has been decreasing in the Portuguese coast (Lemos and Pires, 2004). Additionally, data from the present study do not support the evidence of contrasting changes in distribution of high- and low-shore species.

Two completely new hypotheses are now suggested. First, although long-term analysis of the SST regime during the past 50 years has shown a consistent increase in temperature (section 3.2), a more detailed inspection of the dataset reveals that increases were not homogeneous in a monthly base (Figure 5.1). During winter months, but particularly during the summer, the increase in temperature was more pronounced (this observation is also in agreement with the previous findings of a recently weaker upwelling). For that reason, it is possible that the different responses among cold-water species are simply the result of differences in their life cycles. Perhaps the most affected species, those retreating towards the north, are more vulnerable during the months in which the temperature has raised the most. This would not be surprising, given that even among closely related species the responses to climate may be quite different (Hodkinson, 1999). Also, many southern limits of Mediterranean and Atlantic species of algae are set by summer lethal temperatures (Yarish *et al.*, 1986).

The second hypothesis is based on the noteworthy observation that the majority of the observed changes occurred among those species which had a distributional gap in Northern Portugal (independently of the size of the gap). If their expansion was being hampered by some adverse climatic factor, for example, low sea temperature during the summer, then a slender warming could have been sufficient for a relaxation of the temperature constrain, allowing the expansion and hence the bridging

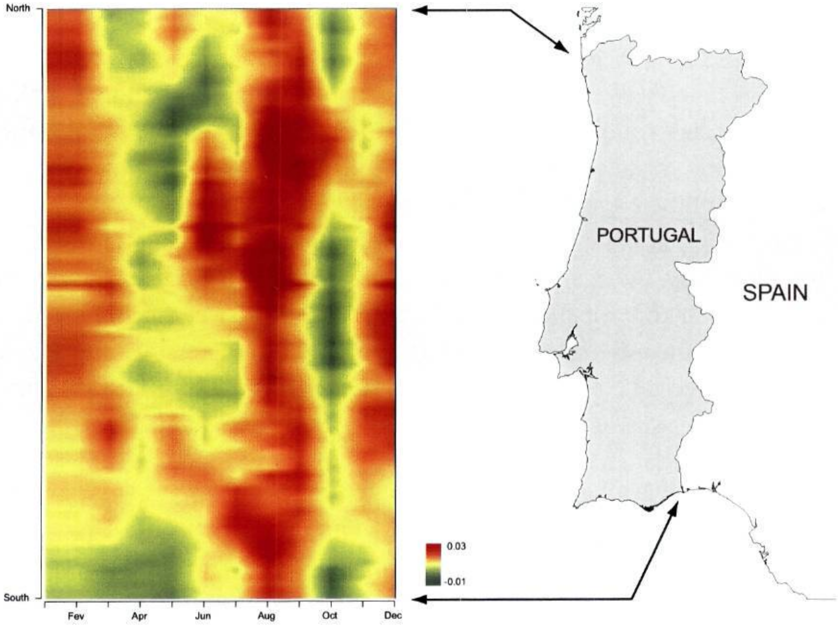

Figure 5.1 Monthly sea surface temperature increase (°C year^{-1}) from 1950 to 2000. The vertical axis represents the Portuguese coast and the horizontal axis shows the different warming trend the thougout the year.

of the distributional gap, albeit only partially in some cases. How could this explain the high diversity of responses among cold-water species? It is probable that the absolute increase in temperature has been too small, affecting only highly sensitive species, or those for which the small threshold between favourable and unfavourable temperature levels is coincident with the observed warming. Thus, only the susceptible group of species would be retreating northwards, while the remaining cold-water species would not change and could even expand their range, driven by a different factor.

It would be interesting to investigate whether the observed patterns can be generalized to other habitats, species and/or communities, since the present results suggest that climate-related distribution changes are most likely noticed in first place within the range limit of species, and only subsequently are they noticed at the distributional borders. Therefore, long-term monitoring of gaps or anomalies in the distribution could provide an early warning system to the effects of climate change.

5.3 The importance of biological interactions

Many recent publications have highlighted the need to investigate the biological interactions thought to interfere in the climate-mediated constraining of species ranges (e.g. Brooker, 2006). Although an increasing number of studies have started to address these challenges (Sanford, 1999; Sanford, 2002; Wethey, 2002; Moore, 2005), substantial research is still required.

The initial objective of the southward transplant of *Himanthalia elongata* (section 3.3) was to assess the susceptibility of its reproductive grow to the warmer waters of Central Portugal, from where the species has completely disappeared in the last decades. However, results indicate that the range retraction was not related with a direct influence of temperature, at least on that specific phase of the life-cycle, since the reproductive organs of the transplanted specimens continued to develop at growth rates comparable with northern, non-transplanted individuals. However, it was interesting to observe a severe herbivorous pressure on the transplanted algae, a phenomenon never registered within the current range of the species. Nonetheless, some caution should be taken when interpreting these results. The seaweed life-span has approximately two years (Kitching, 1981; Stengel *et al.*, 1999) but the experiments lasted only a few months. Thus, since they were not designed to encompass any other stage of the algae's life cycle except reproductive growing, it is impossible to know if temperature is constraining any other life phase and thus being directly responsible for the retreating range (Adahl *et al.*, 2006). Nonetheless, it is very likely that even if all hypothetical physical restraints were removed, the species would still disappear from southern locations, since the observed grazing not only hindered reproductive growth but also caused a complete destruction of many adult forms.

The fact that intensive levels of grazing of *Himanthalia elongata* have never been observed in northern locations (within the species' current range) suggest that the putative grazer range does not reach this area. It is also possible that until the late 1960s this species was absent from the southernmost locations where populations of *H. elongata* were observed. If this is true, it is possible that the disappearance of the algae was caused by a climate-induced northwards migration of that herbivorous species, which is also currently preventing the re-expansion of the algae to its former range. Alternatively, grazing might have been triggered by the temperature increase. Consequently, the two species may have coexisted sympatrically in part, if not all of their ranges, but the algae was only recently excluded from the area where the temperature has crossed a certain threshold (Leonard, 2000). Herbivory pressure was not the only biological interaction apparently affecting *Himanthalia elongata*. Results also suggested the possibility of competition for space with *Sabellaria alveolata*. Thus, biological interactions might have played a more significant role in the retraction of *H. elongata* range than previously anticipated

Although further research is required to eliminate many uncertainties, these results contribute to strengthen a relatively new and emerging 'biogeographic rule' which states that high-latitudinal borders are controlled by physical factors while the low-latitudinal range boundaries are set by biological interactions. This theory, whose rudiments were suggested by Loehle (1998) to explain why boreal tree species were able to grow in temperate climates, has been occasionally invoked to explain the rarity of documented contractions in the lower latitudinal limits of species in response to climate change (see Parmesan *et al.*, 2005; Wilson *et al.*, 2005). The present work seems to support the validity of this hypothesis by a wide range of examples. If the northern limit is in general controlled by physical factors, then even a slight increase in temperature would allow a high number of warm-water species to break their northern distributional barrier and to expand their range, or filling distributional gaps. Species would be simply following the displacement of their 'bioclimatic envelope'. On the other hand, if the southern boundaries are in general controlled by biological interactions, a small increase in temperature would only affect a minority of cold-water species, such as those affected by an increase in abundance of their competitors, parasites, predators or consumers. This response would be much more variable, complex and non-linear, precisely as observed in the field. Similar trends showing a consistently stronger signal of poleward shifts at high-latitude range edges (when compared with their low-latitude equivalents) were recently reported by several independent studies (Parmesan and Yohe, 2003; Parmesan *et al.*, 2005; Helmuth *et al.*, 2006).

These ideas are still in an initial stage and certainly need more evidence to support them. Specifically, they will require numerous independent datasets describing patterns of changes in distribution at low-latitude range margins, which are presently scarce (Wilson *et al.*, 2005; Franco *et al.*, 2006). The understanding of the mechanisms underlying the species-mediated responses to climate change would also be largely improved by a deeper knowledge on the biotic relationships between the different species within the community. This knowledge would be crucial to create more realistic models on species responses to climate change.

5.4 Modelling species responses to climate change

Modelling species and ecological responses taking into account the expected climate change has been used to circumvent the problem of trying to understand how natural systems will respond to environmental conditions that have no analogue at present or in a recent past (Harley *et al.*, 2006). However, as discussed in a previous chapter (Chapter 4), the widespread use of bioclimate envelope approaches has been recently criticized on the basis of their limited and deterministic nature, which seems to be conceptually inadequate while making projections of future events. Support for these suggestions was found when modelling the distribution of *Patella rustica*, given that the model did not pass the validation phase, inaccurately hindcasting the northern limit of the species distribution. Nonetheless, by failing to do so, it emphasised the importance of the non-physiological control of the distributional range, strongly suggesting that dispersal limitations might be playing a fundamental role. These new clues might be of primary importance in designing and interpreting future studies of this and even other related species. Thus, bioclimatic models certainly still have an important role in ecology by helping to effectively put forward some explanatory hypotheses which can be subsequently tested.

Many recent papers have stressed the importance of research aimed at developing hybrid-models that integrate the best of mechanistic and theoretical models (including information on biotic interactions and dispersal mechanisms) with the best of correlative bioclimatic modelling (Pearson *et al.*, 2002; Guisan and Thuiller, 2005; Araújo and Guisan, 2006). This overwhelming task can be made easy by carefully prioritize key species, which can then be used as surrogates for studying whole communities, at least during an exploratory phase. The limpet *Patella rustica* may be an ideal candidate for several reasons: (i) its distribution is currently changing, providing a unique chance of studying many physiological and ecological aspects; (ii) these changes have been studied practically from their beginning; (iii) the fact that the expansion is still in its early stage means that probably in the near future it will provide interesting new data and the opportunity to test several hypotheses, and (iv) preliminary results indicate that the expansion is driven by a complex interaction of factors, thus offering the possibility to study non-linear processes. Therefore, an ideal approach to forecast the distribution of this species would be to include two different components in the model. First, an exhaustive knowledge on several critical parameters of *P. rustica*'s life cycle, as the length of its reproductive period in relation to latitude, reproductive output, growing rates, the average age for attaining sexual maturity and the duration of the plancktonic phase would permit the construction of an accurate model on the organismal responses to physical variables. On the other hand, a circulation model including effects of coastal dispersal barriers and stochastic long-distance transport events would also be considered. These two complementary approaches would then be coupled into a comprehensive model, allowing to test a variety of hypotheses on the relative importance of different life-cycle physiological requirements, environmental constrains and dispersion over the distribution of species.

Chapter 6
Concluding remarks

This chapter integrates and synthesizes the work in the thesis. It is suggested that modifications in distributional ranges are complex and highly variable in intensity, direction and causal factors from species to species. Therefore, generalizations about poleward range shifts due to increasing temperature should be made with caution.

The present work has contributed to update distribution records of more than two hundred rocky intertidal macrospecies along the Portuguese coast. Given their taxonomic, temporal and spatial coverage, these data provide a reliable and comprehensive baseline to contrast with against future changes in species distributions. Data concerning the distribution of epifaunal assemblages suggest that these are not strongly conditioned by the identity of the algal species in which they inhabit, but rather controlled by climatic factors. These factors also seemed to be major determinants of the distribution of many other species, in particular molluscs and algae. It was proposed that the peculiar species pattern found in the northern Portuguese coast results mainly from upwelling influence during summer and autumn.

Several species were identified as sensitive indicators of climate change.

Many are currently shifting their ranges towards the north, most likely driven by the recent increase in temperature and associated changes in coastal sea circulation. Therefore, the future monitoring of their distribution is proposed as a way to track such environmental changes. However, contrarily to what would be expected, many species ranges were not changing at the same rate and/or in the same direction. These results are extremely relevant since they illustrate that generalizations about poleward shifts should not be taken lightly. Even species that are apparently responding to climate warming revealed complex, non-linear interactions with third-party factors like habitat availability or other organisms. Additionally, it is very likely that the relative importance of the factors determining species distribution varies along their range. One of the advanced hypotheses states that while the northern range limit of many species is physically-driven, biological factors are controlling their southern distributional border.

Modelling species distributions provided some insights into a few of these problems. Despite the fact that large-scale climate envelope approaches are currently being criticized for both ignoring indirect effects of warming and the influence of non-climate factors, they proved to be of great utility in exploratory analysis, by allowing to propose and to refine hypotheses on species responses to climate change. Nonetheless, further efforts are required to better understand the processes controlling species distributions. Although some advances in that direction have been made with the current work, it has probably raised an even higher number of novel questions. Among them, it is essential to emphasize the difference between regional warming originated by low-upwelling and the steady increase in temperature derived from global warming. This could be achieved by comparing changes in physical factors (such as SST and upwelling) and in species distributions in different geographic areas (for example, from Portugal to the U.K). It is also imperative to compare differences in direction and strength of species' range shifts with their particular physiological requirements and life-trait characteristics. Also, the influence of temperature in other phases of the life-cycle of *Himanthalia elongata* ought to be addressed, using laboratorial controlled trials. In addition, it would be interesting to repeat transplant experiments, but removing space competitors and using fences to protect both vegetative and reproductive forms from grazing. Finally, population genetic studies and dispersal modelling should be coupled to identify the source of colonizing individuals of *Patella rustica* in northern Portugal, as well as to deepen the knowledge on the factors limiting its northern distributional range.

In conclusion, intertidal assemblages here investigated are ideal for a continued study, which will certainly help to build more accurate predictive models on how species ranges are likely to shift in response to global climate change.

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