UNIVERSITY OF SOUTHAMPTON

FACULTY OF NATURAL AND ENVIRONMENTAL SCIENCES

SCHOOL OF OCEAN AND EARTH SCIENCES

IN COLLABORATION WITH

UNIVERSITY OF THE AZORES

INFLUENCE OF CLIMATE CHANGE AND OTHER IMPACTS ON ROCKY INTERTIDAL COMMUNITIES OF THE AZORES

MARIA LUÍS ADRIÃO DO VALE

DOCTOR OF PHILOSOPHY

NOVEMBER 2015

UNIVERSITY OF SOUTHAMPTON

ABSTRACT

FACULTY OF NATURAL AND ENVIRONMENTAL SCIENCES

School of Ocean and Earth Sciences

Doctor of Philosophy

INFLUENCE OF CLIMATE CHANGE AND OTHER IMPACTS ON ROCKY INTERTIDAL COMMUNITIES OF THE AZORES

by Maria Luís Adrião do Vale

Biodiversity is under increasing pressure from human activities driving global environmental change. Global climate driven change interacts with regional (e.g. eutrophication) and local scale impacts (e.g. overexploitation). Long-term and broad-scale data are required to distinguish human-induced changes from natural fluctuations. The aim of this thesis was to explore the responses of intertidal ecosystems to climate change and other impacts, using the Azores as a model system, by describing patterns and experimentally testing processes. Relevant long-term environmental data on surface air and sea temperature plus wave action were collected. Baseline data collected in the 1980s was compared to the 2010s. Descriptive studies examined the patterns at the individual and community level providing evidence of long-term changes in response to greater stress due to changing environmental conditions. At the individual level, changes in phenology of two Azorean species of limpets (*Patella aspera* and *Patella candei gomesii*) were assessed over time (1980s versus 2010s) and space across the Archipelago. Evidence of temporal and spatial changes were found in the reproductive cycle of the limpets; these can probably be related with climate change and spatial gradients in environmental conditions across the archipelago. At the community level, long-term changes in distribution of key intertidal species were assessed. Changes were found not only in the abundance but also in the vertical distribution of the species. Some of these may be ascribed to recent climate change, whereas other may be better explained by the overexploitation of keystone limpet grazers. Finally, community response to the loss of a key intertidal northern species (*Fucus spiralis*) was experimentally simulated. *Fucus spiralis* showed fast recovery rates and, unlike expected, its loss had minimal effect on the associated assemblages. Overall, results indicate that there have been some significant changes on the Azorean rocky shores. These included changes in the phenology, abundance and distribution of species. My results suggest *F. spiralis* in the Azores is not a key species as found elsewhere; so its potential loss may have little to no impact on the remainder of the community. My research highlights the key role of enforced marine reserves in distinguishing between the long-term effects of changes in climate from other anthropogenic activities such as fishing. Whilst there was some evidence of climate driven change, it is likely that human overexploitation of limpets has a greater effect.

LIST OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

DECLARATION OF AUTHORSHIP

I, Maria Luís Adrião do Vale declare that the thesis entitled “Influence of climate change and other impacts on rocky intertidal communities of the Azores” and the work presented in the thesis are both my own, and have been generated by me as the result of my own original research. I confirm that:

- This work was done wholly or mainly while in candidature for a research degree at this University.
- No part of the thesis has previously been submitted for a degree or any other qualification at this University or any other institution.
- Where I have consulted the published work of others, this is always clearly attributed.
- Where I have quoted from the work of others, the source is always given. With the exception of such quotations, this thesis is entirely my own work.
- I have acknowledged all main sources of help.
- The thesis is based on work done by myself, and jointly with others. Steve J. Hawkins, Ana I. Neto and Gustavo M. Martins advised on concepts and questions in chapters 1 to 6 and helped with some fieldwork. Various colleagues from the Azores - Afonso Prestes, Eva Cacabelos, Isadora Moniz, João Faria, Nuno Álvaro and Rita Patarra, contributed to fieldwork in chapters 3 to 5. Steve J. Hawkins, Helen Martins, Ricardo S. Santos, Ana I. Neto, Norberto Serpa, Carmelina Leal and others contributed to historic data in chapters 3 and 4. Carlos Mendes, Norberto Serpa, Pedro Ribeiro, Marco Branco, Bruno Couto and Marco Ferreira contributed to recent limpet collections in chapter 3. Diamantino Henriques provided some of the environmental data in chapter 2.
- None of this work has been published before submission.

Signed:…………………………………………………………..

Date:……………………………………………………………..

ACKNOWLEDGEMENTS

This research was supported by a PhD grant awarded by Foundation for Science and Technology (FCT, Portugal) (SFRH/BD/70374/2010) and also partially supported by the European Regional Development Fund (ERDF) through the COMPETE - Operational Competitiveness Programme and national funds through FCT - Foundation for Science and Technology, under the project “PEst-C/MAR/LA0015/2013, by the Strategic Funding UID/Multi/04423/2013, in the framework of the programme PT2020 and by cE3c funding (UID/BIA/00329/2013). Logistic support was also provided by CIRN/UAç (Centre of Natural Resources of University of the Azores) and the Department of Biology of the University of the Azores. This research was done at the University of Southampton in collaboration with the University of the Azores (Portugal).

I would like to thank to my supervisors, Dr Steve J. Hawkins, Dr Ana I. Neto and Dr Gustavo M. Martins, for their personal and professional support, input and advice throughout the all thesis.

I am very grateful and indebted to Professor Steve J. Hawkins for his patience, confidence, guidance and his words of encouragement (always present). His knowledge and input were vital during the several stages of this process and an additional source of motivation.

I am very grateful to my co-supervisor Professor Ana I. Neto, who welcomed me in her workgroup giving me the opportunity to develop my research in the Azores. Her knowledge, attention to detail and emotional support were very important throughout my thesis.

I am very grateful to my co-supervisor Dr Gustavo M. Martins, for his knowledge and support in guiding me through all the stages of this process. His personal and professional supports were essential. His guidance, especially in the experimental design and multivariate analysis, had an influence in the development of the thesis and in my own knowledge and points of view.

I would like to thank Dr Diamantino Henriques from the Regional Delegation in the Azores of the national government agency Instituto Português do Mar e da Atmosfera (IPMA), for his availability to discuss and kindly provide me some of the environmental data sets used in my thesis.

I would like to thank Bruno Couto, Carlos Mendes, Isadora Moniz, Marco Cabral, Marco Ferreira, Norberto Serpa and Pedro Ribeiro, for their help in the limpet's collection.

I would like to thank Nuno Álvaro, for his valuable help with the maps.

I would like to thank to some people that were also very important during my stays in Southampton – Angeliki Zisi, Alanoud Al-Ragum, Amani Alshatti, Carla Pueyo, Christos Loukas, Daniela Biesot, Eithne Tynan, Eleni Anagnostou, Greggy Davies, Hachem Kassem, Hector Moreno, Isma Himar Falcon, Konstantina Rizopoulou, Lauren Hall, Lena Tzortzi, Maria Aspiroz, Mario Esposito, Miquel Martinez-Boti, Raquel Vanes and Rui Vieira, for their friendship, emotional support and excellent sense of humor that always brought joy to the lunch time and breaks.

I would like to acknowledge a big thank you to my friends - Ana Mafalda Cruz, Ana Moreira, Ana Roma, Andrew Cordeiro, Afonso Prestes, Carla Rodrigues, Cátia Pereira, Eva Cacabelos, Francisco Wallenstein, Gonçalo Murta, Gustavo Martins, Isadora Moniz, Isnaba Miranda, Joana Bustorff, João Faria, Luz Paramio, Maria Martins, Marina Cabral, Moira MacLean, Nuno Álvaro, Rita Brum and Rita Patarra, who have helped me sometime during this long process in several different ways, through field and laboratory work, breaks (coffee, dinners or just breaks), their friendship and amazing emotional support.

I would like to thanks Isadora Moniz, for her friendship, emotional support and valuable help in the majority of the fieldwork developed along this thesis.

I would like to thank to my "other parents" - Moira MacLean and Gary Fischer, for their amazing friendship, incredible emotional support, words of encouragement and for all the times that I stayed at their house during this process.

I would like to thank the family Patarra-Wallenstein (Rita, Francisco and little André), for their friendship, constant presence, unconditional emotional support, words of encouragement and for always helping me see the bright side of life.

Finally, I would like to express my deepest gratitude and love to my family, especially to Pappi, Mummy, Godinha, and Titia, who have always gave me their unconditional love and support, believing in my capabilities, without them this thesis would never have been possible.

"I need the sea because it teaches me."

Pablo Neruda

1. GENERAL INTRODUCTION

1.1. INTRODUCTORY COMMENTS

Global biodiversity is under increasing pressure from anthropogenic activities driving environmental changes (Parmesan and Yohe, 2003; Helmuth *et al.*, 2006b; Burrows *et al.*, 2011, 2014). Global climate driven change interacts with regional and local scale impacts (Firth and Hawkins, 2011). In the ocean, global environmental change includes increased warming and stormier seas (Trenberth *et al.*, 2007), reduction of pH (Caldeira and Wickett, 2003) - although not strictly climate and widespread global homogenisation of biodiversity as non-native species invade (Stachowicz *et al.*, 1999) from different biogeographic realms. These all interact with regional scale processes such as eutrophication (Philippart, 2011) and overexploitation of resources (e.g. overfishing, Worm *et al.*, 2006) and local impacts such as habitat loss or destruction (Airoldi and Beck, 2007; Firth *et al.*, 2014) and pollution (Thompson *et al.*, 2002).

The main focus of my thesis was to investigate changes in marine life in the Azores in response to global and local pressures. I used rocky shores as a tractable study system to describe patterns and experimental processes by comparing historical data from the 1980s with contemporary re-surveys in the 2010s. Changes in relation to climate at the individual level were assessed in terms of the phenology of limpets over time and using spatial environmental gradients across the Archipelago. At the assemblage level, changes in abundance and distribution of species over time were assessed. Experimental work focussed on the main ecosystem engineer *Fucus spiralis* (Linnaeus 1753), a canopy-forming northern species located towards the southern limit of its distribution. *Fucus spiralis* is at risk from both extreme hot events and general warming at the upper limit of its distribution and greater pressure from herbivory at the lower limit of distribution on the shore. Greater storminess including extreme storms will cause disturbance throughout its vertical range.

This general introduction (Chapter 1) sets the scene for the rest of the thesis by reviewing the pertinent literature, starting with a brief overview of anthropogenically driven climate change in the oceans globally, before focussing on recent changes in the North-East Atlantic. This is followed by a review of long-term research, essential to distinguish between long wave-length, low amplitude climate signals from the background noise of other sources, such as natural variability plus regional and local scale human impacts (Mieszkowska *et al.*, 2014b). These are interwoven by considering the influence of climate fluctuations and recent rapid change on nearshore and coastal ecosystems. Finally, the basic ecology of intertidal ecosystems is briefly outlined at various levels of biological organisation from the individual, through to populations, communities and ecosystems to provide background on the model system chosen for study. I conclude by outlining the overall aims and rationale of the thesis.

1.2. CLIMATE CHANGE IN GLOBAL OCEANS

The recent rapid increase in atmospheric greenhouse gas levels (GHG) (i.e. carbon dioxide (CO_2), methane (CH_4), nitrous oxide (N_2O), ozone (O_3) and fluorinated gases (e.g. CFCs, PFCs, HFCs and SF_6)) is widely accepted to be the result of anthropogenic activities driving global changes in climate conditions (Hegerl *et al.*, 2001; IPCC, 2001, 2007, 2013; Tett *et al.*, 2002; Zwiers, 2003; IDAG, 2005; Zhang *et al.*, 2006). It is generally accepted that anthropogenically driven global warming has already affected the biota of the Earth, in both terrestrial (Jeffree and Jeffree, 1996; Parmesan *et al.*, 1999; Parmesan and Yohe, 2003; Root *et al.*, 2003; Parmesan, 2006) and marine ecosystems (Barry *et al.*, 1995; Southward *et al.*, 1995; Sagarin *et al.*, 1999; IPCC, 2001, 2007, 2013; Benson and Trites, 2002; Walther *et al.*, 2002; Parmesan and Yohe, 2003; Alheit and Niquen, 2004; Helmuth *et al.*, 2006b; Parmesan, 2006; Hoegh-Guldberg and Bruno, 2010; Philippart *et al.*, 2011; Poloczanska *et al.*, 2014; Beaugrand *et al.*, 2015; Firth *et al.*, 2015). The Intergovernmental Panel on Climate Change (IPCC, 2001, 2007, 2013) has assessed the extent to which recent observed changes in both physical and biological systems have been caused by anthropogenic warming. It is expected that in the coming years, climate change will cause major changes to the ecosystems of our planet both physically and biologically, with major social and economic consequences (IPCC, 2001, 2007, 2013; Füssel, 2008).

Climate change is expected to cause global disruption of marine systems. Most model predictions suggest that ocean circulation will be altered (Meehl *et al.*, 2007), sea levels will rise (Trenberth *et al.*, 2007), evaporation will increase (Trenberth and Shea, 2005; Trenberth *et al.*, 2007), sea temperatures will rise (Trenberth *et al.*, 2007) and there will be more frequent severe storms at sea (Trenberth *et al.*, 2007) that will, in turn, increase coastal erosion and flooding. Precipitation will be much more variable with more frequent drought and flood extreme events (Trenberth *et al.*, 2003; Wentz *et al.*, 2007). These changes will affect inshore waters and semi-enclosed estuaries, lagoons plus rias, fjords and sea lochs. Hurricane frequency and intensity will increase (Elsner *et al.*, 2008) and runoff from rivers will be amplified (Milly *et al.*, 2002; Philippart *et al.*, 2011), affecting ocean productivity and disturbance regimes.

In addition, increased levels of carbon dioxide in the atmosphere are leading to acidification of the ocean (Riebesell *et al.*, 2000; Caldeira and Wickett, 2003; Feely *et al.*, 2004; Sabine *et al.*, 2004; Orr *et al.*, 2005; Raven *et al.*, 2005; Kleypas and Langdon, 2006; Hoegh-Guldberg *et al.*, 2007; Kurihara, 2008; Veron, 2008; Kroeker *et al.*, 2010; Azevedo *et al.*, 2015). Although not strictly climate change, ocean acidification is an inevitable consequence of a high atmospheric CO_2 concentration dissolving in seawater (Sundquist, 1993; Houghton, 2007).

Through the reduction of sea ice cover (Comiso *et al.*, 2008; Philippart *et al.*, 2011), there will be increased opportunities for shipping in high latitudes (IPCC, 2007; Reid *et al.*, 2007) resulting in major shifts of biogeographic regions with exchange between oceans that last occurred 3-4 million years ago (Vermeij, 2005; Reid *et al.*, 2007; Greene *et al.*, 2008). Some of these impacts, as a result of climate change have already been reported in recent years (e.g. IPCC, 2007, 2013; Heip *et al.*, 2009; Hoegh-Guldberg and Bruno, 2010; Philippart *et al.*, 2011). These include changes in the range and spatial distribution of species (Beaugrand *et al.*, 2002b; Helmuth *et al.*, 2006b; Hawkins *et al.*, 2008, 2009; Burrows *et al.*, 2011, 2014; Poloczanska *et al.*, 2013; Firth *et al.*, 2015; Hiddink *et al.*, 2015) leading to changes in diversity which are likely to accelerate in the future (Helmuth *et al.*, 2006b). These shifts increase the risk of increased incidence of disease (Harvell *et al.*, 2002), and alteration of food web dynamics (Petchey *et al.*, 1999; Clarke *et al.*, 2007). Climate change may interact with and worsen marine eutrophication (Philippart *et al.*, 2011) by increasing the likelihood of harmful algal blooms (Anderson *et al.*, 2008; Moore *et al.*, 2008; Hallegraeff, 2010).

Globally climate change will induce different events on a latitudinal gradient; for example an increase of temperature will be more evident at the poles than at the equator (MacDonald *et al.*, 2005). Marine environments are changing rapidly (Bell *et al.*, 2000; Church *et al.*, 2001; Bindoff *et al.*, 2007; Hoegh-Guldberg and Bruno, 2010;

Burrows *et al.*, 2011; Johnson *et al.*, 2011; Menge *et al.*, 2011; Philippart *et al.*, 2011; Schiel, 2011; Wernberg *et al.*, 2011; Poloczanska *et al.*, 2013, 2014). These changes are forecasted to continue and accelerate, leading to a global warming of about 0.3°C to 0.7°C, over the next two decades (IPCC, 2013). Sea temperatures are expected to rise by 0.6°C to 2.0°C at the sea surface and by 0.3°C to 0.6°C at the depth of about 1000 m (IPCC, 2013), posing a severe risk of degradation to marine ecosystems, with consequences for human health and welfare (Harley *et al.*, 2006). The goods and services provided by marine ecosystems will be affected as sea temperatures rise (Cheung *et al.*, 2010) (see also Figure 1.1).

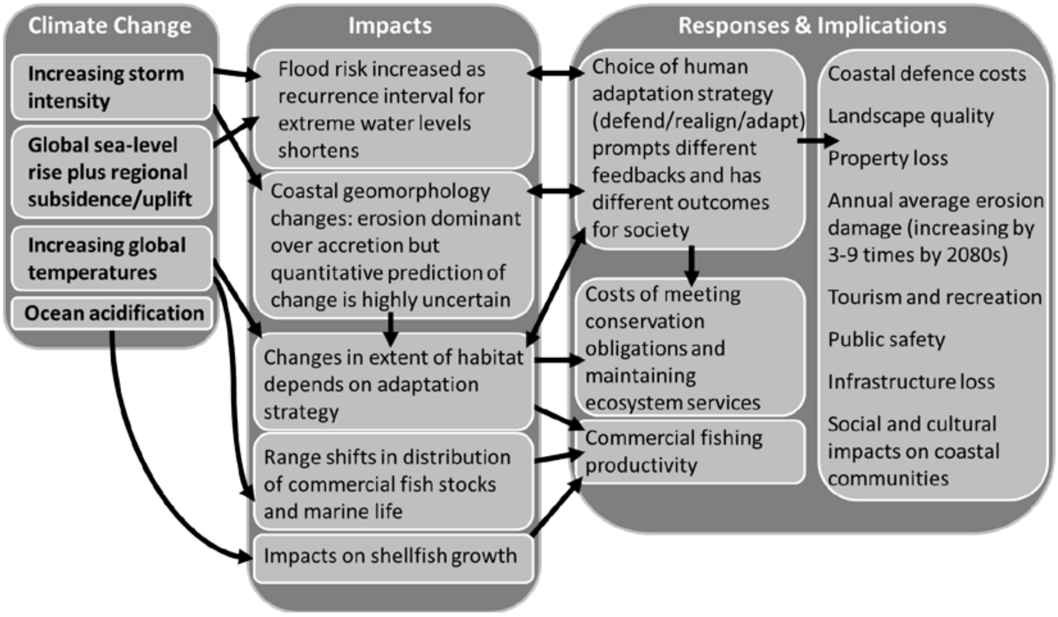


Figure 1.1. Climate change impacts on the marine and coastal environment and the social and economic situation of coastal communities (adapted from Heip *et al.*, 2011)

According to Pereira *et al.* (2010) future scenarios consistently indicate that biodiversity will continue to decline over the 21st century (Thomas *et al.*, 2004). Global biodiversity is under increasing pressure from human activities generating environmental change. Regardless of the amount of effort that has been made in defining the biological impacts of climate change in the ocean (e.g. Southward *et al.*, 1995; Harley *et al.*, 2006; Helmuth *et al.*, 2006b; Poloczanska *et al.*, 2013, 2014), the effects of this global driver on marine biodiversity and ecosystems are still very poorly known and understood (Wernberg *et al.*, 2012). Basic predictions of the responses of marine species to climate change were summarized by Harley *et al.* (2006), who state that as the temperature increases species abundance will change and distributions will shift according to the thermal tolerance and adaptability of the species. Thus responses of different marine species to climate change will vary (Hawkins *et al.*, 2009; Hoegh-Guldberg and Bruno, 2010; McGinty *et al.*, 2011); the marine species will also be subject to interactions with other human-induced changes in the marine environment (Firth and Hawkins, 2011; Philippart *et al.*, 2011).

According to Meehl *et al.* (2007) a predicted outcome of global warming is the change in large scale patterns of ocean circulation. These predicted changes will probably have effects on assemblage composition and community structure (Reid *et al.*, 1998; Beaugrand *et al.*, 2002b; Beaugrand and Reid, 2003; Edwards and Richardson, 2004; Sarmiento *et al.*, 2004; Hays *et al.*, 2005; Harley *et al.*, 2006; Johnson *et al.*, 2011). Changes in oceanic conditions such as water temperature, circulation and coastal upwelling are likely to affect distribution and productivity of plankton and marine fisheries (Beaugrand and Reid, 2003; Brander *et al.*, 2003; Alheit and Niquen, 2004; Beare *et al.*, 2004; Beaugrand and Ibañez, 2004; Genner *et al.*, 2004, 2010; Beaugrand, 2005; Hays *et al.*, 2005; Perry *et al.*, 2005; IPCC, 2007, 2013; Cheung *et al.*, 2009, 2010, 2011, 2012, 2013; Beaugrand *et al.*, 2015; McQuatters-Gollop *et al.*, 2015). The effects of global warming will continue, until measures to reduce the greenhouse gas emission have been taken (IPCC, 2007, 2013; Friedlingstein *et al.*, 2011). The only way to slow climate change is to decrease the dependence on carbon-based sources of energy (IPCC, 2007, 2013; Edenhofer *et al.*, 2010; Russell and Connell, 2010). Even if a reduction in carbon based sources of energy is taken, a minimum time lag will be needed to see any effects, due to the inertia of the climate system. If emissions were cut now by 90%, the global temperature would reach 2°C, above pre-industrial levels, by the end of the millennium (Friedlingstein *et al.*, 2011). Until then human society has to adapt to the effects of climate change (Adger *et al.*, 2005; Parry *et al.*, 2007) and manage the interactions of global change with regional and local scale impacts (Firth and Hawkins, 2011). Nevertheless, human adaptations to climate change, such as coastal defences, can have a severe impact on coastal ecosystems (Hawkins *et al.*, 2009; Chapman and Underwood, 2011; Philippart *et al.*, 2011; Firth *et al.*, 2014), through the loss and alteration of available natural habitats for species composition in coastal communities (Thompson *et al.*, 2002; Airoldi *et al.*, 2005; Bulleri, 2005; Bulleri *et al.*, 2005; Martin *et al.*, 2005; Moschella *et al.*, 2005; Martins *et al.*, 2009; Firth *et al.*, 2013, 2014).

1.3. CLIMATE CHANGE IN THE NORTH-EAST ATLANTIC

The North-East (NE) Atlantic Ocean can be defined as the region between the European Western Shores out to the Mid-Atlantic Ridge and constrained to the North by the Greenland-Scotland Ridge. The Azorean archipelago and Iceland lie at the outer boundaries. The North-East Atlantic has an important moderating effect on the European climate, through the effects of the North Atlantic current (extension of the Gulf Stream). This current has the capability to warm the atmosphere over Europe by about 5°C (Heip *et al.*, 2011).

The North Atlantic Oscillation (NAO) is the normalized gradient in sea-level air pressure between Iceland and the Azores (Hurrell, 1995; Reid *et al.*, 1998; Paeth *et al.*, 1999; Hurrell *et al.*, 2001; MacDonald *et al.*, 2005). It is uncertain if the multi-decadal NAO variability is associated with climate change (Paeth *et al.*, 1999). This meteorological phenomenon affects the surface air temperature, wind strength, precipitation levels and storm intensity as well as the frequency of events over the Atlantic and adjacent continents (Hurrell, 1995; Hurrell *et al.*, 2001; Stenseth *et al.*, 2002; Trenberth *et al.*, 2007; Heip *et al.*, 2009; Hurrell and Deser, 2009). According to Hurrell and Deser (2009) the ocean is also affected by the NAO, through fluctuations in the heat content, gyre circulation, location of the mixed layer depth, salinity, high latitude deep water formation and sea ice cover. Therefore, several studies have linked NAO with changes in the structure and functioning of marine ecosystems including phenological shifts (Sims *et al.*, 2001, 2004), population dynamics (Ottersen *et al.*, 2001), abundance, spatial distribution and interspecific relationships (Ottersen *et al.*, 2001; Mieszkowska *et al.*, 2014a). According to Alexander and Tett (2005) over the past 20 years, mean wave heights and frequency of severe wind events have increased; it is predicted that these trend will continue (Bacon and Carter, 1991; Wang *et al.*, 2004; deYoung *et al.*, 2008). North Atlantic sea surface temperatures (SST) display a cyclical variation (0.35°C range) with a periodicity of 65-75 years (Trenberth and Shea, 2006): a cold phase occurred between 1905-1925 and 1970-1990, while between 1930-1960 a warm phase occurred (Kerr, 2000). This variability in the SST in the North Atlantic Ocean is termed the Atlantic Multi-decadal Oscillation (AMO) (Kerr, 2000; Knight *et al.*, 2006; Delworth *et al.*, 2007). Mieszkowska *et al.* (2014a) studied the influence of the AMO on inter-annual population dynamics of warm and cold water intertidal species and determined that the fluctuations in relative abundance of boreal versus Lusitanian barnacles are driven by wider underlying forces - perhaps influencing circulation patterns and direction of flow into the English Channel and also the more proximate effects of SST.

Several authors have stated that the North-East Atlantic region has shown signs of rapid temperature increase above global averages, as a response to global climate warming (Lima *et al.*, 2006, 2007; Mieszkowska *et al.*, 2006a, 2006b; IPCC, 2007, 2013; Hawkins *et al.*, 2008; Lima and Wethey, 2012). Change in sea surface temperature for the North Atlantic Ocean have been well documented, showing a upward trend with a averaged warming of 0.49°C for the period of 1850-2007. This increase was attributed to the combined effects of anthropogenic global warming and the oscillations of the ocean-atmosphere system (Heip *et al.*, 2011). These changes are, however, not uniformly linear (Philippart *et al.*, 2011). There have been periods of warm conditions (e.g. 1880s to 1890s, 1920s to early-1960s), followed by colder periods (1914 to 1918, 1960s to mid-1980s) (Thompson *et al.*, 2010; Lima and Wethey, 2012). From the 1980s there has been a period of rapid warming interspersed with cold winters. During the period from 1982 to 2006, through satellite observational studies, the estimated sea surface temperature rise was at a rate of 0.03-0.06°C yr^{-1} for the North Atlantic and European Seas (Coppini *et al.*, 2011). Philippart *et al.* (2007) stated that the sea surface temperature observed in 1975-2005 on the North-East Atlantic Ocean increased by 1°C; moreover an increase of +2°C on SST in 1990s-2090s has been forecast (Philippart *et al.*, 2011). Lima and Wethey (2012) also detected a warming on the coastlines around the world. Oceans are the main global sink for carbon dioxide (CO_2), however the distribution of the anthropogenically sourced CO_2 is irregular, with the largest vertically integrated concentration of CO_2 (23%) found in the North Atlantic (Philippart *et al.*, 2011).

Several studies in the North-East Atlantic have linked large shifts in marine ecosystem structure and dynamics with changes in the oceanic conditions due to fluctuations in climate over the past century. These encompass studies of plankton (Russell, 1973; Southward *et al.*, 1995; Hawkins *et al.*, 2003; Beaugrand and Ibañez, 2004; Beaugrand, 2005; Beaugrand *et al.*, 2013; McQuatters-Gollop *et al.*, 2015), fish (Brander *et al.*, 2003; Beare *et al.*, 2004; Genner *et al.*, 2004, 2010; Perry *et al.*, 2005; Simpson *et al.*, 2011), squid (Sims *et al.*, 2001), benthos (Hawkins *et al.*, 2003; Hiscock *et al.*, 2004; Clare *et al.*, 2015), marine birds (Durant *et al.*, 2005), and whole ecosystems (Southward, 1980; Southward *et al.*, 1995, 2005; Hawkins *et al.*, 2003).

1.4. LONG-TERM STUDIES ON THE MARINE ENVIRONMENT

Long-term and broad-scale data are required to understand and distinguish human-induced change from natural spatial variation and temporal fluctuations in a system (Southward, 1980; Underwood, 1991, 1992, 1994; Southward *et al.*, 1995, 2005; Hawkins *et al.*, 2003; Mieszkowska *et al.*, 2006b; Hughes and Heap, 2009; Poloczanska *et al.*, 2011; Wethey *et al.*, 2011). Long-term data sets provide a baseline against which we can compare changes; however the robustness of the data depends on the quality and frequency of the sampling (Schiel, 2011).

Climate is an important factor in the distribution of biodiversity (Parmesan and Yohe, 2003). Long-term data sets are particularly valuable in placing these recent changes into context, since current abundances and biogeographic distributions of species can be compared to those of previous periods (e.g. Southward and Crisp, 1954b, 1956; Southward, 1963, 1967, 1991; Hawkins *et al.*, 2008, 2009; Poloczanska *et al.*, 2008). Several scientific long-term studies have been developed, focusing on climate change and marine ecosystems, contributing to an increased knowledge and understanding of the current and future potential impacts of climate change on the marine environment (Heip *et al.*, 2011). The majority of the long-term studies on climate change and marine ecosystems have focussed on the North-East Atlantic (see Table 1.1), benefiting from historical data stretching back many decades (e.g. Southward *et al.*, 2005).

Table 1.1. Summary of selected long-term studies on marine ecosystems (CPR: Continuous Plankton Recorder).

Topic	Location	e.g. Publications
Hydrography and Plankton	North Sea	CPR: Radach *et al.*, 1990; Edwards and Richardson, 2004; Greve *et al.*, 2004; Wiltshire *et al.*, 2008, 2010
	Irish Sea	Allen *et al.*, 1998
	Western English Channel	Southward, 1963, 1980; Russell *et al.,* 1971; Maddock *et al.*, 1981, 1989; Southward *et al.*, 1995, 2005; Hawkins *et al.*, 2003
	North-East Atlantic	CPR: Edwards *et al.*, 2001; Beaugrand and Reid, 2003; Hays *et al.*, 2005; McGinty *et al.*, 2011
	North Atlantic Ocean	CPR: Beaugrand and Ibañez, 2004; Beaugrand, 2005; McQuatters-Gollop *et al.*, 2015
Fish and Nekton	Irish Sea	Geffen *et al.*, 2011
	Bristol Channel (Britain)	Genner *et al.*, 2004; Henderson and Seaby, 2005; Henderson, 2007; Henderson *et al.*, 2011
	English Channel (Thames estuary)	Attrill and Power, 2002; Power and Attrill, 2002
	Western English Channel	Southward, 1963, 1980; Russell, 1973; Southward and Boalch, 1986; Southward *et al.*, 1988, 1995; Genner *et al.*, 2004, 2010
	North-East Atlantic	Brander *et al.*, 2003; Beare *et al.*, 2004; Perry *et al.*, 2005; Cheung *et al.*, 2011; Simpson *et al.*, 2011
	South America	Alheit and Niquen, 2004
	Atlantic Ocean	Sims *et al.*, 2001
	Global scale	Cheung *et al.*, 2009, 2010, 2013
Benthos	Irish Sea	Pennington *et al.*, 1998; Hill *et al.*, 1999; Bradshaw *et al.*, 2002
	North Sea	Frid, 2011; Clare *et al.*, 2015
	Western English Channel	Holme, 1961, 1983, 1984; Hinz *et al.*, 2009; Capasso *et al.*, 2010
	Britain and Ireland	Hiscock *et al.*, 2004
Intertidal organisms	Western English Channel	Southward, 1991; Southward *et al.*, 1995, 2005; Hawkins *et al.*, 2003, 2008, 2009; Mieszkowska *et al.*, 2014a
	British Isles	Mieszkowska *et al.*, 2006a, 2006b, 2007
	North-East Atlantic	Lima *et al.*, 2006, 2007; Wethey *et al.*, 2011
	North-West Atlantic	Merzouk and Johnson, 2011
	West Coast North America	Barry *et al.*, 1995; Sagarin *et al.*, 1999; Helmuth *et al.*, 2006a; Menge *et al.*, 2011
	East Coast North America	Bertness *et al.*, 1999

Most of the studies related to climate research in marine environments concentrate on temperature and on work conducted at the level of individual organisms (Harley *et al.*, 2006; Helmuth *et al.*, 2006b). One of the most comprehensive long-term data sets with regard to species distributions over time has been collected in the Western English Channel (Southward, 1963, 1980; Russell, 1973; Southward *et al.*, 1995, 2005; Hawkins *et al.*, 2003, 2008, 2009). Despite the rich legacy of monitoring responses of species to climate fluctuations in the North-East Atlantic, there are still several other regions that have not been so intensively studied and those need further work (Hawkins *et al.*, 2008). Through analyses of long-term datasets collected in the Western English Channel, there is strong evidence that climate driven fluctuations and more recent directional changes (e.g. increasing temperature) have taken place. These interact with regional anthropogenic impacts such as fishing (Araújo *et al.*, 2006; Genner *et al.*, 2010) to have major impacts on the ecosystem (Russell, 1973; Southward, 1980; Southward *et al.*, 1995, 2005; Hawkins *et al.*, 2003). Helmuth *et al.* (2006b), state that the results of long-term monitoring have shown that the changes can be rapid and are evident across a wide range of marine taxa, causing major shifts in biogeographic distributions, which are occurring on a sub decadal scale. According to IPCC (2007, 2013), changes may be more rapid in the future. In order to understand the influences of climate on community structure, dynamics and ecosystem functioning, routine monitoring of species abundances, range and assemblage composition is essential. Changes in spatial and temporal patterns have already been described; however less work has been done on the consequences for community and ecosystem processes (but see Leonard, 2000; Moore *et al.*, 2007a; Hawkins *et al.*, 2008, 2009; Poloczanska *et al.*, 2008).

Through the analysis of long-term data sets and the physiological responses of organisms to relevant environmental variables, and consequently the indirect impacts of these responses on species interactions, we can predict effects on natural assemblages given various scenarios of global climate change (Helmuth *et al.*, 2006b). Southward *et al.* (1995) stated that in order to refine predictive models (e.g. Poloczanska *et al.*, 2008) we need continued monitoring of representative or key species at a number of sites, enabling us to detect biological changes and assess the degree of stability of the ecosystem. Such work is now underway (Mieszkowska *et al.*, 2006a, 2006b) to predict future distributions of several organisms; bioclimatic envelope approaches have been used. These approaches estimate the distribution patterns of species through the environmental variables, mapping suitable climate (niche) space (Pearson and Dawson, 2003; Helmuth *et al.*, 2006a), neglecting the effects of species interactions and dispersal capabilities (Davis *et al.*, 1998), which will result in inaccurate model predictions (Hawkins *et al.*, 2008). These models can also be used to predict the potential movement of invasive species, which can also be a consequence of climate change (Stachowicz *et al.*, 1999, 2002; Hijmans and Graham, 2006; Hellmann *et al.*, 2008; Jeschke and Strayer, 2008; Sorte *et al.*, 2010). According to Poloczanska *et al.* (2008), predicting the future distribution of species, requires extrapolation beyond the present range of observations, and therefore requires the application of basic, mechanistic ecological principles to new situations.

In order to adapt to climate change, future research and monitoring have to be closely connected to flexible, responsive and adaptive management systems. To accomplish this, the designs of monitoring strategies have to be able to detect critical changes in species composition and ecosystems functioning (Heip *et al.*, 2011). Overall, broad-scale and long-term observations are vital for an accurate knowledge of the state of our seas and coasts (Hawkins *et al.*, 2008, 2009), and since change is unavoidable, it is crucial to incorporate current patterns and future forecasts into marine conservation and management plans (Mieszkowska *et al.*, 2006a; Firth and Hawkins, 2011; Hawkins *et al.*, 2013b).

1.5. RESPONSES OF NEARSHORE AND COASTAL ECOSYSTEMS TO CLIMATE CHANGE AND OTHER IMPACTS

Globally, changes are occurring in the biogeochemistry and ecology of the oceans, especially in response to increasing temperatures (Parmesan and Yohe, 2003; Helmuth *et al.*, 2006b; Burrows *et al.*, 2011; Poloczanska *et al.*, 2014) and reducing pH (Caldeira and Wickett, 2003; Cheung *et al.*, 2011). As a result, changes will occur in the physiology (see Helmuth and Hofmann, 2001; Helmuth *et al.*, 2002, 2010; Somero, 2002; Ferreira *et al.*, 2014), phenology (see Edwards and Richardson, 2004; Sims *et al.*, 2004; Hays *et al.*, 2005; Parmesan, 2006; Giménez, 2011; McGinty *et al.*, 2011; Moore *et al.*, 2011; Poloczanska *et al.*, 2014), and species distribution and assemblage composition (see Southward *et al.*, 1995; Sagarin *et al.*, 1999; Perry *et al.*, 2005; Lima *et al.*, 2007; Hiddink and ter Hofstede, 2008; Hiddink *et al.*, 2015). Ecological responses to climate change depend on the interactions between the abiotic environment, organism-level processes, population dynamics and community structure (Harley *et al.*, 2006). At the organism-level, the direct effects of climate change will have impacts on the performance of individuals at several stages of life history (Moore *et al.*, 2011), through changes in physiology (Dahlhoff *et al.*, 2002), morphology and behaviour (Sanford, 2002). Climate change will have effects on the transport processes that impact dispersal and recruitment influencing population dynamics (Menge *et al.*, 2011). Community-level effects will occur due to changes in interactions between species (e.g. facilitation, Moore *et al.*, 2007b; predation, Sanford, 2002; competition, Southward and Crisp, 1954b and Poloczanska *et al.*, 2008) and include climate-driven variations in both the abundance and the per capita interaction strength of these species (Harley *et al.*, 2006). The combination of these responses will have outcomes via emergent ecological responses, encompassing changes in species distribution, biodiversity, productivity, population genetics and microevolution (Harley *et al.*, 2006; Hawkins *et al.*, 2008, 2009) (Figure 1.2).

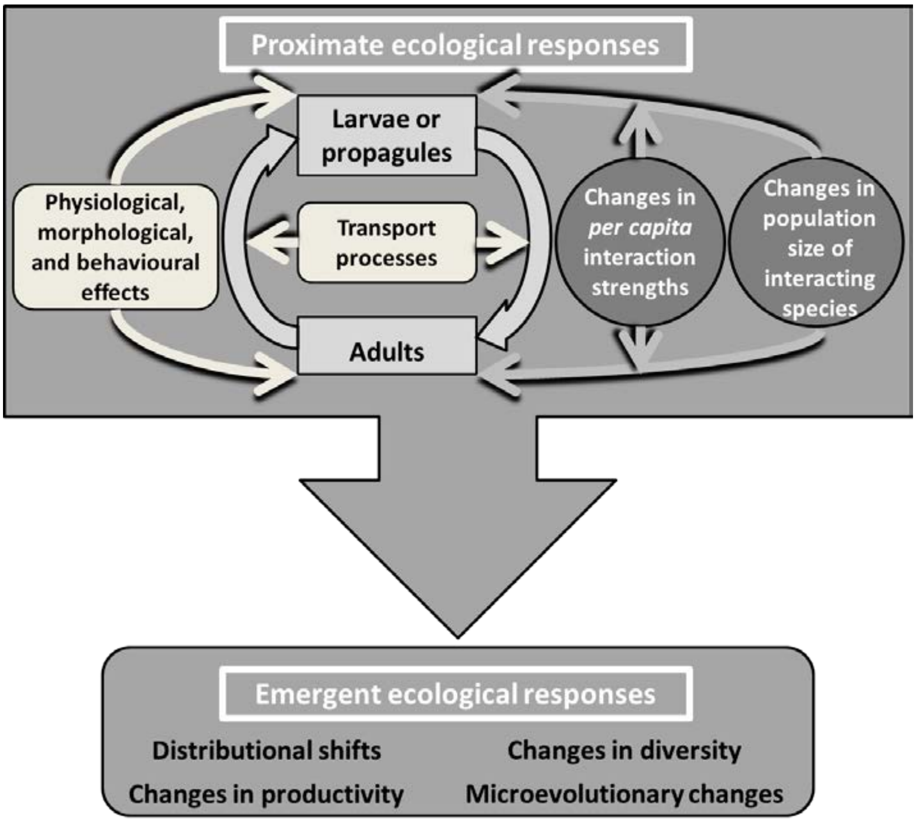


Figure 1.2. Potential ecological responses to climate change (light grey boxes - life cycle of a generic marine species; yellow boxes - direct effects of climate change at the individual level and population level; dark grey circles - community level responses) (adapted from Harley *et al.*, 2006).

Climate change affects all levels of biological organization, from the molecular to the ecosystem. One of the most significant impacts of global climate change on biological processes is through variation in organism body temperature (Helmuth *et al.*, 2011). Temperature change is a significant direct driver of change in marine organisms, as it has a strong control over all metabolic and physiological processes (Heip *et al.*, 2011; Helmuth *et al.*, 2011). Temperature variations can affect development rates of organisms at all life stages (Helmuth *et al.*, 2006b), as well as having significant consequences for biochemical processes, cell biology, physiology and the performance of organisms (e.g. growth and reproduction, Giménez, 2011). The influence of other factors such as disturbance due to storms may be stage-dependent (Giménez, 2011; Heip *et al.*, 2011). Extreme temperatures will cause stress and ultimately mortality (Denny *et al.*, 2011; Firth *et al.*, 2011; Seabra *et al.*, 2011; Sorte *et al.*, 2011; Wethey *et al.*, 2011), but other factors such as rainfall will have an influence on the survival of organisms (Morritt *et al.*, 2007; Firth and Williams, 2009).

At the population-level, responses to climate change, especially at biogeographic boundaries, are driven by reproductive output and recruitment success leading to range extensions and retractions (Hutchins, 1947; Mieszkowska *et al.*, 2007; Menge *et al.*, 2011; Wethey *et al.*, 2011). Changes in phenological events (e.g. reproductive timing, migrations, and seasonal peaks of abundance) as response to climate change have also been detected (Sims *et al.*, 2001, 2004; Edwards and Richardson, 2004; Genner *et al.*, 2004, 2010; Greve *et al.*, 2004; Moore *et al.*, 2011). These changes can induce a trophic mismatch (differential shifts in the timing of events in resources and consumers), leading to negative consequences for consumers at the population level (Beaugrand *et al.*, 2002b; Edwards and Richardson, 2004; Giménez, 2011). Population-level responses are fairly easy to identify and measure; in contrast, community-level responses are often subtle and changed by both direct and indirect effects (Harley *et al.*, 2006; Hawkins *et al.*, 2008; Poloczanska *et al.*, 2008; Kordas *et al.*, 2011), with consequences for ecosystem functioning (Harley *et al.*, 2006; Hawkins *et al.*, 2008, 2009; Johnson *et al.*, 2011).

Clarke *et al.* (2007) stated that when the extent of environmental variability is minor, many organisms can adjust physiologically; however, when a population experiences environmental variability out of the normal range, they may respond in three ways:

(i) Migration - the species shifts to a more favourable area;
(ii) Adaptation - the species evolves to shift the phenotypic reaction norm to match the new environment;
(iii) Extinction - the species fails to adapt or migrate, and becomes extinct (Clarke, 1996).

The latter will be initially at a local scale, but ultimately such local extinctions could scale up to global extinctions, especially where species have nowhere to go (e.g. Polar Seas, Cheung *et al.*, 2009; Northern Adriatic, Ben Rais Lasram *et al.*, 2010; and Mediterranean Sea, Lejeusne *et al.*, 2009). Biological communities react to climate change through changes in the abundance and phenology (Moore *et al.*, 2007b; Poloczanska *et al.*, 2014) of the organisms and through poleward shifts in distribution (Southward *et al.*, 1995; Parmesan, 1996; Sagarin *et al.*, 1999; Walther *et al.*, 2002; Hawkins *et al.*, 2003; Parmesan and Yohe, 2003; Helmuth *et al.*, 2006b; Lima *et al.*, 2006; Mieszkowska *et al.*, 2006b; Hiddink and ter Hofstede, 2008; Sexton *et al.*, 2009; Wethey *et al.*, 2011). The structure and functioning of communities can be greatly affected by the changes in distribution and associated species interactions (Hawkins *et al.*, 2009; Burrows *et al.*, 2011; Firth *et al.*, 2011; Poloczanska *et al.*, 2014).

Several studies have documented shifts in distribution patterns for a number of marine species and communities, such as plankton (Southward *et al.*, 1995; Beaugrand *et al.*, 2002a; Beaugrand and Reid, 2003; Beaugrand and Ibañez, 2004; Edwards and Richardson, 2004; Beaugrand, 2005; Hays *et al.*, 2005), fish (Southward *et al.*, 1995; Brander *et al.*, 2003; Hawkins *et al.*, 2003; Genner *et al.*, 2004, 2010; Perry *et al.*, 2005; Dulvy *et al.*, 2006; Cheung *et al.*, 2009; Drinkwater *et al.*, 2010; Pereira *et al.*, 2010; Simpson *et al.*, 2011), and subtidal benthic invertebrates (Ling *et al.*, 2008, 2009). Beaugrand *et al.* (2002a), through data collected monthly by the Continuous Plankton Recorder (CPR) survey over the North Atlantic and the North Sea from 1958-1997, were able to detect changes in copepod assemblages. The mean number of species per assemblage was used as an indicator of change in the biogeographical range of copepod communities (Beaugrand, 2005). Biogeographical shifts in all copepod assemblages were identified, with northward extensions of more than 10° in latitude of warm-water species (southern species), while cold-water species (northern species) showed a decrease in the numbers detected. These changes were attributed to a regional increase in sea surface temperature. Perry *et al.* (2005) studied exploited and non-exploited demersal fish assemblages in the North Sea in relation to recent increases in sea temperature over 25 years (1977-2001). Survey data were used to determine the abundance (over a range of latitudes and depths) for 36 species. Among the species studied, 15 showed a latitudinal shift; 13 of these were northwards and 2 southwards; these shifts ranged from 48 to 403 km. Most of the species that shifted in latitude also moved into deeper waters. The authors concluded that 21 out of 36 studied species showed distributional responses to the increase in sea temperature. In this study, however, they did not consider other factors such as phenological changes that could lead to trophic mismatches (e.g. Beaugrand *et al.*, 2002b; Edwards and Richardson, 2004; Beaugrand, 2005).

In marine coastal ecosystems, due to global warming, ecological responses are observed through the poleward shifts in the geographic range of species (Herbert *et al.*, 2003, 2007; Zacherl *et al.*, 2003; Rivadeneira and Fernández, 2005; Lima *et al.*, 2006, 2007; Mieszkowska *et al.*, 2006a, 2007; Jones *et al.*, 2009; Müller *et al.*, 2009; Johnson *et al.*, 2011; Merzouk and Johnson, 2011; Pinsky *et al.*, 2013) and also through changes in the composition of nearshore benthic communities (Barry *et al.*, 1995; Southward *et al.*, 1995, 2005; Mathieson *et al.*, 1998; Bertness *et al.*, 1999; Sagarin *et al.*, 1999; Hiscock *et al.*, 2004; Simkanin *et al.*, 2005; Harley *et al.*, 2006; Helmuth *et al.*, 2006b; Kirihara *et al.*, 2006; Hawkins *et al.*, 2008, 2009; Ling *et al.*, 2009; Poloczanska *et al.*, 2014). In the Northern Hemisphere it is expected that the southern limit of the range of cold-adapted species will move polewards, as well as the northern limit of warm-adapted species (Parmesan and Yohe, 2003). According to Helmuth *et al.* (2006b) in general cold-water species are decreasing in abundance and withdrawing poleward, while warm-water species are increasing in abundance and moving northward, in some cases by as much as 50 km per decade. Kordas *et al.* (2011) stated that some species ranges are shifting rapidly (e.g. Beaugrand *et al.*, 2002b; Hays *et al.*, 2005; Chen *et al.*, 2011), while others are shifting gradually (e.g. Sorte *et al.*, 2010; Pinsky *et al.*, 2013; Poloczanska *et al.*, 2013), and others are either not shifting at all (e.g. Herbert *et al.*, 2007) or are moving in the opposite direction (e.g. Perry *et al.*, 2005; Lima *et al.*, 2007). These reductions and extensions of the geographic ranges of species leads to a loss of species from communities, but on the other hand leads to the introduction of new species to established communities (Mieszkowska *et al.*, 2006a). Schneider (1993) stated that southern species will outperform northern species at the same location. Recent work challenges this assumption, especially in the intertidal zone where northern species often perform better and are more competitive than southern species (Connell, 1961b; Boaventura *et al.*, 2002a, 2003; Moore *et al.*, 2007b; Poloczanska *et al.*, 2008; Hawkins *et al.*, 2009).

Mieszkowska *et al.* (2006a, 2006b, 2007), through the MarClim project (a 4 year multi-partner project), investigated the effects of climatic warming on marine biodiversity using well-studied rocky shore species as indicators. The project used long-term series data (in some cases back to the 1950s) and contemporary data collected during the project (2001-2005). They were able to provide strong evidence that recent climate change has affected the abundance, population structure and biogeographic ranges of several intertidal indicator species (Hawkins *et al.*, 2003, 2008, 2009; Southward *et al.*, 2005). Examples included: northwards shift of northern limits of several southern species and small retractions of some northern species at the southern distributional limit (Southward, 1991; Mieszkowska *et al.*, 2006a); and increase in the abundance of southern trochid snails (Mieszkowska *et al.*, 2007). Changes in the annual reproductive cycles of the southern trochids and also increased survival of newly settled recruits were also seen (Mieszkowska *et al.*, 2007). Changes have also been observed in the annual reproductive cycles of limpets. The southern species *Patella depressa* (Pennant 1777) is starting to reproduce earlier and the reproductive season is lasting longer, while the northern species *Patella vulgata* (Linnaeus 1758), in some years, is not reaching the gonad development stages at which spawning can occur, leading to reproductive failure (Moore *et al.*, 2011).

1.5.1. Responses of rocky shore organisms

While most evidence of recent shifts in organism distribution has been obtained using intertidal organisms, similar changes in distribution of subtidal species should also be expected (Merzouk and Johnson, 2011; Wernberg *et al.*, 2013).

Rocky shores are distributed worldwide, typically being open systems with abrupt environmental gradients, which support different communities of animals and plants (Thompson *et al.*, 2002). According to Hawkins *et al.* (2008), these ecosystems are relatively simple which makes them an excellent model system for testing and understanding the consequences of climate change in marine communities and ecosystems. Due to these characteristics, these ecosystems are one of the most thoroughly experimentally studied (Connell, 1972; Paine, 1994), providing good baseline information to quantify the ecological effects of climate change (Helmuth *et al.*, 2006b).

Organisms present in rocky intertidal habitats experience steep environmental gradients, on the tidal elevation gradient between fully marine and fully terrestrial conditions and the horizontal gradient between wave exposed and wave sheltered conditions (Raffaelli and Hawkins, 1996). These conditions make rocky shore organisms and assemblages good indicators of the effects of climate change on natural ecosystems (Barry *et al.*, 1995; Southward *et al.*, 1995; Sagarin *et al.*, 1999; Helmuth, 2002; Thompson *et al.*, 2002, 2004; Hawkins *et al.*, 2003; Harley *et al.*, 2006; Helmuth *et al.*, 2006b; Mieszkowska *et al.*, 2006a; Denny *et al.*, 2011), since intertidal seaweeds and animals should be sensitive to direct and indirect effects of environmental temperature change (Sanford, 2002; Somero, 2002; Helmuth *et al.*, 2006a, 2011; Poloczanska *et al.*, 2008; Denny *et al.*, 2011; Lockwood and Somero, 2011). Somero (2002) stated that, at low tide, the body temperature of intertidal invertebrates and algae is a crucial determinant of organism survival and performance. Since, these intertidal organisms are influenced by marine and terrestrial environmental conditions; they often experience temperatures near their thermal tolerance limits (Somero, 2002).

The use of rocky shore organisms as sentinel species in the detection of changes is less expensive than the use of other marine systems that are less accessible and more expensive to survey (Lewis, 1986; Southward *et al.*, 1995, 2005; Hawkins *et al.*, 2008). According to several authors (Lewis, 1996, 1999; Sagarin and Gaines, 2002; Hiscock *et al.*, 2004; Helmuth *et al.*, 2006b; Lima *et al.*, 2006) sedentary rocky shore species are the best candidates to monitor climate change, since they are visible, simple to identify and move slowly. Several studies have used intertidal systems to record rapid changes in the abundance and distribution of intertidal species linked to changes in climate (see reviews in Southward *et al.*, 1995; Helmuth *et al.*, 2006b; Hawkins *et al.*, 2009).

However, most of the best-documented climate-related changes in rocky intertidal organisms studies are focussed in Europe and in North America (e.g. Barry *et al.*, 1995; Sagarin *et al.*, 1999; Herbert *et al.*, 2003; Zacherl *et al.*, 2003; Simkanin *et al.*, 2005; Mieszkowska *et al.*, 2006a; Lima *et al.*, 2007), with far fewer studies in the Southern Hemisphere (e.g. Rivadeneira and Fernández, 2005; Smale *et al.*, 2007b; Smale, 2008; Smale and Barnes, 2008; Poloczanska *et al.,* 2011; Wernberg *et al.*, 2013).

Of all the environmental stressors during emersion (e.g. temperature, desiccation, solar radiation) that affect intertidal organisms, temperature has been one of the most studied and has been identified as one of the most important factors that affect the physiology, ecology and biogeography of intertidal organisms (Southward, 1958; Porter and Gates, 1969; Southward *et al.*, 1995; Helmuth, 1998; Sagarin *et al.*, 1999; Dahlhoff *et al.*, 2001; Helmuth, 2002, 2006b, 2011; Somero, 2002; Wethey, 2002; Lima *et al.*, 2007; Wethey and Woodin, 2008; Yamane and Gilman, 2009; Berke *et al.*, 2010; Fuller *et al.*, 2010; Hofmann and Todgham, 2010; Lockwood and Somero, 2011; Seabra *et al.*, 2011; Sorte *et al.*, 2011). While exposed to the air, several invertebrate species are subjected to daily fluctuations in body temperatures, which can exceed 20°C (Helmuth and Hofmann, 2001; Helmuth, 2002; Helmuth *et al.*, 2010). The heat flux on an organism is determined by several climatic factors (e.g. air temperature, surface temperature, solar radiation, cloud cover, wind speed, relative humidity, and fog). It is also affected by characteristics of the organism, such as size, colour, shape, behaviour, and material properties (Porter and Gates, 1969; Gates, 1980; Helmuth, 1998; Gilman *et al.*, 2006). Evidence at a physiological level suggests that in addition to the magnitude of extreme temperatures determining the survival of the organism, factors such as duration and frequency of these events are also important (Buckley *et al.*, 2001; Halpin *et al.*, 2004; Wright *et al.*, 2004; Helmuth *et al.*, 2006a). During aerial exposure the body temperature of an intertidal organism is also influenced by factors such as absolute tidal height of the organism on the shore, the wave splash that it receives and the local tidal cycle. The interaction of these factors determines the time and duration of exposure to terrestrial conditions that the organism is subjected to during low tide. In addition, factors such as substratum angle and topographic complexity including shading are also important since they determine the amount of solar radiation received by the organism, which will modify the degree of desiccation or exposure (Helmuth and Hofmann, 2001; Helmuth *et al.*, 2006a; Seabra *et al.*, 2011). According to Bertness and Leonard (1997) and Bertness *et al.* (1999), local environmental conditions can also be modified by the biota, for example, some species are sheltered by beds of seaweeds (Peterson, 1982; Moore *et al.*, 2007a) and mussels (Witman, 1987). So, the precise environmental characteristics of one place on the shore are also dependent of these microhabitat features (Hawkins and Jones, 1992; Johnson *et al.*, 2003; Seabra *et al.*, 2011), whether topographically or biologically generated.

To date most studies focusing on the effects of climate change have looked at the impacts of increased temperature, usually considered in isolation. Much less is known about the influence of factors other than temperature or interactive effects. Moreover, much experimental work has focused on the response of a single species to change in environmental conditions. Evidence suggests that some species will be negatively affected whilst others may thrive under new environmental conditions (Mieszkowska *et al.*, 2007). Given the importance of biological interactions in driving community structure, it is not known how predictions made at the species-level can be scaled up to the ecosystem-level. A more holistic approach, considering the community or ecosystem as the response variables and the impacts of several environmental factors together, is necessary if we are to accurately predict future changes in the structure and functioning of ecosystems (Helmuth *et al.*, 2006b).

Beyond the effects of climate change, due to other human activities, coastal ecosystems have also been impacted at regional (e.g. eutrophication) and local (e.g. habitat loss - due to land reclamation and coastal development) scale processes. Several studies have focused on the impacts of anthropogenic habitat modification, such as coastal defence structures, on intertidal communities, assessing that these structures can have a major influence over the abundance and distribution of the species and in the overall community structure (Airoldi *et al.*, 2005, 2008; Martin *et al.*, 2005; Moschella *et al.*, 2005; Martins *et al.*, 2009; Firth *et al.*, 2014; Yesson *et al.*, 2015).

Evidence that the overexploitation of intertidal living resources, mainly for human consumption, also have a major effect at the community structure, have been provided by several studies (Martins *et al.*, 1987b; Griffiths and Branch, 1997; Castilla, 1999; Crowe *et al.*, 2000; deBoer and Prins, 2002; Roy *et al.*, 2003; Guidetti and Sala, 2007; Fenberg and Roy, 2008; Martins *et al.*, 2008a, 2009, 2010, 2011; Griffiths *et al.*, 2010; Jimenez *et al.*, 2011; Sala *et al.*, 2012).

1.6. FACTORS AFFECTING THE DISTRIBUTION AND ABUNDANCE OF ROCKY INTERTIDAL ORGANISMS

1.6.1. Environmental gradients

Patterns of distribution and abundance of species result from responses to the physical environment and the outcomes of biological rocky shore interactions (Connell, 1972; Lewis, 1972; Stephenson and Stephenson, 1972; Raffaelli and Hawkins, 1996; Jonsson *et al.*, 2006; Little *et al.*, 2010). Changes in the environmental regime will impact both directly (Holmes *et al.*, 2005; Harley *et al.*, 2006) and indirectly by modifying biological interactions (Hawkins *et al.*, 2008, 2009; Poloczanska *et al.*, 2008) and patterns of species distribution. Such changes are likely to have important consequences for the structure and functioning of ecosystems (Southward *et al.*, 1995; Helmuth *et al.*, 2006b; Hawkins *et al.*, 2008, 2009).

Distribution and abundance of intertidal organisms is affected locally by four major physical environmental gradients (reviewed in Raffaelli and Hawkins (1996): the vertical gradient (air-sea interface see Colman, 1933; Southward, 1958; Connell, 1972), the horizontal gradient (wave action see Lewis, 1964; Connell, 1972), the particle size gradient (from deposing sedimentary shores to rocky shores) and the salinity gradient (transition from seawater-freshwater)). Superimposed on these gradients are mosaics of microhabitats influenced by the topographic template as a consequence of the geology of the shore (Connell, 1972; Raffaelli and Hawkins, 1996; Johnson *et al.*, 2003; Sugden *et al.*, 2009).

1.6.2. Vertical patterns

The sea shore represents a unidirectional vertical stress gradient for most marine organisms, along the intertidal or vertical gradient. This gradient extends from the low water mark to the splash zone, which is the maximum limit of seawater influence on the shore (Lewis, 1964; Raffaelli and Hawkins, 1996). Species are vertically distributed along the shore determined by tolerance to physical factors (e.g. desiccation and temperature see Dayton, 1971; Connell, 1972; Williams, 1994; Williams and Morritt, 1995) and variation in responses to biological processes, such as competition (Connell, 1961a; Dayton, 1971; Menge, 1976; Lubchenco and Menge, 1978; Johnson *et al.*, 1998a) and predation (Connell, 1961a; Paine, 1966, 1969, 1976; Dayton, 1971; Menge, 1976; Castilla and Paine, 1987). According to Connell (1972) the upper limit of species distribution is generally determined by physical factors (e.g. Southward, 1958; Connell, 1961b; Lewis, 1964; Frank, 1965; Foster, 1971; Schonbeck and Norton, 1978, 1980; Hawkins and Hartnoll, 1985), such as increased desiccation, higher temperatures or stronger solar radiation; while the lower limits of the species seem to be set by biological interactions with competitors (e.g. Menge, 1976; Lubchenco and Menge, 1978) or predators (e.g. Paine, 1966; Dayton, 1971). Biologically generated habitat structure and complexity (Johnson *et al.*, 2003), biological productivity, species diversity (Hawkins and Hartnoll, 1980) and the intensity of biological interactions (Janke, 1990) all increase towards the low shore (Raffaelli and Hawkins, 1996).

On the upper reaches of the shore, marine organisms experience increasingly longer periods of emersion while the relative humidity can vary considerably (Branch, 1981). In temperate and tropical areas the most dominant stress is desiccation, due to the combined effects of heat and low relative humidity (Moore, 1972; Williams, 1994; Williams and Morritt, 1995; Raffaelli and Hawkins, 1996). Precipitation and evaporation can affect the salinity and water on the surface (e.g. rocky pools or rock surface see Morris and Taylor, 1983; Huggett and Griffiths, 1986; Little *et al.*, 1990), which can cause osmotic problems for species (Segal and Dehnel, 1962; Wolcott, 1973; Branch and Cherry, 1985; Hawkins and Jones, 1992). At higher shore levels the time available for respiration and feeding also decreases, since many intertidal animals are more efficient when the tide is in (Branch, 1981; Hawkins and Hartnoll, 1983b; Little, 1989; Hawkins and Jones, 1992). Organisms at high shore levels survive long periods without being submerged in sea water, due to their morphology (Moore, 1934; Segal, 1956a; Vermeij, 1973; Lowell, 1984), physiology (Segal, 1956b; Davies, 1969; Wolcott, 1973) and behaviour (Frank, 1965; Branch, 1975; Creese, 1980), while low shore species are completely marine and can cope only with brief periods of emersion (Little, 1989; Raffaelli and Hawkins, 1996).

Since Connell (1972), various studies have shown that the upper limit of mid and low shore species also can be set directly by biological factors such as competition (Hawkins and Hartnoll, 1985; Jenkins *et al.*, 1999b; Jenkins and Hawkins, 2003) and grazing (Southward and Southward, 1978; Underwood and Jernakoff, 1984; Boaventura *et al.*, 2002a). On the high shore upper limits still seem generally set by physical factors (Hawkins and Hartnoll, 1985).

1.6.3. Horizontal patterns

The horizontal gradient of exposure to wave action, from sheltered bays out to exposed cliffs is determined by fetch (Thomas, 1986; Burrows *et al.*, 2008). When the fetch is sufficiently large, such as in the Azores, shores will experience heavy wave action (Raffaelli and Hawkins, 1996), which has a profound effect on the biological characteristics of a shore. Along this exposure gradient stress is not unidirectional (Raffaelli and Hawkins, 1996) since for some species, such as suspension feeders or sessile predators, exposed conditions provide benefits, such as transportation of food and dispersal of reproductive material (Lewis, 1968). For other species, however, these conditions prevent attachment to the shore, dislodgement or inhibit foraging (Dayton, 1971; Lubchenco and Menge, 1978; Hawkins and Jones, 1992; Jonsson *et al.*, 2006). Foraging should be dependent on the searching costs required to find prey, the metabolic costs of handling the prey and the risks associated with its search and handling (Mangel and Clark, 1986). Burrows and Hughes (1989) stated that these costs are variable according with the physical conditions of the environment and with different microhabitats. Nonetheless, low water movement may also be problematic, leading to situations of restricted oxygen supply for both plants and animals and resulting in a lack of dissolved nutrients for seaweeds and food for filter feeders. According to Airoldi and Hawkins (2007) silt deposition can also be a problem for the grazing activity of limpets. Therefore the widespread assumption that exposed shores are more stressful is not always true (Raffaelli and Hawkins, 1996). The composition of shore communities will be influenced by disturbance due to wave action, as organisms are removed from the surface, creating free space ready for recolonization (Connell, 1961a, 1972; Raffaelli and Hawkins, 1996; Little *et al.*, 2010) and biological interactions such as grazing (Hawkins and Hartnoll, 1983b; Jenkins *et al.*, 2005; Coleman *et al.*, 2006; Jonsson *et al.*, 2006). This is of extreme importance because on sheltered shores, the available free space is limited, and the current occupants can live for long periods; this maintains relatively constant community composition which can span decades (Ingólfsson and Hawkins, 2008). In contrast, on exposed shores growth can be fast but survival rates can be low as individuals are removed by wave action (Connell, 1961a; Jenkins *et al.*, 1999a; Jenkins and Hawkins, 2003; Ingólfsson and Hawkins, 2008; Little *et al.*, 2010). For example, the establishment of fucoid canopies on exposed shores is determined by grazing, but persistence is determined by wave action (Jonsson *et al.*, 2006).

A salinity gradient is created where the freshwater influence is significant, going from marine to completely freshwater conditions (Raffaelli and Hawkins, 1996). Variations of this gradient happen along the vertical gradient, where water is trapped in rock depressions and hollows, and where there is a film of water covering organisms attached to rocky shores, or in the interstitial water trapped by finer sediments (Raffaelli and Hawkins, 1996).

1.6.4. Biogeography

Geographic location and hence climate regime plays a role in the distribution of intertidal organisms, and can be considered an overarching but gentle fifth environmental gradient. Several studies have provided evidence of the importance of geographic location in the distribution of organisms globally (Lewis, 1972; Stephenson and Stephenson, 1972; Branch and Branch, 1981). The environmental stress at a particular location will depend on the interaction of multiple stress gradients in addition to latitude (Helmuth *et al.*, 2006b; Lima and Wethey, 2012). Since, in temperate regions stress will be less extreme on the upper levels in comparison with the low latitudes, where heat extremes occur. Similarly upper-shore organisms in temperate regions will experience less stress than at high latitudes, where freezing is common (Raffaelli and Hawkins, 1996). Disturbance due to ice scouring will also be greater at higher latitudes (Smale *et al.*, 2007a,b). Different major biogeographic groups have been identified along geographic gradients (Briggs, 1974; Lüning *et al.*, 1990), since some groups of characteristic taxa are present only within particular temperature ranges. Cold temperate and polar sublittoral species do not survive freezing and, like mid-intertidal forms, may suffer lethal damage around -20°C; tropical sublittoral species show limited tolerance below 10°C with upper lethal limits of 33-35°C; boreal and cold temperate species of the midshore survive temperatures below the freezing point of sea water (Lüning and Asmus, 1991).

1.6.5. Geology, topography and microhabitats

Factors such as the geology, topography and microhabitats also have an influence on the distribution and abundance of intertidal organisms. Small-scale variation in environmental conditions and spatial heterogeneity provides refuges from physical extremes as well as biological factors (Raffaelli and Hawkins, 1996; Johnson *et al.*, 2003). Places like cracks, crevices, gullies and pools, ultimately determined by the geology of the bed rock, create microhabitats that can provide refuges from which predators and grazers emerge to forage (Hawkins and Jones, 1992; Johnson *et al.*, 1998b, 2008).

Originally the distribution and abundance of organisms on intertidal shores was thought to be related primarily with physical factors, mainly with the vertical gradient or the degree of exposure to waves (Lewis, 1964; Stephenson and Stephenson, 1972). However, whilst being an ultimate factor, subsequent experimental work has shown that physical stresses associated with these two physical gradients do not explain all patterns of abundance for many intertidal organisms (Underwood, 1980; Chapman, 2000); biological factors are thought to be also important in directly setting distributions along these environments (for review see Connell, 1972; Raffaelli and Hawkins, 1996), although their intensity is modulated by physical factors (e.g. Hawkins and Hartnoll, 1983b).

Biological factors such as competition and predation have been shown as being important in the setting of lower limits of algae and sessile animals (Southward, 1958; Paine, 1966; Dayton, 1971; Connell, 1972; Wolcott, 1973; Menge, 1976; Lubchenco and Menge, 1978). For mobile animals, evidence is much scarcer; there is some evidence that biological factors can play an important role in determining the lower limits of distribution of mobile animals (Benedetti-Cecchi *et al.*, 1999; Perez *et al.*, 2009; Silva *et al.*, 2010). In conclusion, species are distributed or zoned along the gradients described according to their capability to cope with the changes in physical factors and response to biological interactions associated with each gradient (Raffaelli and Hawkins, 1996).

Other studies (e.g. Menge, 2000) have focused on other broad-scale processes, such as upwelling regime and currents in determining patterns of recruitment and other ecological patterns. In many cases the behaviour of settling larvae is the direct cause of distribution patterns of intertidal organisms (Jenkins, 2005). Settlement behaviour ensures that an organism will live in a region where they are likely to survive the physical environment and where the risk of biological interactions is reduced (Crisp, 1961; Hawkins and Hartnoll, 1982; Raimondi, 1990; Hawkins and Jones, 1992; Thompson *et al.*, 2000; Jenkins, 2005). Populations limited by reduced recruitment success would be expected to have irregular age structures, missing year classes or a bias towards old animals (Hutchins, 1947; Lewis *et al.*, 1982; Wethey *et al.*, 2011).

1.7. OVERALL AIMS AND RATIONALE OF THESIS

The overall aim of this thesis is to explore the responses of intertidal ecosystems to climate change and other impacts, using the Azores as a test system. The literature review (Chapter 1) has set the scene for the rest of the thesis. A brief overview of the Azores archipelago (Chapter 2) is then given, focussing on the biota of rocky shores and impacts to which they are subject, and a summary of environmental changes from publically available data and other sources.

The specific objectives of this thesis follow two themes:

> **(A)** *Descriptive studies of patterns: Evidence of long-term and broad-scale changes at the individual, population and community levels*;
>
> **(B)** *Experimental studies of processes: How might intertidal communities respond to changes in environmental conditions*?

Theme (A) examines the patterns of the communities and species providing evidence of long-term changes at various levels in response to greater stress due to changing environmental conditions, being addressed by Chapters 3 - *Reproductive phenology of limpets*, and 4 - *Evidence of long-term changes in the distribution of key intertidal species*. Theme (B) investigates the processes that influence the distribution of a key intertidal northern species via experimental manipulations, addressed in Chapter 5 - *Experimental simulation of how Azorean intertidal communities might respond to changes in environmental conditions?*

Some baseline data exist for the Azores from the 1980s mainly collected by S. J. Hawkins and Azorean colleagues from the Department of Oceanography and Fisheries (DOP-UAç) as part of wider studies on management limpet populations in particular and rocky shores in general. Chapter 3 investigates at the individual level the reproductive phenology of the two Azorean species of limpets - *Patella aspera* (Röding 1798) and *Patella candei gomesii* (D'Orbingly 1840). Differences in seasonality of reproduction were compared from unpublished records and grey literature (Martins *et al.*, 1987a,b) from the 1980s with repeat studies between 2012-2014. The spatial gradient in environmental conditions across the Azorean archipelago was also used to better understand patterns in reproductive seasonality.

Chapter 4 seeks evidence of changes in distribution and abundance at the population and community level of key intertidal species and functional groups. Transect studies made in the late 1980s were repeated. These followed up on work by Hawkins *et al.* (1990a) published in the grey literature for São Miguel. Unpublished data collected during an expedition to Faial in 1989 (Martins *et al.*, 1992) were also collected and compared to present day surveys.

Processes influencing how intertidal communities might respond to changes in environmental conditions were experimentally investigated in Chapter 5. A northern canopy forming species (*Fucus spiralis*) was experimentally manipulated to simulate the likely species loss in the future due to climate change. The potential for recovery of *F. spiralis* and consequences for the rest of the community were then investigated.

Finally, Chapter 6 synthesises and discusses my main findings including the relative importance of recent climate change and other impacts on Azorean rocky shores. Suggestions for future work were also made.

2. AZORES: STUDY AREA, ROCKY SHORES AND ENVIRONMENTAL CHANGES

In this chapter I describe the study area and summarize knowledge on Azorean rocky shores. Publically collected environmental data of relevance to the rest of the thesis are summarised and briefly discussed to show differences with time and across the Archipelago.

2.1. STUDY AREA

The Azorean archipelago has a volcanic origin with the islands being formed through an accumulation of eruptive debris over the oceanic platforms of the mid-Atlantic ridge. The nine islands range in age between the youngest, Pico at <1 million years and the oldest, Santa Maria at 8 million years (Azevedo *et al.*, 1991; Serralheiro and Madeira, 1993). The Azorean archipelago extends for more than 400 km along a NNW-SSE orientation in the Northern Atlantic (IH, 2000; Morton and Britton, 2000). The archipelago is composed of nine islands separated in three groups: Western, Central and Eastern. It is located between 37° to 40°N and 25° to 31°W (Figure 2.1), in a warm temperate region, being considered part of Macaronesia along with Madeira, the Salvage islands, the Canaries and the Cape Verde islands.

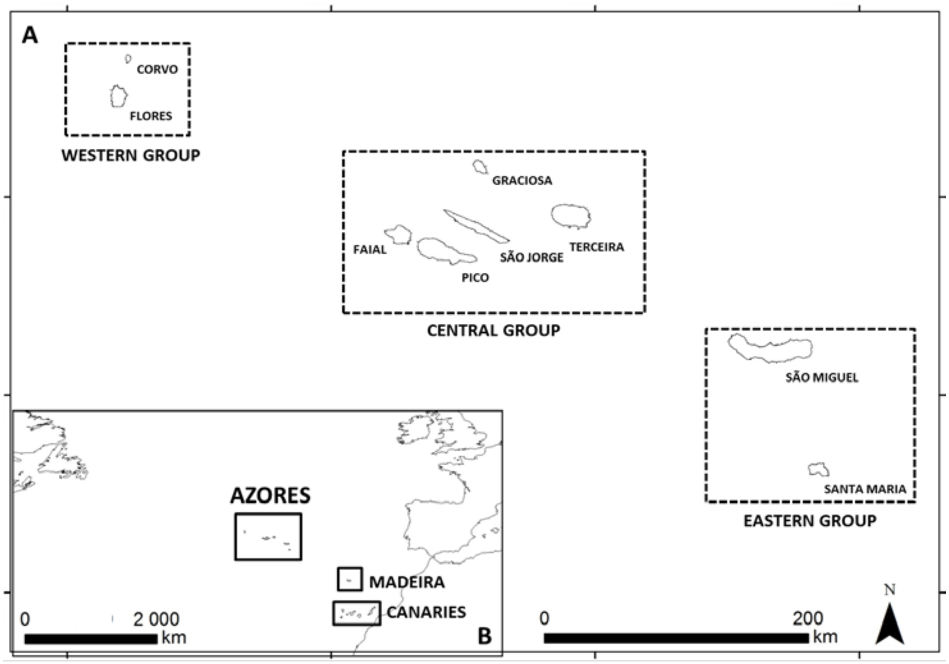


Figure 2.1. A) Azores archipelago with the location of the three groups (Western, Central and Eastern) and the nine islands; **B**) the Azores relative to Madeira and Canaries archipelagos of Macaronesia (Cape Verde Islands not shown).

Prevailing meteorological conditions are determined by the subtropical anticyclone of the Azores, giving a humid oceanic climate with low annual variation. The average annual air temperature is between 16.7-17.7°C; August is the hottest month (~23°C) and February the coldest (~15°C). Highest monthly average rainfall occurs between October-March in the Eastern and Western groups and between September-March and April in the Central group of the archipelago (IH, 2000; Santos *et al.*, 2004).

The Azores are located in an area of relatively cold water, with the sea surface temperature normally increasing from the Western to the Eastern groups. Sea surface temperatures, in the Azores, ranges between 13°C (March) and 25°C (August-September), whilst salinity varies between 35.9 and 36.5 at the surface (IH, 2000; Santos *et al.*, 2004). The tidal cycle is semi-diurnal with maximum amplitude less than 2m (Martins, 2009). The surface currents in the Azores form part of the general circulation of the North Atlantic. The current that separates from the North Atlantic main current to the South is known as the Azores Current (Klein and Siedler, 1989) (see Figure 2.2).

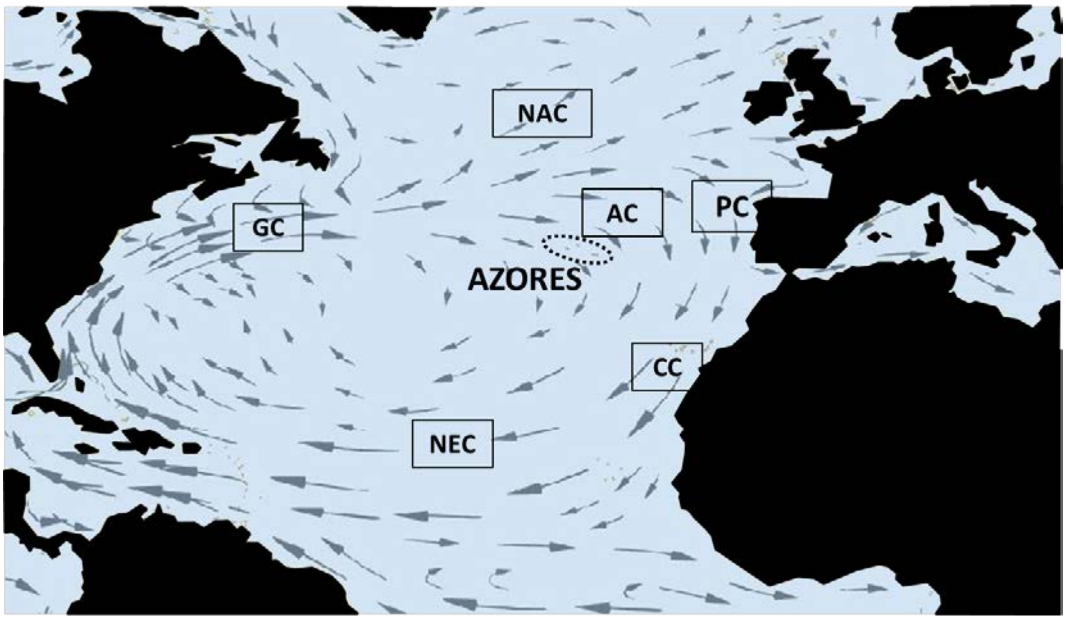


Figure 2.2. The Azores in the context of North Atlantic currents (GC - Gulf Current, NAC - North Atlantic Current, AC - Azores Current, PC - Portugal Current, CC - Canaries Current, NEC - North Equatorial Current) (adapted from Instituto Geográfico Português (IGEO)).

The Azores Current is weak, rarely reaching one knot with a South-South-Easterly predominantly direction. From December to April South-Easterly currents predominate, whilst from May to November the direction switches southwards. Local winds may significantly alter the direction and flow of the current, together with the effect of the location of the Azores anticyclone (Klein and Siedler, 1989; IH, 2000). The islands are exposed to strong winds, mostly from South-West, West and North-West in the Central and Eastern groups; while in the Western group the wind blows mainly from the North-East (Martins, 2009).

The islands are bordered by very deep waters. The coastline topography is very complex with high and steep cliffs broken with rocky beaches and occasional black volcanic sandy beaches (Morton *et al.*, 1998). The archipelago is subject to high levels of wave action with sheltered areas restricted to harbours and breached volcanic cones (“*caldeiras*”). Wave height is lowest during June-August (between 0.9 and 1.1 m) and highest between January and March reaching 2.6 m in height (IH, 2000).

2.2. AZOREAN ROCKY SHORES - BIOTA AND IMPACTS

Oceanic islands are isolated from the continent, increasing the difficulties for colonization of those systems by terrestrial and intertidal biota. The colonization of islands, by organisms, can be considered as an invasive procedure, which could and has been enhanced through anthropogenic vectors, such as shipping, aquaculture, deliberate introductions (Hawkins *et al.*, 2000). In open systems, with long-lived larvae (e.g. barnacles), local reproductive output has little influence on local recruitment, especially in dispersive environments such as isolated islands (Caley *et al.*, 1996; Jenkins, 2005).

In terms of floristic and faunistic affinities the Azores show many affinities with the rest of Macaronesia (Madeira, Canaries and Cape Verde), with these similarities between the archipelagos being sufficient to consider the Macaronesia (Azores, Madeira, Canaries and Cape Verde) as a biogeographical unit (Morton *et al.*, 1998; Hawkins *et al.*, 2000; Morton and Britton, 2000). According to Santos *et al.* (1995a) the Azores are considered a crossroads in the middle of the Atlantic, since the flora and fauna show similarities with Europe, but also with the Caribbean.

Oceanic islands, such as the Azores, consist of isolated areas of intertidal habitats typically with simpler and less resilient communities (Williamson, 1981). Their small size and isolation makes them extremely vulnerable to degradation and system disruption (Hawkins *et al.*, 1999; Henderson and Whittaker, 2003). Comparing the Azores with the rest of Macaronesia and continental shores, impoverishment or absence of certain key species and guilds is clear (Hawkins *et al.*, 2000; Morton and Britton, 2000). For example on the mid to upper shores of the Azores and Madeira, space-occupying organisms are reduced only to *Chthamalus stellatus* (Poli 1791); while on the mainland and the Canaries, mussels, stalked barnacles and other barnacle species such as *Chthamalus montagui* (Southward 1976) and *Balanus perforatus* (Bruguière 1789), are also present. In the Azores, patellid limpets are reduced to two species: *Patella aspera* and *Patella candei gomesii* (Hawkins *et al.*, 1990b; Côrte-Real *et al.*, 1992; 1996; Koufopanou *et al.*, 1999; Weber and Hawkins, 2002; Sá-Pinto *et al.*, 2005; Weber and Hawkins, 2005; Sá-Pinto *et al.*, 2008), whereas in Madeira and Canaries there are three species, and in the Mediterranean, continental coasts of Africa and Southern Europe there are at least four species (Ridgway *et al.*, 1999; Hawkins *et al.*, 2000). Mussels, kelps and seagrass beds are largely absent in the Azores, with the exception of a relict subtidal population of *Laminaria ochroleuca* (Bachelot de la Pylaie 1824) in the Formigas islets (Tittley *et al.*, 2001; Wallenstein *et al.*, 2008). Until recently intertidal trochids of the genus *Phorcus* (Donald et al., 2012) were absent from the Azores, but they have recently colonized the Eastern group (Ávila *et al.* (2015) and M. Vale *personal observation*).

In the Azores, the rocky intertidal shore can be classified into three broad vertical areas. The upper shore (splash and spray zone) is dominated by littorinids - *Tectarius striatus* (King 1832) and *Melarhaphe neritoides* (Linnaeus 1758), lichens (*Verrucaria* sp. and *Lichina* sp.), ephemeral algae (in season) and cyanobacteria (Hawkins *et al.*, 1990a, 2000; Martins, 2009). The mid shore zone is daily immersed by the tide and is dominated by filter feeding barnacles - *Chthamalus stellatus* and grazing limpets - *Patella candei gomesii* and *Patella aspera*. *Chthamalus stellatus* is the major space occupier except in sheltered conditions. The abundance of *Patella candei gomesii* generally increases with the exposure to wave-action (Hawkins *et al.*, 1990a, 2000; Martins, 2009). At this level, on moderately exposed conditions, an algal association between the turf-forming *Gelidium microdon* (Kützing 1849) and the fucoid canopy consisting of *Fucus spiralis* (probably the recently split form *Fucus giuryi* (Zardi, Nicastro, Serrão and Pearson, 2011) see Zardi *et al.*, 2011) forming scattered patches is common (Martins, 2009). During the course of my work, doubts were raised about the nomenclature of the only fucoid species present in the Azores; whether it is *Fucus giuryi* instead of *Fucus spiralis* (K. R. Nicastro and G. I. Zardi *personal communication*). Since, both fucoid species (*F. guiryi* and *F. spiralis*) show the same distribution and are considered northern species (Zardi *et al.*, 2011, 2015; Guiry and Guiry, 2015) the underlying logic of subsequent work is not affected. For the purposes of this thesis, I decided to continue to use *Fucus spiralis* to designate the fucoid species present in the Azores. In the Azores, this species has a prolonged fertile period, being reproductively active all year (Neto, 1997).

On the lower shore, the upper part is dominated by turf-forming species of algae. Other taxa such as *Patella aspera*, *Stramonita haemastoma* (Linnaeus 1766), *Halopteris scoparia* ((Linnaeus) Kützing 1843), *Cystoseira* spp., *Paracentrotus lividus* (Lamarck 1816), *Arbacia lixula* (Linnaeus 1758) and *Megabalanus azoricus* (Pilsbry 1916) are also present depending on the conditions, particularly wave exposure (Hawkins *et al.*, 1990a, 2000; Morton and Britton, 2000; Martins, 2009). Mobile species such as *Pachygrapsus marmoratus* (Fabricius 1787) freely range over the whole shore. Articulated coralline algae are the dominant taxa either side of the low water mark (Martins, 2009). According to Hawkins *et al.* (1990a), on Azorean shores the large amplitude of wave action in relation to tidal range amplifies microhabitat differences, obscuring zonation patterns.

The grazing limpet *Patella ulyssiponensis* (Gmelin 1791) which occurs on continental and its Macaronesia sister *P. aspera* (Weber and Hawkins, 2005; Sá-Pinto *et al.*, 2008), occur predominantly in the low intertidal of exposed shores, but it can also occur in the shallow subtidal (Thompson, 1979; Côrte-Real *et al.*, 1992). According to Martins *et al.* (1987b), *P. aspera* is a protandrous hermaphrodite species that reaches sexual maturity between 41-45 mm shell length, with the peak of maximum gonad development being in January and the gonad resting period in May-June. *Patella candei gomesii* is an endemic subspecies of the Azores (Côrte-Real *et al.*, 1996; Weber and Hawkins, 2002; Sá-Pinto *et al.*, 2005, 2008) which occurs predominantly in the mid and high intertidal zone (Hawkins *et al.*, 2000). According to Martins *et al.* (1987b), *P. candei gomesii* is a gonochoristic species with an early sexual maturity (16-20 mm shell length). No clear peak of spawning was determined, however, they suggest that this species spawns throughout the year and that there is no defined resting period (Martins *et al.*, 1987b). More recently, Cúrdia *et al.* (2005) were able to determine that this species shows a synchronous spawning peak at the end of summer. Menezes (1991) determined that *P. candei gomesii* reaches first sexual maturation around 10 mm in shell length. Both species are external fertilizers and their larval stage probably lasts between 1-2 weeks as in other limpets (Hawkins *et al.*, 2000; Ribeiro *et al.*, 2009).

The Azores, due to their location, isolation and unpolluted conditions are considered an excellent model for the study of recent climate changes and possible interactions with other impacts such as overexploitation of the littoral zone. The Azorean archipelago represents the southern range limit of several northern species, so recent changes, such as global warming, could be expected to have a major effect over the populations and communities present at several levels. Responses of marine species to temperature increase include both shifts in species distribution and changes in abundance, according to the thermal tolerance and adaptability of the species. So, it is expected that the southern limit of the range of cold-adapted species will move polewards, as well as the northern limit of warm-adapted species. According to Morton and Britton (2000), there is also evidence of introduced exotic marine species in the Azores, such as *Balanus eburneus* (Gould 1841) and *Littorina saxatilis* (Olivi 1792). These species have only localized distribution and are absent from the majority of the Azorean rocky shores. Also, arrival in the Azores of tropical species, with southern range limits of distribution, has been reported. This was the case of the fishes *Parablennius sanguinolentus parvicornis* (Valenciennes 1836), *Squaliolus laticaudus* (Smith and Radcliffe 1912) and *Seriola fasciata* (Bloch 1793) (Santos *et al.*, 1995b; Silva *et al.*, 1998; Machado and Barreiros, 2006), and the algae *Caulerpa webbiana* (Montagne 1837) (Cardigos et al., 2006). Chainho *et al.* (2015) registered a total number of 64 non indigenous marine species for the Azores, with 20% of these known as established species, 13% unestablished species and 21% of unknown population status. Also Martins *et al.* (2014) presented evidence of new species arriving in the archipelago. From the 190 epibiont species present in limpets shells (*P. aspera*), 17 algae were warm-water species.

According to Petit and Prudent (2008), in the Macaronesia region the recently built infrastructure to support tourism is exerting pressure on coastal areas, which added to the threats of invasive species and climate change could lead to major disruptions of ecosystems. In the Azores, the tourist industry is poorly developed, compared with other regions of Macaronesia. Even so, a big increase of coastal tourist infrastructures such as marinas has been observed over the last years (Petit and Prudent, 2008). It is predicted that the tourist industry will increase in the Azores, especially now, since low-cost flight companies recently started to operate to the Azores region.

As in several coastal areas with long established human populations, in the Azores, the harvesting of marine resources is traditional part of the culture, leading to an overexploitation of many stocks (Martins *et al.*, 1987a,b; Santos *et al.*, 1995a; Morton *et al.*, 1998; Hawkins *et al.*, 2000; Morton and Britton, 2000; Martins, 2009, 2010). The overexploitation of keystone grazers (*P. aspera* and *P. candei gomesii*) for human consumption is well known in the Azores and has led to a decline in the populations of these species in much of the archipelago (Martins *et al.*, 1987b; Santos *et al.*, 1990, 1995a; Hawkins *et al.*, 2000; Martins *et al.*, 2010). In the 1980s, a collapse in the stocks of limpets led to several investigations funded by the regional government (Martins *et al.*, 1987a,b; Santos *et al.*, 1990, 1995a, 2010), resulting in fishery regulations (e.g. D.R.R. 14/93/A Diário da República - I Série B, 178) for the collection of limpets. This regulation declared that between the periods - 1st of October to 31st of May, the collection of limpets was forbidden. For the rest of the year, the collection of limpets was allowed, outside the protected areas, but only above the established minimum sizes (*P. aspera* - 5 cm and *P. candei gomesii* - 3 cm in shell length) and to a maximum of 1 Kg per person per day. Due to the lack of enforcement of these management measures, limpet populations continue to suffer overexploitation and are still much reduced in the Azores, particularly in the Central and Eastern groups (Menezes, 1991; Ferraz, 1998; Ferraz *et al.*, 2001; Martins *et al.*, 2010; Santos *et al.*, 2010). Their reduction has a strong impact on the community structure (Martins *et al.*, 2011). Even so, very recently, the regional government of the Azores has changed the management measures (D.L.R. 31/2012/A - Portaria n. 74/2015/A, 15th June 2015). Presently, the closed season is between the 1st of October and the 30th of April; while over the rest of the year the collection of limpets is allowed, outside of the protected areas, above the established minimum sizes to a maximum of 80 Kg per day per legal license holder. These new measures are likely to have an impact on limpet populations, since the populations are already under pressure due to the overexploitation. Low population densities, especially in species that are external fertilizers will reduce the likelihood of fertilization success, since the opportunities for an encounter between the gametes are reduced (Levitan, 1991; McCarthy, 1997; Hawkins *et al.*, 2000). Also, overexploited populations tend to show an overall decrease in their average size (Siegfried *et al.*, 1994; Hawkins *et al.*, 2000; Moreno, 2001; Fenberg and Roy, 2008, 2012; Fenberg *et al.*, 2010; Jimenez *et al.*, 2011). In the case of *P. aspera*, because it is a protandrous hermaphrodite species, this will result in a lower number of females, which could increase the likelihood of recruitment failure.

2.3. ENVIRONMENTAL CHANGES

There is growing evidence that environmental changes are taking place in the North-East Atlantic (e.g. Kushnir *et al.*, 1997; Wang *et al.*, 2004; deYoung *et al.*, 2008; Burrows *et al.*, 2011; Lima and Wethey, 2012). For the Macaronesia region, it is predicted that the temperature will increase by an average of 2.1°C (range - 1.9 to 2.4°C) by the year 2099 (IPCC, 2007). According to Cropper (2013), a significant increase in temperature for the whole region has already been observed. In the Azores, an increase of 0.24-0.76°C was detected for the period between 1973-2012; there are predictions that the temperature will continue to increase by between 0.82-2.87°C until the year 2100 (Cropper, 2013).

In order to set the scene in terms of the possible environmental changes occurring in the Azores, analyses were made of the following environmental variables - surface air temperature (SAT), sea surface temperature (SST) and wave heights, to determine any changes that might have affected rocky intertidal communities over the course of interest of my work (1980s to the present).

2.3.1. Material and Methods

Environmental data sets, *surface air temperature* (°C) (SAT) and *sea surface temperature* (°C)(Gauss SST), were accessed through the National Oceanic and Atmospheric Administration (NOAA) website (NOAA, 2015). Monthly means were re-analysed using the tool - *National Center for Environmental Prediction/National Center for Atmospheric Research - reanalysis monthly means* (NCEP/NCAR) (Kalnay *et al.*, 1996). These data sets extended from 1948 to 2014. The analyses were made at the surface level for the Azores archipelago (Lat. 39°45'-36°55'N, Long. 31°16'-25°0'W), and for four islands: Flores (Western group: Lat. 39°33'-39°23'N, Long. 31°16'-31°6'W), Faial (Central group: Lat. 38°30'-38°38'N, Long. 28°50'-28°35'W), São Miguel (Eastern group: Lat. 37°55'-37°41'N, Long. 25°51'-25°7'W), and Santa Maria (Eastern group: Lat. 37°1'-36°55'N, Long. 25°11'-25°0'W).

The wave action data for *monthly average significant wave height* (m) (SWHave), *monthly maximum significant wave height* (m) (SWHmax) and *monthly total wave* *energy density per unit area* (KJ/m^2) (WEDave), were obtained through spatial averaging of ECMWF (European Centre for Medium-range Weather Forecasts) and analyses of the WAve Model (WAM) operational datasets for UTC 00, 06, 12 and 18 times, using a grid resolution of 0.25° x 0.25°.

Total wave energy density (WED) was computed for each area from the averaged significant wave height (SWH) using the following expression (where ρ is the sea water density (1029 g m^{-3}) and g the acceleration of gravity (9.8 ms^{-2})):

$$WED = \frac{1}{8}\rho g\, SWH^2$$

SWHave and WEDave monthly values were computed averaging all SWH and WED values respectively for each month. Monthly maximum SWHave values were found from the SWH hourly values for each month. These data sets were collected between 1985 and 2014. These analyses were made for four islands: Flores (East coast: Lat. 39°30'-39°60'N, Long. 31°25'-31°00'W; West coast: Lat. 39°30'-39°60'N, Long. 31°50'-31°25'W), Faial (South coast: Lat. 38°30'-38°60'N, Long. 29°00'-28°50'W), São Miguel (South coast: Lat. 37°50'-37°80'N, Long. 26°00'-25°00'W), and Santa Maria (South coast: Lat. 36°70'-37°00'N, Long. 25°5'-24°75'W), in order to inform the ecological studies. These data sets were kindly provided by the national government agency Instituto Português do Mar e da Atmosfera (IPMA) through its Regional Delegation in the Azores.

Initially, in order to detect a long-term trend in the environmental data, a Mann-Kendall trend test was made for the all range of data collected (SAT and SST: from 1948 to 2014; wave action variables: from 1985 to 2014), using *XLSTAT2015*. The Mann-Kendall test is a non-parametric test used to identify increasing or decreasing trends in time series data (e.g. Allen *et al.*, 1998; Drápela and Drápelová, 2011).

To investigate if there were significant differences in the monthly average environmental variables between 1980s and 2010s, a Wilcoxon matched pair signed-rank test was made (W critical value α=0.05) (Quinn and Keough, 2002). For analyses of SAT and SST a time window of 20 years was used; this was because the long-lived organisms present in the rocky shores will be influenced by the conditions of the previous 10-15 years. The 1980s period comprise the monthly averaged data from 1970 to 1989, while the 2010s period covers the monthly averaged data from 1995 to 2014. For wave action, since there were no data available before 1985, a time window of 10 years was selected (1980s: 1985-1994; 2010s: 2005-2014), using the first and last 10 years of data available for these variables.

To investigate if there were significant differences in the annual average environmental variables (annual average, hottest month - August and coldest month - February) between 1980s and 2010s, a Mann-Whitney test was made for a time window of 10 years. For SAT and SST the 1980s period comprise the annual averaged data from 1980 to 1989, while the 2010s period covers the annual averaged data from 2005 to 2014. For the wave action the 10 years' time window period used the annual averaged data from 1985 to 1994 (1980s) and 2005 to 2014 (2010s), as there were no data available before 1985.

2.3.2. Environmental analysis

Surface air temperature and sea surface temperature exhibited a cyclical pattern of climate variability through time. In both surface air temperature and SST data (1948-2014), for all the locations, the presence of two warm periods with the peaks in the early 1950s and 2000s are evident, interwoven with a cool period around the 1970s and 1980s (Figures 2.3 to 2.7). Even so, it is quite clear that for all the selected locations, both the surface air temperature and the SST data show higher values in the second warmer period (2000s) than in the first warmer period (Figures 2.3 to 2.7). Averaged surface air temperature and sea surface temperature exhibited the same pattern throughout the four islands, with the lowest temperatures being recorded in Flores and the highest in Santa Maria, showing increasing temperatures from the West to the East (FLW<FAI<SMG<SMA). Mann-Kendall trend tests, detected a significant increase trend of the surface air temperature for the Azores archipelago, and also for three of the four selected islands (Faial, São Miguel and Santa Maria islands), for the period 1948-2014 (Table 2.1). An increase of surface air temperature is apparent between the early (1950) and later (2000) warm periods (Figures 2.3 to 2.7). SST did not show any significant trend for the period 1948-2014 (Table 2.1). Even so, in all the locations, SST in recent periods has been warmer than in the previous warmer period of the 1950s (Figures 2.3 to 2.7). The Wilcoxon matched signed rank tests on the monthly averaged surface air temperature and sea surface temperature between the 1980s (1970-1989) and the 2010s (1995-2014), detected a significant increase of temperature (SAT and SST) for the Azores archipelago and for the four selected islands (Flores, Faial, São Miguel and Santa

Maria) over the course of the year (Table 2.2 and Figures 2.8 and 2.9). The Mann-Whitney tests on the annual averaged surface air temperature and sea surface temperature between the two selected periods - 1980s (1980-1989) and the 2010s (2005-2014), detected a significant increase of temperature (SAT and SST) for the Azores archipelago as a whole and for the four selected islands (Flores, Faial, São Miguel and Santa Maria), the exception being for the SAT in Flores Island that did not showed a significant result (Table 2.3). The Mann-Whitney tests analysis on the hottest (August) and coldest (February) months surface air temperature and sea surface temperature between the 1980s (1980-1989) and the 2010s (2005-2014), only detected a significant increase of SST for the coldest month (February) for the Azores archipelago as a whole and three of the four selected islands (Flores, São Miguel and Santa Maria) (Table 2.3). These analyses show some geographic and seasonal differences. The changes in the Central and Eastern groups are more apparent than in the milder Western group. Much of the increase in average annual temperature is attributable to raised winter temperatures.

For the three wave action variables, a pattern of increase in wave action from the East to the West was detected (SMA<SMG<FAI<FLW) (Figures 2.10 to 2.14). However, the Mann-Kendall trend test was not able to detect any temporal trend in all the selected locations for the period 1985-2014 (Table 2.4), which could be because the duration of the available data for these variables is rather short. Looking at the maximum wave height data, overall there was some evidence of more extreme events in the preceding decade (2005-2014) than in the period of historic data (Figures 2.10 to 2.14). The Wilcoxon matched signed rank tests analysis on the monthly averaged wave action variables, between the two selected periods - 1980s (1985-1994) and the 2010s (2005-2014), detected significant differences in the monthly maximum significant wave height (SWHmax), and on the monthly total wave energy density (WEDave) for some islands with differences between variables (Table 2.5). While the monthly maximum significant wave height (SWHmax) showed a significant increase for Flores (East and West) and Santa Maria between the selected periods; the monthly total wave energy density (WEDave) showed a significant increase for Flores (East and West) and Faial (Table 2.5). The Mann-Whitney tests analysis on the annual averaged wave action variables between the two selected periods - 1980s (1985-1994) and the 2010s (2005-2014), only detected

a significant increase of the monthly maximum significant wave height (SWHmax) for Flores (East and West) (Table 2.6).

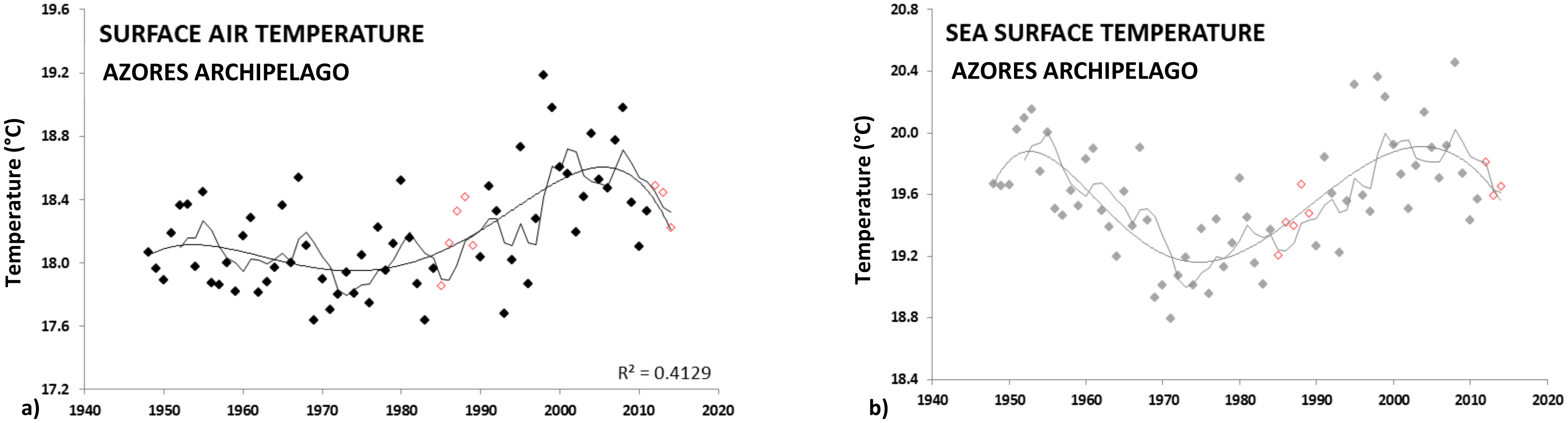


Figure 2.3. Long-term data on **a)** surface air temperature (SAT) and **b)** sea surface temperature (SST) averaged for the whole Azores archipelago (5 year moving average and 6th order polynomial trendline; open red symbols: 2 periods studied in remaining chapters - 1980s (1985-89) and 2010s (2010-14).

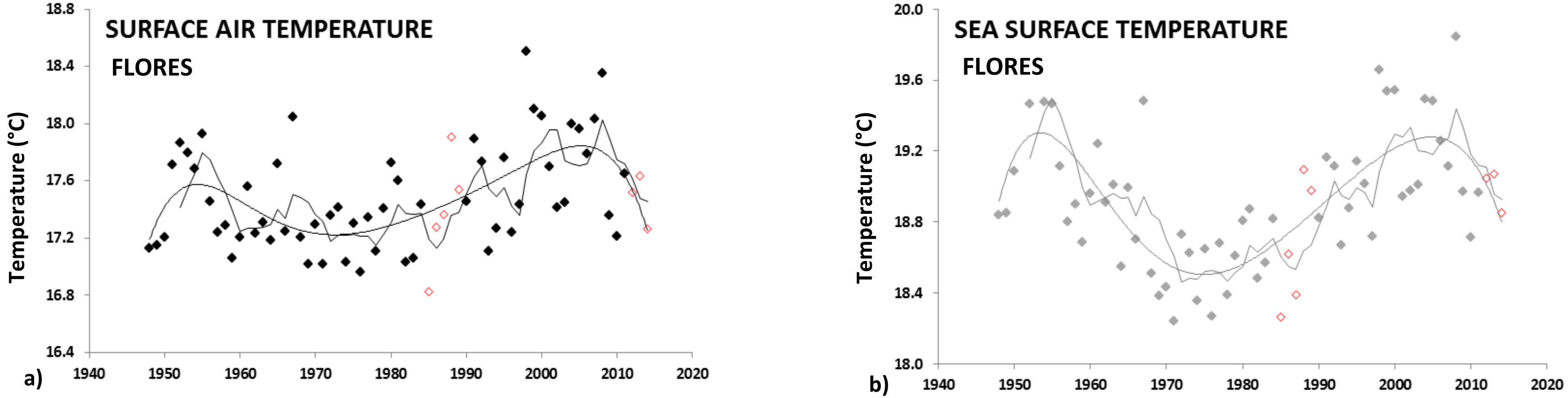


Figure 2.4. Long-term data on **a)** surface air temperature (SAT) and **b)** sea surface temperature (SST) averaged for Flores island (5 year moving average and 6th order polynomial trendline; open red symbols: 2 periods studied in remaining chapters - 1980s (1985-89) and 2010s (2010-14).

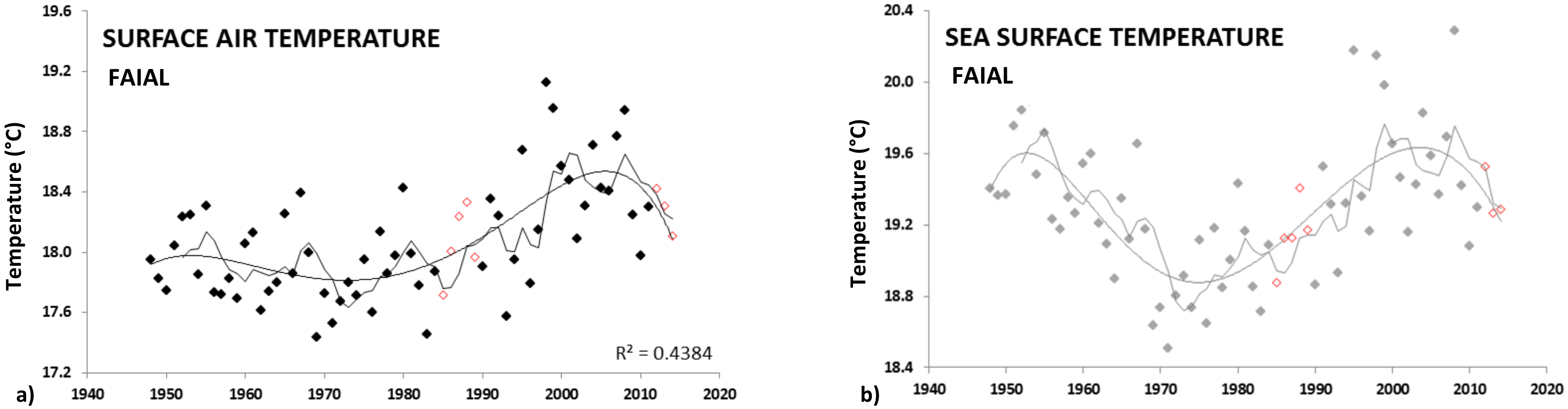


Figure 2.5. Long-term data on **a)** surface air temperature (SAT) and **b)** sea surface temperature (SST) averaged for Faial island (5 year moving average and 6th order polynomial trendline; open red symbols: 2 periods studied in remaining chapters - 1980s (1985-89) and 2010s (2010-14).

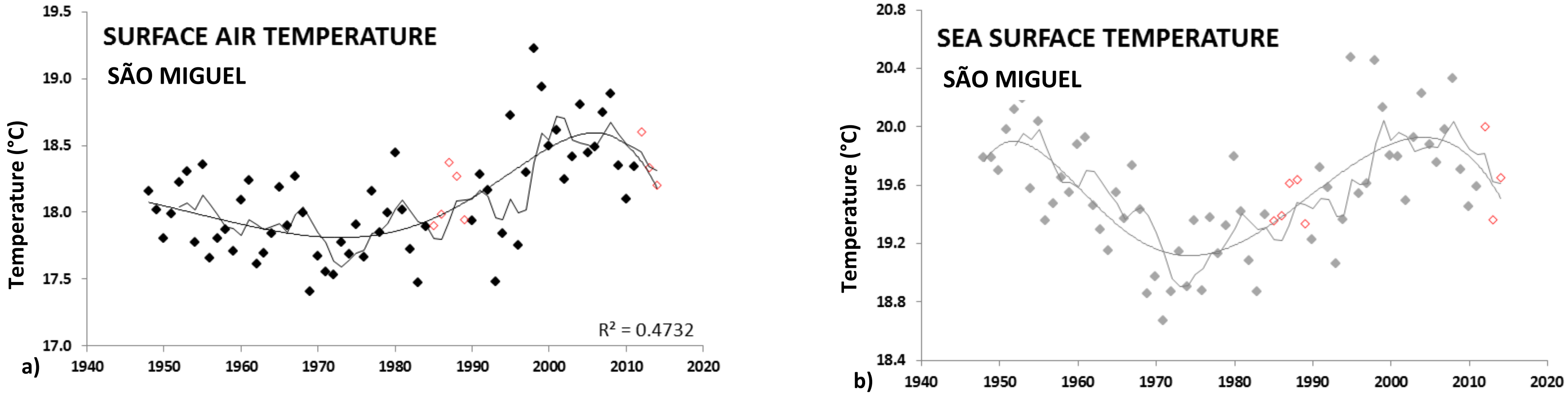


Figure 2.6. Long-term data on **a)** surface air temperature (SAT) and **b)** sea surface temperature (SST) averaged for São Miguel island (5 year moving average and 6th order polynomial trendline; open red symbols: 2 periods studied in remaining chapters - 1980s (1985-89) and 2010s (2010-14).

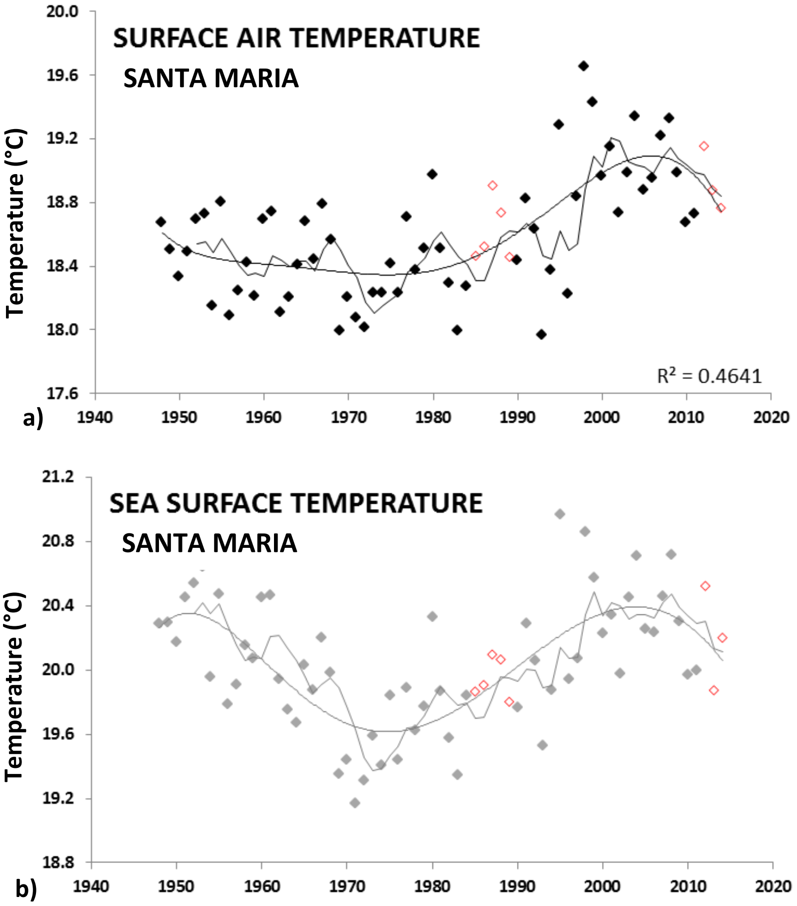


Figure 2.7. Long-term data on **a)** surface air temperature (SAT) and **b)** sea surface temperature (SST) averaged for Santa Maria island (5 year moving average and 6th order polynomial trendline; open red symbols: 2 periods studied in remaining chapters - 1980s (1985-89) and 2010s (2010-14).

Table 2.1. Mann-Kendall statistics for surface air temperature (SAT) and sea surface temperature (SST) in the Azores archipelago, and in the four selected islands: Flores, Faial, São Miguel and Santa Maria, for the period 1948-2014 (in box - statistically significant).

MANN-KENDALL TREND TEST (1948-2014)	AZORES	FLORES	FAIAL	S.MIGUEL	SANTA MARIA
SURFACE AIR TEMPERATURE					
Kendall's tau	0.053	0.035	0.059	0.063	0.066
S	17250	11301	19056	20219	21205
Var(S)	57853976.7	57853963.0	57853966.7	57853969.0	57853966.3
p-value (Two-tailed)	**0.023**	0.137	**0.012**	**0.008**	**0.005**
SST					
Kendall's tau	0.021	0.016	0.018	0.024	0.025
S	6684	5305	5734	7632	8056
Var(S)	57853972.7	57853966.3	57853941.3	57853943.3	57853948.0
p-value (Two-tailed)	0.380	0.486	0.451	0.316	0.290

Table 2.2. Wilcoxon signed rank test statistics for the monthly average of surface air temperature (SAT) and sea surface temperature (SST) in the Azores archipelago, and in the four selected islands: Flores, Faial, São Miguel and Santa Maria, between the periods 1980s-2010s (1980s: 1970-1989; 2010s: 1995-2014; in box - statistically significant).

WILCOXON SIGNED RANK TEST (1980s-2010s)	AZORES	FLORES	FAIAL	S.MIGUEL	SANTA MARIA
SURFACE AIR TEMPERATURE					
Variance (V)	162.5	162.5	162.5	162.5	162.5
p-value (Two-tailed)	**0.003**	**0.003**	**0.003**	**0.003**	**0.003**
SST					
Variance (V)	162.5	162.5	162.5	162.5	162.5
p-value (Two-tailed)	**0.003**	**0.007**	**0.003**	**0.003**	**0.003**

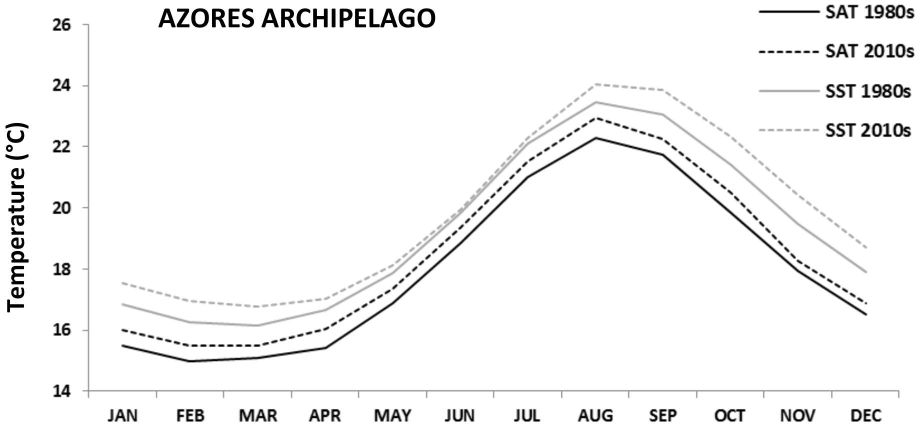


Figure 2.8. Surface air temperature (SAT) and sea surface temperature (SST) for Azores archipelago in the periods 1980s and 2010s (1980s: 1970-1989 and 2010s: 1995-2014).

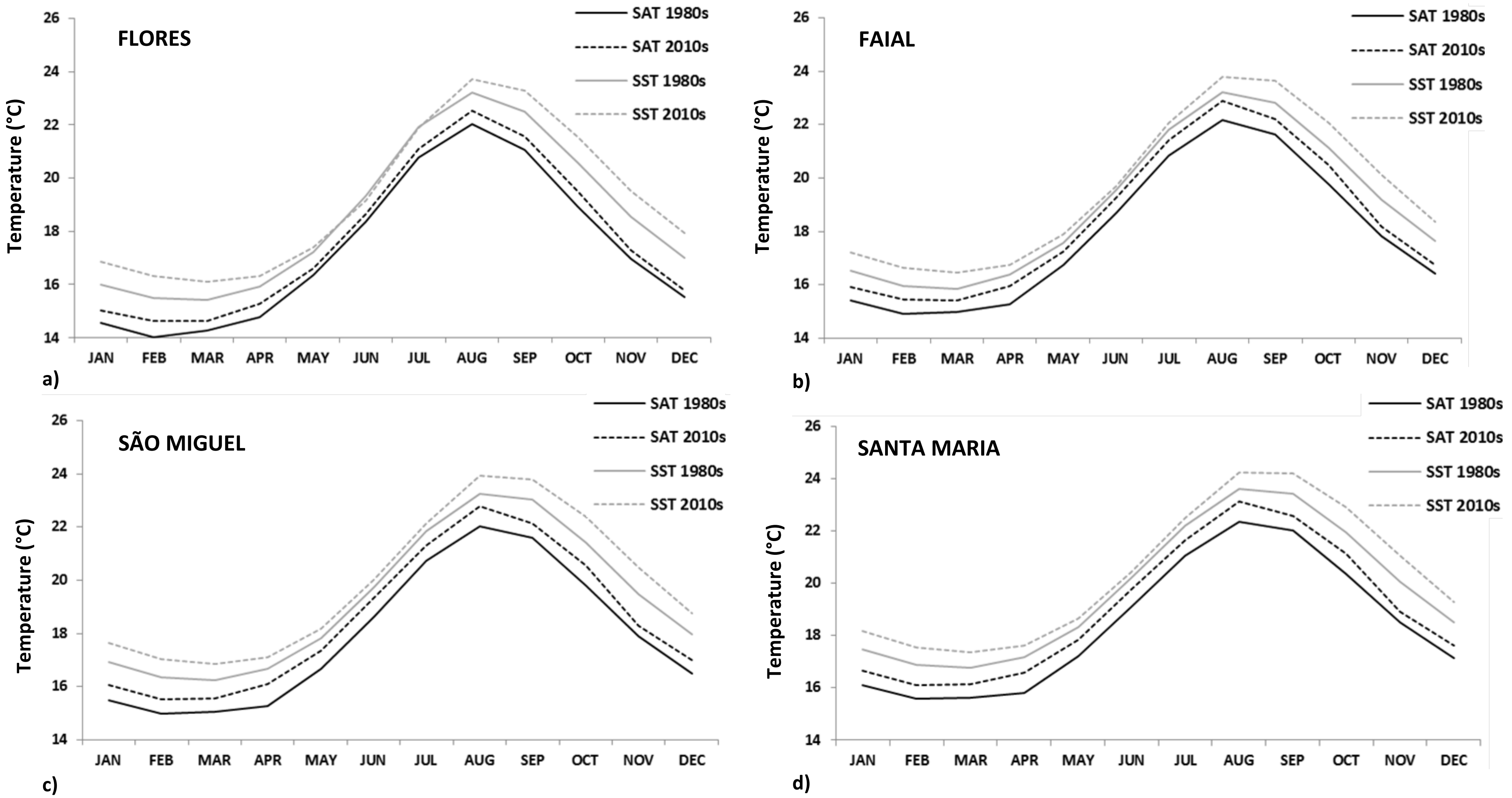


Figure 2.9. Surface air temperature (SAT) and sea surface temperature (SST) in the periods 1980s and 2010s for: **a)** Flores, **b)** Faial, **c)** São Miguel and **d)** Santa Maria (1980s: 1970-1989 and 2010s: 1995-2014).

Table 2.3. Mann-Whitney test statistics for the annual average, hottest month (August) and coldest month (February) of surface air temperature (SAT) and sea surface temperature (SST) in the Azores archipelago, and in the four selected islands: Flores, Faial, São Miguel and Santa Maria, between the periods 1980s-2010s (1980s: 1980-1989; 2010s: 2005-2014; in box - statistically significant).

MANN-WHITNEY TEST (1980s-2010s)		AZORES	FLORES	FAIAL	S.MIGUEL	SANTA MARIA
ANNUAL AVERAGE	**SURFACE AIR TEMPERATURE**					
	U	16.0	29.0	17.0	13.0	13.0
	p-value (Two-tailed)	**0.011**	0.121	**0.014**	**0.006**	**0.006**
	SST					
	U	11.0	14.0	16.0	15.0	14.0
	p-value (Two-tailed)	**0.004**	**0.007**	**0.011**	**0.009**	**0.007**
AUGUST	**SURFACE AIR TEMPERATURE**					
	U	37.0	26.0	34.0	38.0	36.0
	p-value (Two-tailed)	0.345	0.076	0.241	0.385	0.307
	SST					
	U	38.0	31.0	40.0	45.0	43.0
	p-value (Two-tailed)	0.385	0.162	0.473	0.734	0.623
FEBRUARY	**SURFACE AIR TEMPERATURE**					
	U	31.0	36.0	29.0	31.0	30.0
	p-value (Two-tailed)	0.162	0.307	0.121	0.162	0.140
	SST					
	U	18.0	17.0	24.0	21.0	21.0
	p-value (Two-tailed)	**0.017**	**0.014**	0.054	**0.031**	**0.031**

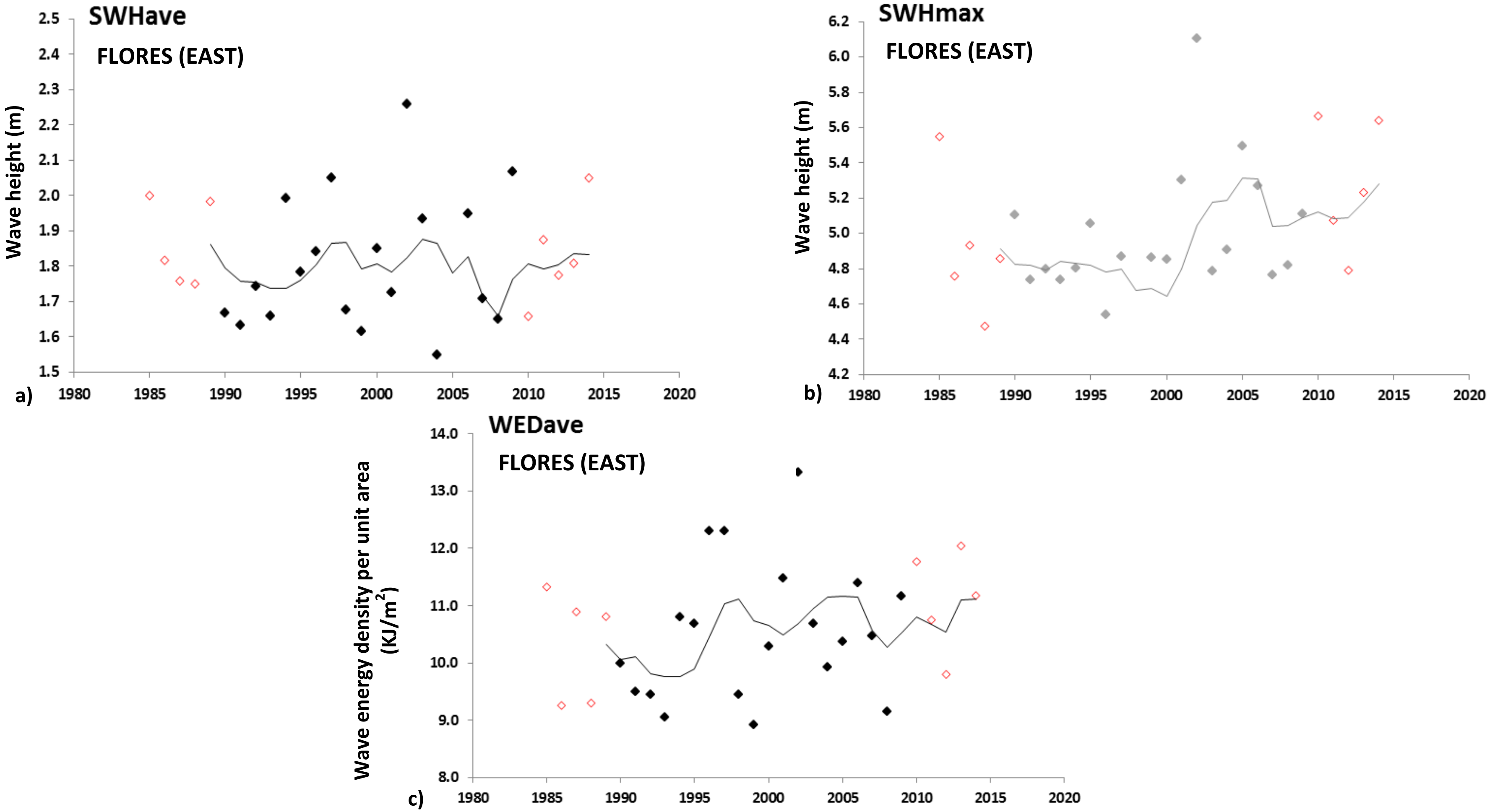


Figure 2.10. Long-term data on **a)** monthly average significant wave height (m) (SWHave), **b)** monthly maximum significant wave height (m) (SWHmax) and **c)** monthly total wave energy density per unit area (KJ/m2) (WEDave) for Flores island (East coast) (5 year moving average trendline; open red symbols: 2 periods studied in remaining chapters - 1980s (1985-89) and 2010s (2010-14).

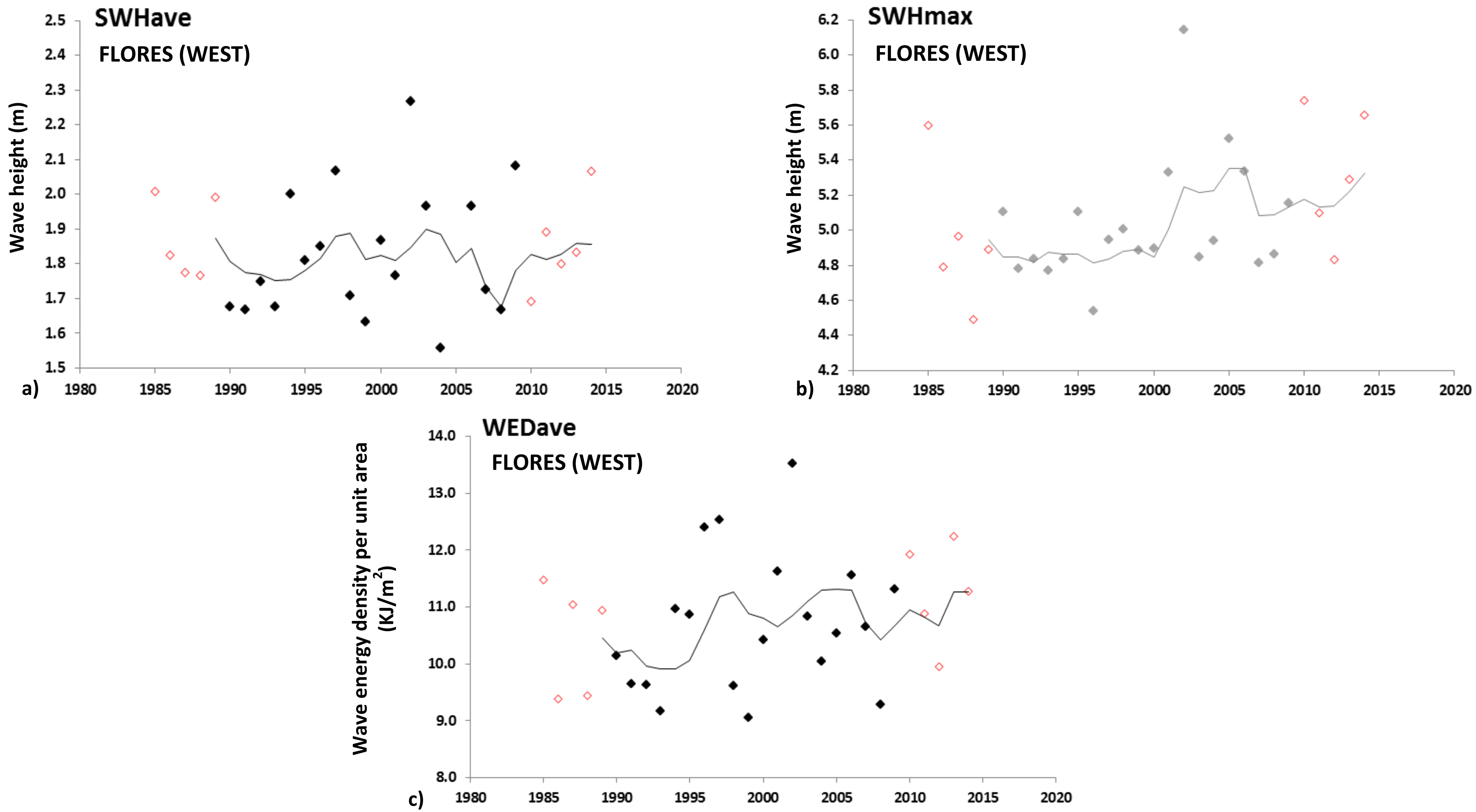


Figure 2.11. Long-term data on **a)** monthly average significant wave height (m) (SWHave), **b)** monthly maximum significant wave height (m) (SWHmax) and **c)** monthly total wave energy density per unit area (KJ/m^2) (WEDave) for Flores island (West coast) (5 year moving average trendline; open red symbols: 2 periods studied in remaining chapters - 1980s (1985-89) and 2010s (2010-14).

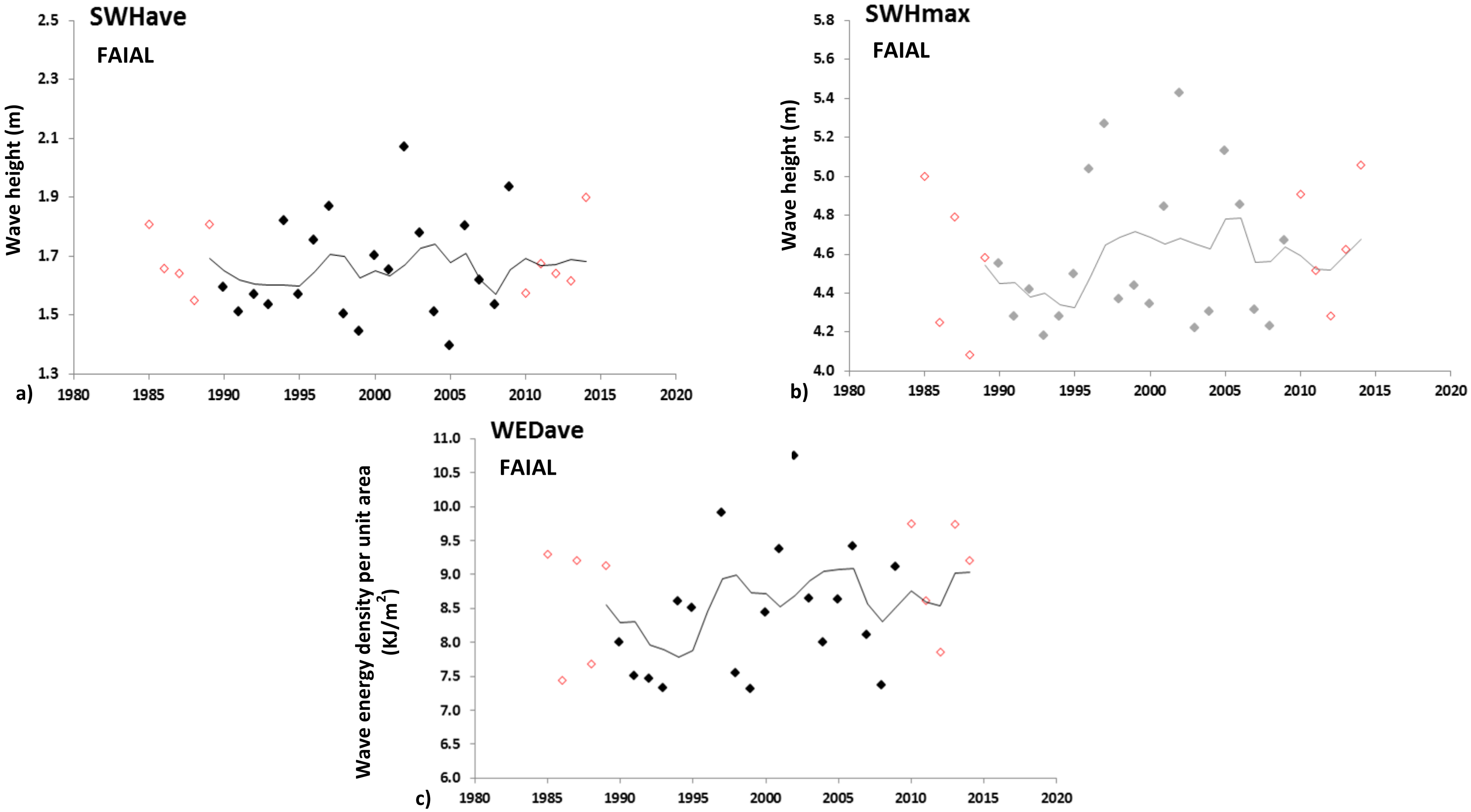


Figure 2.12. Long-term data on **a)** monthly average significant wave height (m) (SWHave), **b)** monthly maximum significant wave height (m) (SWHmax) and **c)** monthly total wave energy density per unit area (KJ/m^2) (WEDave) for Faial island (5 year moving average trendline; open red symbols: 2 periods studied in remaining chapters - 1980s (1985-89) and 2010s (2010-14).

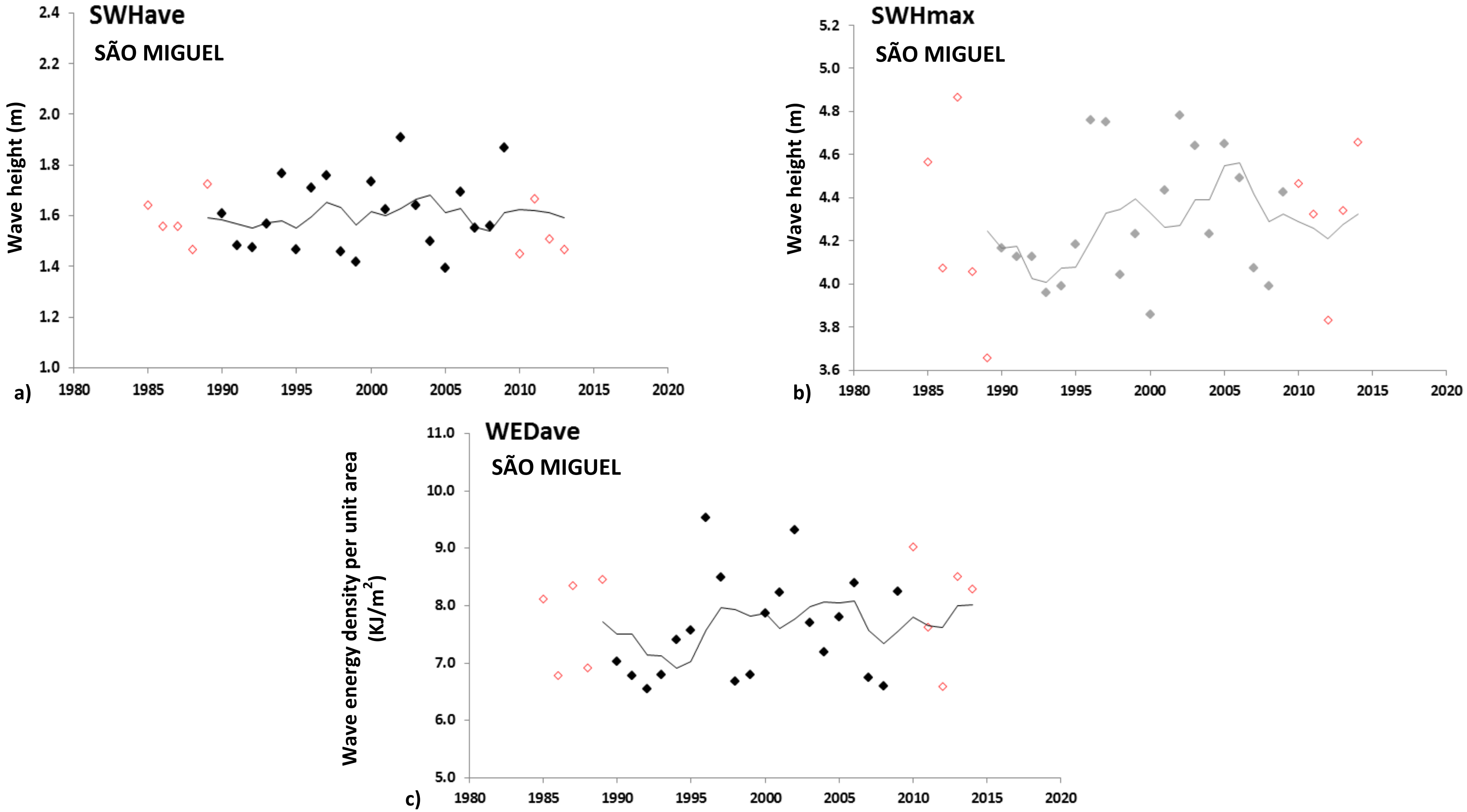


Figure 2.13. Long-term data on **a)** monthly average significant wave height (m) (SWHave), **b)** monthly maximum significant wave height (m) (SWHmax) and **c)** monthly total wave energy density per unit area (KJ/m^2) (WEDave) for São Miguel island (5 year moving average trendline; open red symbols: 2 periods studied in remaining chapters - 1980s (1985-89) and 2010s (2010-14).

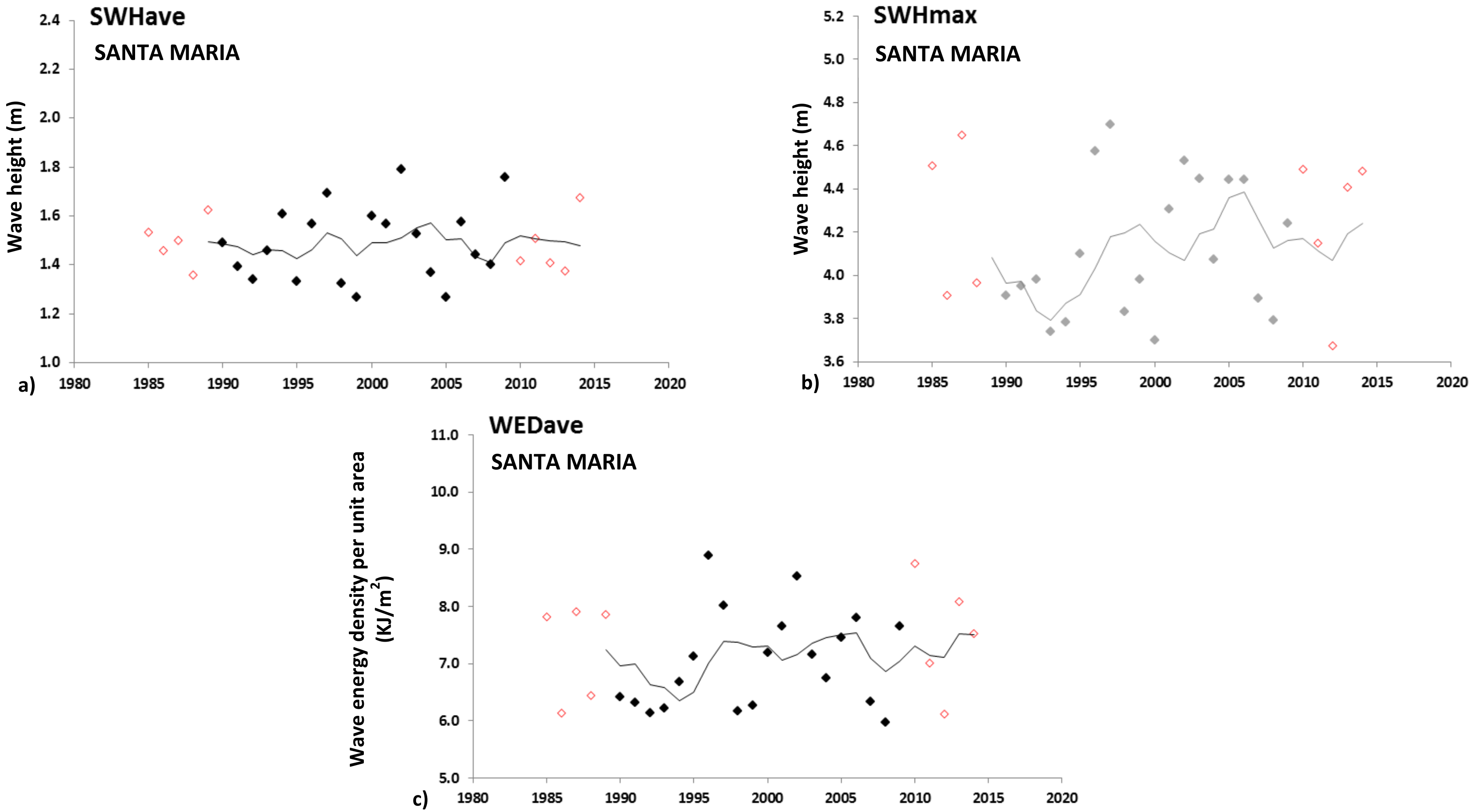
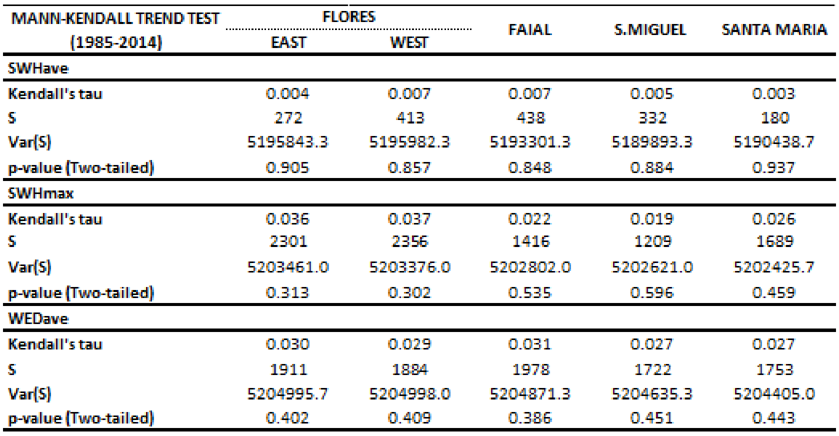


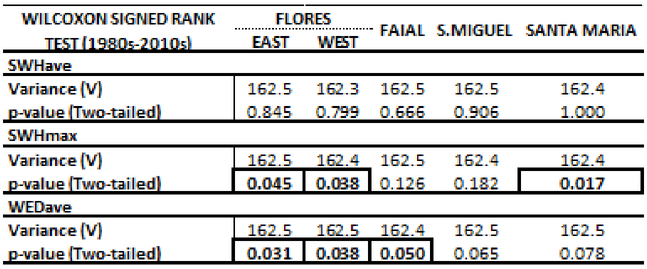
Figure 2.14. Long-term data on **a)** monthly average significant wave height (m) (SWHave), **b)** monthly maximum significant wave height (m) (SWHmax) and **c)** monthly total wave energy density per unit area (KJ/m^2) (WEDave) for Santa Maria island (5 year moving average trendline; open red symbols: 2 periods studied in remaining chapters - 1980s (1985-89) and 2010s (2010-14).

Table 2.4. Mann-Kendall statistics for wave action (SWHave: monthly average significant wave height (m), SWHmax: monthly maximum significant wave height (m), and WEDave: monthly total wave energy density per unit area (KJ/m2)), in the four selected islands: Flores (East and West coast), Faial (South coast), São Miguel (South coast) and Santa Maria (South coast), for the period 1985-2014 (in box - statistically significant).



MANN-KENDALL TREND TEST (1985-2014)	FLORES EAST	FLORES WEST	FAIAL	S.MIGUEL	SANTA MARIA
SWHave					
Kendall's tau	0.004	0.007	0.007	0.005	0.003
S	272	413	438	332	180
Var(S)	5195843.3	5195982.3	5193301.3	5189893.3	5190438.7
p-value (Two-tailed)	0.905	0.857	0.848	0.884	0.937
SWHmax					
Kendall's tau	0.036	0.037	0.022	0.019	0.026
S	2301	2356	1416	1209	1689
Var(S)	5203461.0	5203376.0	5202802.0	5202621.0	5202425.7
p-value (Two-tailed)	0.313	0.302	0.535	0.596	0.459
WEDave					
Kendall's tau	0.030	0.029	0.031	0.027	0.027
S	1911	1884	1978	1722	1753
Var(S)	5204995.7	5204998.0	5204871.3	5204635.3	5204405.0
p-value (Two-tailed)	0.402	0.409	0.386	0.451	0.443

Table 2.5. Wilcoxon signed rank test statistics for the monthly average of wave action (SWHave: monthly average significant wave height (m), SWHmax: monthly maximum significant wave height (m), and WEDave: monthly total wave energy density per unit area (KJ/m2)), in the four selected islands: Flores (East and West coast), Faial (South coast), São Miguel (South coast) and Santa Maria (South coast), between the periods 1980s-2010s (1980s: 1985-1994; 2010s: 2005-2014; in box - statistically significant).



WILCOXON SIGNED RANK TEST (1980s-2010s)	FLORES EAST	FLORES WEST	FAIAL	S.MIGUEL	SANTA MARIA
SWHave					
Variance (V)	162.5	162.3	162.5	162.5	162.4
p-value (Two-tailed)	0.845	0.799	0.666	0.906	1.000
SWHmax					
Variance (V)	162.5	162.4	162.5	162.4	162.4
p-value (Two-tailed)	**0.045**	**0.038**	0.126	0.182	**0.017**
WEDave					
Variance (V)	162.5	162.5	162.4	162.5	162.5
p-value (Two-tailed)	**0.031**	**0.038**	**0.050**	0.065	0.078

Table 2.6. Mann-Whitney test statistics for the annual average, hottest month (August) and coldest month (February) of wave action (SWHave: monthly average significant wave height (m), SWHmax: monthly maximum significant wave height (m), and WEDave: monthly total wave energy density per unit area (KJ/m2)), in the four selected islands: Flores (East and West coast), Faial (South coast), São Miguel (South coast) and Santa Maria (South coast), between the periods 1980s-2010s (1980s: 1985-1994; 2010s: 2005-2014; in box - statistically significant).

MANN-WHITNEY TEST (1980s-2010s)		FLORES		FAIAL	S.MIGUEL	SANTA MARIA
		EAST	WEST			
ANNUAL AVERAGE	SWHave					
	U	48.5	44.0	36.5	53.5	51.0
	p-value (Two-tailed)	0.940	0.678	0.325	0.820	0.970
	SWHmax					
	U	21.5	21.5	28.0	34.0	37.0
	p-value (Two-tailed)	**0.034**	**0.034**	0.104	0.241	0.344
	WEDave					
	U	28.0	28.0	29.0	38.0	41.0
	p-value (Two-tailed)	0.104	0.104	0.121	0.384	0.520
AUGUST	SWHave					
	U	57.0	57.0	63.0	54.5	54.0
	p-value (Two-tailed)	0.621	0.621	0.341	0.754	0.789
	SWHmax					
	U	58.5	56.5	57.0	58.0	54.0
	p-value (Two-tailed)	0.542	0.647	0.621	0.569	0.789
	WEDave					
	U	37.0	36.0	41.5	40.0	40.5
	p-value (Two-tailed)	0.343	0.307	0.543	0.465	0.493
FEBRUARY	SWHave					
	U	44.0	41.0	40.0	44.0	42.0
	p-value (Two-tailed)	0.675	0.519	0.472	0.677	0.570
	SWHmax					
	U	41.5	42.5	47.0	42.0	40.5
	p-value (Two-tailed)	0.545	0.596	0.850	0.570	0.496
	WEDave					
	U	42.0	42.0	42.0	45.0	48.0
	p-value (Two-tailed)	0.571	0.571	0.571	0.734	0.910

2.3.3. Discussion

The analyses of the surface air temperatures are in agreement with works such as Lima and Wethey (2012), which have shown a warming of coastlines around the world. A general trend of SST increase was not detected through the Mann Kendall trend test. However, an increase of the SST was detected using other analyses with a selected subset of data (Wilcoxon signed rank test and Mann-Whitney test) in all the selected locations, these results being in agreement with past work in the North-East Atlantic by Thompson *et al.* (2010) and Lima and Wethey (2012).

My analysis of wave action variables differed from the works published by Wang *et al.* (2004) and Wolf and Woolf (2006) for the North-East Atlantic, since it was not possible to detect a significant increased trend for the three wave action variables over the last

~30 years in the Azores. This may be because the Azores archipelago is located in the middle of the Atlantic, totally unprotected and subject to all the fluctuations of the currents and climate throughout the year. Additionally these analyses only considered the mean monthly values of the environmental variables. However, more focussed analyses detected that there has been an increase of the maximum significant wave height, mainly in the Western group (Flores island), reinforcing the idea of the occurrence of more frequent extreme events. According to Young *et al.* (2011), over the past two decades there was a non-significant trend in mean monthly values of wave height; however, when considering extreme conditions a significant trend of increasing in wave height was detected especially at higher latitudes. There were no obvious trends in wave action data; however, some cues were obtained that reinforce the assumptions that the North Atlantic is becoming stormier (Wang *et al.*, 2004). Most importantly, the environmental information highlights the cyclical nature of climate fluctuations, in line with the AMO (Atlantic Multidecadal Oscillation) (Mieszkowska *et al.*, 2014a).

According to Seabra *et al.* (2015) the use of the appropriate metrics of an environmental variable and the identification of the appropriate environmental pressure variable will provide knowledge to detect, interpret and predict the impacts that these variables will have in the ecosystem. Even so, comparing the two selected periods 1980s and 2010s, I was able to detect a significant difference in the surface air temperature and sea surface temperature, providing evidence that temperature between those two periods has increased in this region. Through this analysis I have shown that the 1980s was at the end of a cold period, while the 2010s period was after a peak warm period. These differences could have a major influence over the rocky shores organisms and communities. Lima and Wethey (2012) demonstrated that 38% of the coastlines are experiencing more extremely hot days, while 46% of the coastlines show a significant decrease in the frequency of extremely cold days. Data were not available for these analyses locally, but it is reasonable to assume that extreme temperatures are more frequent.

The historic ecological data explained in subsequent chapters were collected at the switch from a cold to a warmer period. The resurvey period represented the end of a warm period with a slightly down turn of both air and sea temperatures in recent years. Annual SAT and SST data for the period 1980-1989 and the period 2005-2014 were compared by Mann Whitney tests, showing a significant increase of the general temperature between the selected periods. More importantly several very warm years were recorded for both air and sea surface temperature from the mid-1990s onwards compared to the 1970s and 1980s for all the Azores combined and for each of the individual islands. These warm years exceeded values seen in the previous warm periods of the 1950s. Four or five (depending on island) of the warmest years recorded were observed from the mid-1990s onwards in all islands. The differences in temperature were more pronounced in the Eastern and Central group, but less so for the Western group; while the Western group appeared to have experienced stormier weather in recent years.

3. TEMPORAL AND SPATIAL PATTERNS OF REPRODUCTIVE PHENOLOGY OF LIMPETS

3.1. INTRODUCTION

Recent rapid climate change has driven shifts in the phenology of marine, freshwater and terrestrial organisms (Root *et al.*, 2003; Parmesan, 2007; Devictor *et al.*, 2012; Wolkovich *et al.*, 2012; Poloczanska *et al.*, 2013). Phenology is the study of periodic biological life cycles stages (e.g. reproductive period, larval season), especially their timing and interactions with weather and climate (Schwartz, 2013). These phenological shifts differ among species as different environmental processes and signals drive or trigger idiosyncratic phenological responses (Saikkonen *et al.*, 2012); these also vary between different systems (e.g. terrestrial and marine see Edwards and Richardson, 2004). Phenological shifts can have consequences for aquatic communities and ecosystems due to the potential occurrence of trophic mismatches, and in the case of commercial species, increased risks of recruitment failure (Beaugrand *et al.*, 2002b; Pörtner and Farrell, 2008; Giménez, 2011; Cheung *et al.*, 2013). Thus phenological timing is critical for individual fitness, with potential population and community-level consequences depending on the capability of different species to adapt by using modified environmental cues (Bradshaw and Holzapfel, 2006; Saikkonen *et al.*, 2012).

In marine ecosystems, the majority of phenological studies have focussed on planktonic species (Edwards and Richardson, 2004; Genner *et al.*, 2010) and on vertebrates such as turtles (Mazaris *et al.*, 2008) and marine birds (Gaston *et al.*, 2009). These include observed phenological responses to past climate fluctuations (e.g. in squid and fish see Sims *et al.*, 2001, 2004) and more recent rapid climate changes (Poloczanska *et al.*, 2013).

Rocky shores occur worldwide, being typically open systems with sharp environmental gradients, supporting a diverse community of plants and animals (Lewis, 1964; Stephenson and Stephenson, 1972; Raffaelli and Hawkins, 1996; Thompson *et al.*, 2002). Hawkins *et al.* (2008, 2009), stated that rocky shore ecosystems are relatively simple, which makes them an excellent model system to investigate the consequences of climate change for community structure and ecosystem processes. Their accessibility makes intertidal and shallow-water rocky shore habitats some of the most studied ecosystems, including a plethora of field experimental studies (stemming from the pioneering work of Hatton, 1938; Jones, 1946; Connell, 1961b, 1972; Paine, 1994) providing much insight into processes, particularly interactions amongst species. There is also good broad-scale and long-term baseline information from historical studies (e.g. Southward and Crisp, 1954a; Crisp and Southward, 1958; Fischer-Piette and Crisp, 1959; Fischer-Piette, 1963) against which the ecological effects of climate change can be assessed and quantified (e.g. Helmuth *et al.*, 2006b; Lima *et al.*, 2006; Mieszkowska *et al.*, 2006a, 2007; Firth *et al.*, 2015). Intertidal organisms, in particular, experience large environmental fluctuations as a result of the rising and falling of tides and the consequent exposure to both aquatic and aerial climatic regimes. All the above characteristics make rocky intertidal organisms and assemblages potentially good indicators of the effects of climate fluctuations and change on natural ecosystems (Southward, 1967, 1980, 1991; Barry *et al.*, 1995; Southward *et al.*, 1995; Sagarin *et al.*, 1999; Helmuth *et al.*, 2002, 2006b; Thompson *et al.*, 2002; Hawkins *et al.*, 2003; Harley *et al.*, 2006; Mieszkowska *et al.*, 2006a; Denny *et al.*, 2011).

Patellid grazers are considered keystone species playing an important role in the structure of intertidal communities (Branch, 1981; Hawkins and Hartnoll, 1983b). Removal and exclusion experiments have shown how limpet grazing controls algal biomass (Jones, 1946, 1948; Underwood, 1980; Hawkins, 1981; Hawkins and Hartnoll, 1983b; Jernakoff, 1985; Castilla, 1999; Bulleri *et al.*, 2000; Benedetti-Cecchi *et al.*, 2001a; Jenkins *et al.*, 2005; Coleman *et al.*, 2006; Jonsson *et al.*, 2006; Davies *et al.*, 2007; Martins *et al.*, 2010), sets patterns of vertical distribution (Underwood and Jernakoff, 1984; Boaventura *et al.*, 2002a) and patchiness (Hawkins and Hartnoll, 1985; Burrows and Hawkins, 1998; Johnson *et al.*, 1998a), and interact strongly with space-occupying sessile species such as barnacles (Hawkins, 1983; Miller and Carefoot, 1989; Arrontes *et al.*, 2004) and mussels (Crowe *et al.*, 2011).

Limpet grazing has a major influence on community structure and functioning of coastal ecosystems, which can be disrupted by heavy human exploitation as in Chile (Godoy and Moreno, 1989; Moreno, 2001), South Africa (Siegfried *et al.*, 1994) and the Azores (Martins *et al.*, 2008a, 2009, 2010).

Moore *et al.* (2011) were able to investigate the consequences of recent warming on two species of limpets (*Patella vulgata* and *Patella depressa*) through variations in their phenology. They concluded that the warm-water species (*P. depressa*), near its poleward range limit in the British Isles, was reproducing earlier and more successfully than in the past; often via an extended breeding season leading to increased number of broods (Moore *et al.*, 2011). Meanwhile, the cold-water species (*P. vulgata*), has been failing to reproduce successfully in South-West England due to a delay in the maturation compromising the single autumn spawning period (Moore *et al.*, 2011).

The overall aim of my work was to describe the reproductive phenology of the two Macaronesia endemic patellid species - *Patella candei gomesii* (Côrte-Real *et al.*, 1996; Weber and Hawkins, 2002; Sá-Pinto *et al.*, 2005, 2008) and *Patella aspera* (Weber and Hawkins, 2005; Sá-Pinto et al., 2008), in the Azorean archipelago. Assessment of seasonality of reproductive activity has been prompted by the desire to understand climate sensitivity of these economically and culturally important species in the Azores. Using largely unpublished and "grey" historic data (Martins *et al.*, 1987b) from the 1980s and collections between 2012 and 2014, differences in *Patella* spp. phenology were assessed. Differences in the phenology of reproduction of *Patella* spp. were also compared between the Western and Eastern groups of Azorean islands comprising a gradient of temperature of about ~1.2°C, from the milder less seasonally variable Western to the warmer Eastern groups. This is associated with differences in latitude (2°N) and longitude (6°W) and variable influences of oceanographic conditions of the islands. More formally, the following specific questions were addressed:

1) Is inter-annual variability of reproductive cycles *Patella candei gomesii* and *P. aspera* apparent in the recent data (2012-2014)?
2) Has the duration of the autumn-winter-spring reproductive spawning period of *Patella aspera* altered and shifted over time?
3) Has the duration of the summer reproductive resting period of *Patella aspera* changed over time? We predict that greater stress due to warming would lead to an extended summer resting period.
4) Are there differences in reproductive seasonality of *Patella candei gomesii* and *P. aspera* in response to the spatial environmental gradient from the Western to Eastern groups of islands?

3.2. MATERIAL AND METHODS

The reproductive seasonality of the two species were compared over time (1980s to 2010s) and over a spatial environmental gradient from the Western group (Lat. 39°45'-39°23'N, Long. 31°16'-31°5'W) to the Eastern group (Lat. 37°55'-36°55'N, Long. 25°51'-25°0'W)(Figure 3.1).

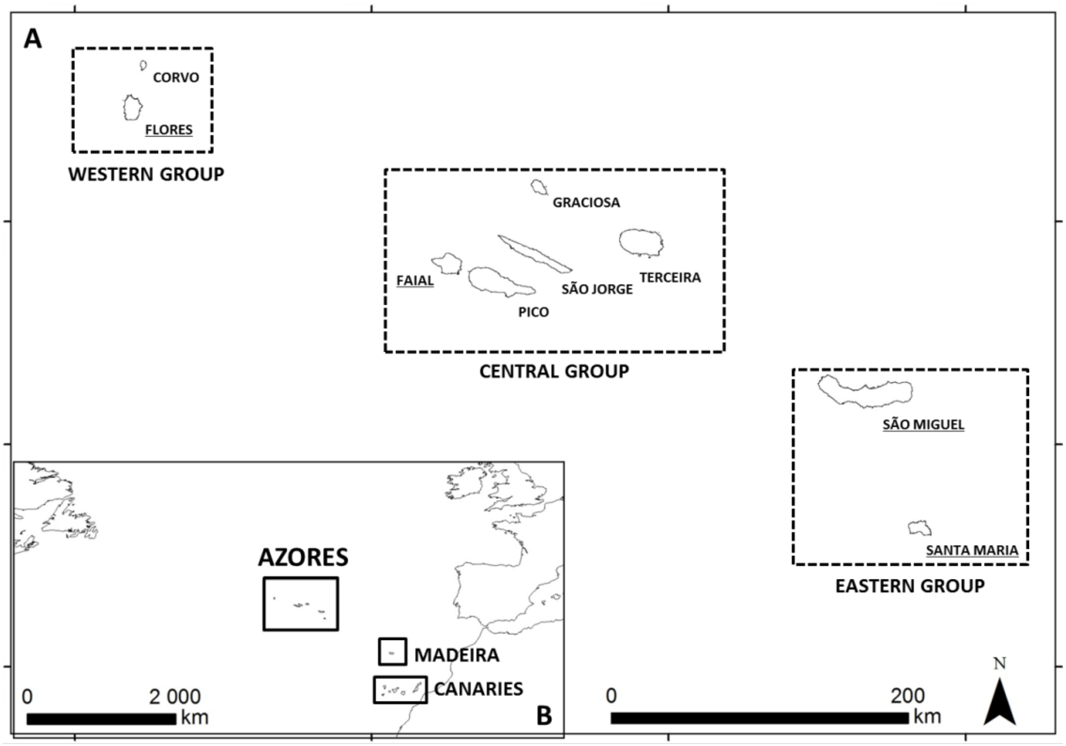


Figure 3.1. A) The Azores archipelago with the location of the three groups (Western, Central and Eastern) and the nine islands (limpet collections were made on the underlined islands); **B)** the Azores relative to Madeira and Canaries archipelagos of Macaronesia (Cape Verde Islands not shown).

3.2.1. Historic data collection: Study area and sampling design

Archived unpublished data on the reproductive phenology of *Patella* spp. were collected by S. J. Hawkins and colleagues (led by Ricardo S. Santos and Helen Martins) in the 1980s and early 1990s (Martins *et al.*, 1987a,b). The data from the 1980s were collected to help establish a management regime to counter the intensive overexploitation, which had led to the collapse of stocks in some islands (Martins *et al.*, 1987a,b). Historic information includes data for both species compiled from several sources. *Patella aspera* and *P. candei gomesii* data from São Miguel and Faial islands were obtained through market samples, opportunistic collections, and stock assessment by standard ½ hour diving collections and also through confiscated illegal catches. For Flores Island data on *P. aspera* were gathered through opportunist collections (Tables 3.1 and 3.2).

Table 3.1. Historic sampling locations for *Patella candei gomesii* in São Miguel and Faial islands (1985-1989) and seasonal coverage of samples.

Island	Sampling period	Locations (and collectors)	Comments
São Miguel (SMG)	1986: August 1987: September 1989: October	Mosteiros, Candelaria, Ponta Delgada, Rabo de Peixe, Ribeira Quente and Feteiras (S. J. Hawkins, R. S. Santos, H. Martins, and other colleagues from Department of Oceanography and Fisheries from University of Azores (DOP-UAç))	Patchy coverage; Mainly intertidal, with occasional subtidal individuals
Faial (FAI)	1986: April-August; October-December 1987: January-December 1988: January-December 1989: January; April; June	Lajinha, Horta, Capelinhos, Varadouro, Ribeirinha, Porto Pim, Pasteleiro, Porto do Alcaíde, Porto Salão, Monte da Guia (S. J. Hawkins, R. S. Santos, H. Martins, and other colleagues from Department of Oceanography and Fisheries from University of Azores (DOP-UAç))	Full coverage; Intertidal, with occasional subtidal individuals
Total number of historic *P. candei gomesii* collected: 24(SMG)+2497(FAI) = **2521 specimens**			

Table 3.2. Historic sampling locations for *Patella aspera* in São Miguel, Flores and Faial islands (1985-1989) and seasonal coverage of samples.

Island	Sampling period	Locations (and collectors)	Comments
São Miguel (SMG)	1985: August-December 1986: January-October 1987: August-September 1989: October	Mosteiros, Porto da Baleia, Porto da Ribeirinha, Rabo de Peixe, Porto Formoso, Ponta Garça, Caloura-Cerco, Maia, Candelária, Ferraria, Ponta Delgada, Feteiras, Lagoa and Ribeira Quente (S. J. Hawkins, R. S. Santos, H. Martins, and other colleagues from Department of Oceanography and Fisheries from University of Azores (DOP-UAç))	Patchy coverage; Mainly subtidal, sometimes working with professional divers
Flores (FLW)	1987: October	Santa Cruz das Flores, Lajes das Flores, Baia da Ribeira da Silva (S. J. Hawkins, R. S. Santos, H. Martins, and other colleagues from Department of Oceanography and Fisheries from University of Azores (DOP-UAç))	Patchy coverage; Mainly subtidal
Faial (FAI)	1986: May; July 1987: January; April; June; November 1989: April; June; November	Capelinhos, Praia do Norte, Varadouro, Ribeirinha, Porto Salão, Capelinhos, Feteira, Praia do Almoxarife, Monte da Guia (S. J. Hawkins, R. S. Santos, H. Martins, and other colleagues from Department of Oceanography and Fisheries from University of Azores (DOP-UAç))	Patchy coverage; Mainly subtidal
Total number of historic *P. aspera* collected: 1293(SMG)+259(FLW)+656(FAI) = **2208 specimens**			

3.2.2. Recent data collection (2012-2014): Study area and sampling design

Limpets were collected in four of the nine islands of the archipelago - Flores (FLW), São Miguel (SMG), Faial (FAI) and Santa Maria (SMA), at two different locations within each island for at least 36 months (Tables 3.3 and 3.4), between 2012 and 2014. Spatial and temporal coverage was limited by various logistic constraints and bad weather compromising collection.

Table 3.3. Recent sampling locations for *Patella candei gomesii* in São Miguel, Flores, Faial and Santa Maria islands (2012-2014) and seasonal coverage of samples.

Island	Sampling period	Locations (and collectors)	Comments
São Miguel (SMG)	2012: May-December 2013: January-December 2014: January-December	Forno de Cal, Ferraria, Cruzeiro and Lagoa - OVGA (A. Prestes, R. Patarra, E. Cacabelos, G. M. Martins, I. Moniz, J. Faria, M. Vale, N. Álvaro)	Full coverage; Intertidal
Flores (FLW)	2012: May-December 2013: January-December 2014: January-December	Rolo da Fajanzinha and Ponta da Caveira (C. Mendes)	Full coverage; Intertidal
Faial (FAI)	2012: May-July; September; December 2013: April-July 2014: July-August	Porto Salão, Castelo Branco, Ribeirinha, Praia do Norte, Praia da Fajã, Monte da Guia and Espalhafatos (Pedreira do Nunes) (N. Serpa, P. Ribeiro)	Patchy coverage due to logistic constraints; Intertidal
Santa Maria (SMA)	2012: May-December 2013: January; August-December 2014: January-December	Costa do Campo, Pedra que Pica, Baía do Cura, Vila do Porto, Ilhéu da Vila, Campo Ponta Ponderado, Baixa S, Praia da Malbusca, Figueiral, Prainha, Praia dos Frades, Baía da Cré, Ponta Castelete and Praia dos Cedros (M. Cabral, B. Couto)	Patchy coverage due to logistic constraints; Intertidal

Total number of recent *P. candei gomesii* collected: 5939(SMG)+2643(FLW)+1099(FAI)+1541(SMA) = **11 222 specimens**

Table 3.4. Recent sampling locations for *Patella aspera* in São Miguel, Flores and Faial islands (2012-2014) and seasonal coverage of samples.

Island	Sampling period	Locations (and collectors)	Comments
São Miguel (SMG)	2012: June-December 2013: January-December 2014: January; March-June; August-December	Mosteiros, Feteiras, Ginetes, Relva, Fenais da Luz, Ponta Delgada, Candelária, São Vicente de Ferreira, Santo António das Capelas, Ferraria, Capelas, Remédios da Bretanha, Ajuda da Bretanha and Ponta da Bretanha (M. Ferreira)	Generally good coverage; Patchy in 2014 due to weather conditions; Subtidal
Flores (FLW)	2012: May-December 2013: January-December 2014: January-December	Rolo da Fajanzinha and Ponta da Caveira (C. Mendes)	Full coverage; Intertidal
Faial (FAI)	2012: May-July; September; December 2013: April-July 2014: July-August	Porto Salão, Castelo Branco, Ribeirinha, Praia do Norte, Praia da Fajã, Monte da Guia and Espalhafatos (Pedreira do Nunes) (N. Serpa, P. Ribeiro)	Patchy coverage due to logistic constraints; Intertidal
Total number of recent *P. aspera* collected: 2979(SMG)+1773(FLW)+224(FAI) = **4976 specimens**			

At each location, at least 40 individuals of each species were collected; between the 4th and the 11th day of each month (logistical and/or weather constraints prevented the collection of animals within this time window a few times). Whenever possible, collections respected standardized individual sizes (*Patella candei gomesii* (endemic subspecies): +10 mm; *Patella aspera* (Macaronesia species): 45 to 65 mm), following Martins *et al.* (1987b) and Menezes (1991).

Samples were frozen (-20°C) for later inspection. In the laboratory, limpets were measured (maximum shell length and height), weighed, and dissected to determine the sex and the gonad stage. Gonad staging used the semi-quantitative scale of Orton *et al.* (1956) that scores gonad development, ranging between empty neuters (sex and gonad indistinguishable) and gonad full and releasing gametes (stage V), with pluses indicating filling and minuses emptying of the gonads (Figure 3.2). Sampling methods and further processing of samples followed the exact methodology used in 1980s, to ensure comparability (Martins *et al.*, 1987b). S. J. Hawkins trained the staff in the Azores in the 1980s and recently trained Maria Vale during the period 2012-2014. S. J. Hawkins was trained by A. J. Southward, who had been trained by J. H. Orton. There was thus some consistency in gonad staging over time.

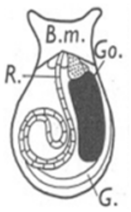
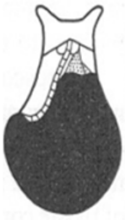
GONAD STAGE	NEUTER (N)	I	II	III	IV	V
FILLING	Limpet sex and gonad indistinguishable	Sex distinguishable and gonad starting to develop	Gonad developing to 1/3 full	Gonad developing between 1/3-2/3 full	Gonad 2/3 full	Gonad full and discharging gametes
EMPTYING		Almost empty, but sex discernible	Emptying 1/3 full	emptying gonad 1/3-2/3 full	Emptying gonad 2/3 full	
SCHEME						

Figure 3.2. Semi-quantitative scale of limpet gonad ripening stages (adapted from Orton *et al.,* 1956 and Moore *et al.,* 2011).

3.2.3. Data analysis

Data were used in two ways to assess both the temporal differences (historic versus recent) and spatial patterns (Eastern to Western groups) in reproductive phenology in relation to the location in the archipelago. In order to compare historic and recent phenology, data for both periods were aggregated as monthly averages. Inter-annual variability in recent data was also assessed. Prior to analyses, a quality assessment of the data was made to ensure the data were balanced and sufficient through the selection of the most complete data series. This resulted in using only part of the data available. For the temporal analysis, the historic (where present between 1985-1989) and recent (2012-2014) data sets from S. Miguel Island for *P. aspera* (+40 mm) were used (Table 3.2). While for *P. candei gomesii* (+10 mm) the selected data sets were the data from Faial Island (where present historic data: 1985-1989; where present recent data: 2012-2014) (Table 3.1). For the spatial analysis of recent data (2012-2014) from two islands (S. Miguel and Flores islands) for *P. aspera* (+40 mm) were used (Table 3.4); whereas for *P. candei gomesii* (+10 mm) the selected data sets were from three islands (S. Miguel, Flores and Santa Maria islands) (Table 3.3).

3.2.3.1. Inter-annual variability in recent reproductive phenology of *Patella* spp.

The developmental stages of gonads were considered in three groups: (i) **I^{-}-N-I^{+}** - earlier stages of gonad development, (ii) **II^{+}- III^{+}-III^{-}-II^{-}** - intermediate stages of gonad development or emptying, and (iii) **IV^{-}-V-IV^{+}** - advanced stages of gonad development, following the approach used by S. J. Hawkins in the historic data (Martins *et al.*, 1987b). To test for inter-annual variability among recent years (2012, 2013 and 2014) in gonad development (IV^{+}-V-IV^{-} and I^{-}-N-I^{+}), a Mann-Whitney test was applied using *XLSTAT 2015* (Bonferroni correction p=0.017) separately for each species. For *P. aspera* the recent data from the islands of S. Miguel and Flores were analysed; while for *P. candei gomesii* the data from the islands of S. Miguel, Flores and Santa Maria were used.

3.2.3.2. Temporal differences in reproductive phenology of *Patella* spp.

Temporal differences in the ripening or fullness in early and advanced stages of gonad development (I^{-}-N-I^{+} and IV^{-}-V-IV^{+}) were assessed using a Wilcoxon signed-rank test using *SigmaPlot v12.5*. This was done separately for each species: *P. aspera* - historic versus recent data (SMG); *P. candei gomesii* - historic versus recent data (FAI). To assess if temporal differences detected previously (historic versus recent data) differed with sex, a Wilcoxon signed-rank test was made separately for both females and males of *P. aspera*. A two-sample Kolmogorov-Smirnov test (K-S test) was also used (*XLSTAT2015*) to examine differences in the total shell length size of limpets between historic and recent data, as this could potentially influence the results.

3.2.3.3. Spatial patterns in reproductive phenology of *Patella* spp.

For the spatial patterns, the same overall approach used in the temporal analyses was followed (i.e. three groups: I^{-}-N-I^{+}, II^{+}- III^{+}-III^{-}-II^{-}, IV^{-}-V-IV^{+}). The differences in the ripening or fullness in early and advanced stages of gonad development (I^{-}-N-I^{+} and IV^{-}-V-IV^{+}) were assessed through a Wilcoxon signed-rank test (W critical value α=0.05) using *SigmaPlot v12.5*. Analyses were run separately for each species: *P. aspera* - São Miguel and Flores; *P. candei gomesii* - São Miguel, Faial and Santa Maria. To assess if the differences detected previously (between islands) varied with sex, a Wilcoxon signed-rank test was applied separately for both females and males of *P. aspera*. For both species, a two-sample Kolmogorov-Smirnov test (K-S test) was also applied using

XLSTAT2015, to examine for differences in the total shell length size of limpets between islands.

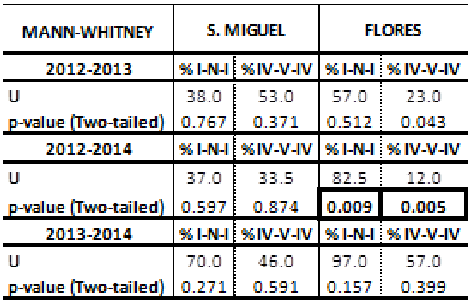
3.3. RESULTS

3.3.1. Inter-annual variability in recent reproductive phenology of *Patella* spp.

In S. Miguel there was no significant inter-annual variability in the annual cycle of gonad development groups (%I-N-I and %IV-V-IV) for *P. aspera*; in contrast significant inter-annual variability was observed in Flores for both the ripening and resting periods between 2012 and 2014 (%I-N-I: *p*=0.009) and %IV-V-IV: *p*=0.005) (Table 3.5).

For *P. candei gomesii,* significant inter-annual variability in the annual cycle of gonad development were only observed in Flores for both gonad development groups (%I-N-I and %IV-V-IV); with resting season and ripeness occurring earlier in 2014 and later in 2012. The inter-annual variability observed for the immature and mature gonad development stages occurred between 2012-2014 (immature: *p*=0.010 and mature: *p*<0.001) and between 2013-2014 (immature: *p*<0.001 and mature: *p*<0.001) (Table 3.6).

Table 3.5. Inter-annual variability among recent years (2012-2014) in gonad development (%I-N-I and %IV-V-IV) for *Patella aspera* in São Miguel and Flores islands (Bonferroni correction: *p*=0.017 (0.05/3 years); in box - statistically significant).



MANN-WHITNEY	S. MIGUEL		FLORES	
2012-2013	% I-N-I	% IV-V-IV	% I-N-I	% IV-V-IV
U	38.0	53.0	57.0	23.0
p-value (Two-tailed)	0.767	0.371	0.512	0.043
2012-2014	% I-N-I	% IV-V-IV	% I-N-I	% IV-V-IV
U	37.0	33.5	82.5	12.0
p-value (Two-tailed)	0.597	0.874	**0.009**	**0.005**
2013-2014	% I-N-I	% IV-V-IV	% I-N-I	% IV-V-IV
U	70.0	46.0	97.0	57.0
p-value (Two-tailed)	0.271	0.591	0.157	0.399

Table 3.6. Inter-annual variability among the recent years (2012-2014) in gonad development (%I-N-I and %IV-V-IV) for *Patella candei gomesii* in São Miguel, Flores and Santa Maria islands (Bonferroni correction: *p*=0.017 (0.05/3 years); in box - statistically significant).

MANN-WHITNEY	S. MIGUEL		FLORES		SANTA MARIA	
2012-2013	% I-N-I	% IV-V-IV	% I-N-I	% IV-V-IV	% I-N-I	% IV-V-IV
U	42.0	42.0	67.0	23.0	26.0	25.0
p-value (Two-tailed)	0.671	0.671	0.153	0.059	0.846	0.949
2012-2014	% I-N-I	% IV-V-IV	% I-N-I	% IV-V-IV	% I-N-I	% IV-V-IV
U	65.0	24.0	82.0	2.0	39.0	60.0
p-value (Two-tailed)	0.203	0.070	0.010	<0.001	0.512	0.375
2013-2014	% I-N-I	% IV-V-IV	% I-N-I	% IV-V-IV	% I-N-I	% IV-V-IV
U	100.0	44.0	137.0	10.0	28.5	39.0
p-value (Two-tailed)	0.112	0.112	<0.001	<0.001	0.512	0.814

3.3.2. Temporal differences in reproductive phenology of *Patella* spp.

3.3.2.1. Temporal differences in reproductive phenology of *Patella aspera* - São Miguel Island

In the historic data (1980s) the percentage of immature individuals (%I-N-I) reached its maximum, indicating the resting season, in May and June (respectively 86% and 89%). Recently, however, the resting period was observed later in the year occurring in June and July (respectively 77% and 70%). This result suggests a delay in the onset of the resting season (Figure 3.3.a,b). Intermediate stages (%II-III, both filling and emptying) were more common throughout the year recently (2012-2014) than historically (1985-1989) (Wilcoxon signed rank test: *p*=0.005) (Figure 3.3.a,b). In the historic data a greater proportion of individuals reached the spawning stage in December and January (respectively 54% and 70%); whereas in the recent data this peak occurred earlier in the months of November and December (respectively 26% and 25%), suggesting that the spawning has been starting earlier (Figure 3.3.a,b). Moreover, in recent years a considerably lower percentage of individuals (less than 25% of individuals) reached the maximum ripening stage, subsequently progressing to spawning (Figure 3.4.a,b). Wilcoxon signed-rank tests revealed that the changes in the advanced (%IV-V-IV) and in the intermediate (%II-III) gonad stage development between the historic and the recent data were statistically significant (respectively *p*= 0.002 and *p*= 0.005).

There were more neuters present during the resting period in the summer (May to August) and in the remaining months of the year, with more neuters being present historically (ranging between 0-67%, respectively November-February and June) than recently (0-26%, respectively November to February and June), especially during the resting phase. The percentage of males historically ranged between 14-75% (respectively June and February), whereas recently they ranged between 45-78% (respectively October and February). Historically the percentage of females ranged between 13-43% (respectively March and October), while in the recent data they ranged between 22-54% (respectively February and October) (Figure 3.3.c,d).

The shell lengths of *P. aspera,* used for gonads analysis, were significantly greater in the historic sample compared to the recent sample (Kolmogorov-Smirnov test: $p < 0.0001$) (averaged shell length: historic data - 51.38 mm (±7.51 mm); recent data - 50.26 mm (±6.59 mm)) (Figure 3.5.a).

Although, the percentage of reproductive active females and males has increased recently, fewer individuals reached the advanced gonad stage development IV-V-IV, in comparison with the historic data (Figure 3.4.c,d). For both males and females, advanced gonad development (IV-V-IV) was significantly greater historically than at present (Wilcoxon signed-rank test - females: $p=0.002$ and males: $p=0.007$). Analysis of total shell length of *P. aspera* separately for females and males also revealed significant differences for both sexes (Kolmogorov-Smirnov test: females - $p=0.013$ and males - $p<0.0001$) (averaged shell length: historic data - female 52.33 mm (±7.85 mm), male 51.65 mm (±7.48 mm); recent data - female 51.25 mm (±6.65 mm), male 50.02 mm (±6.48 mm)) with the largest shell lengths being recorded for both sexes in the historic data (Figure 3.5.b,c).

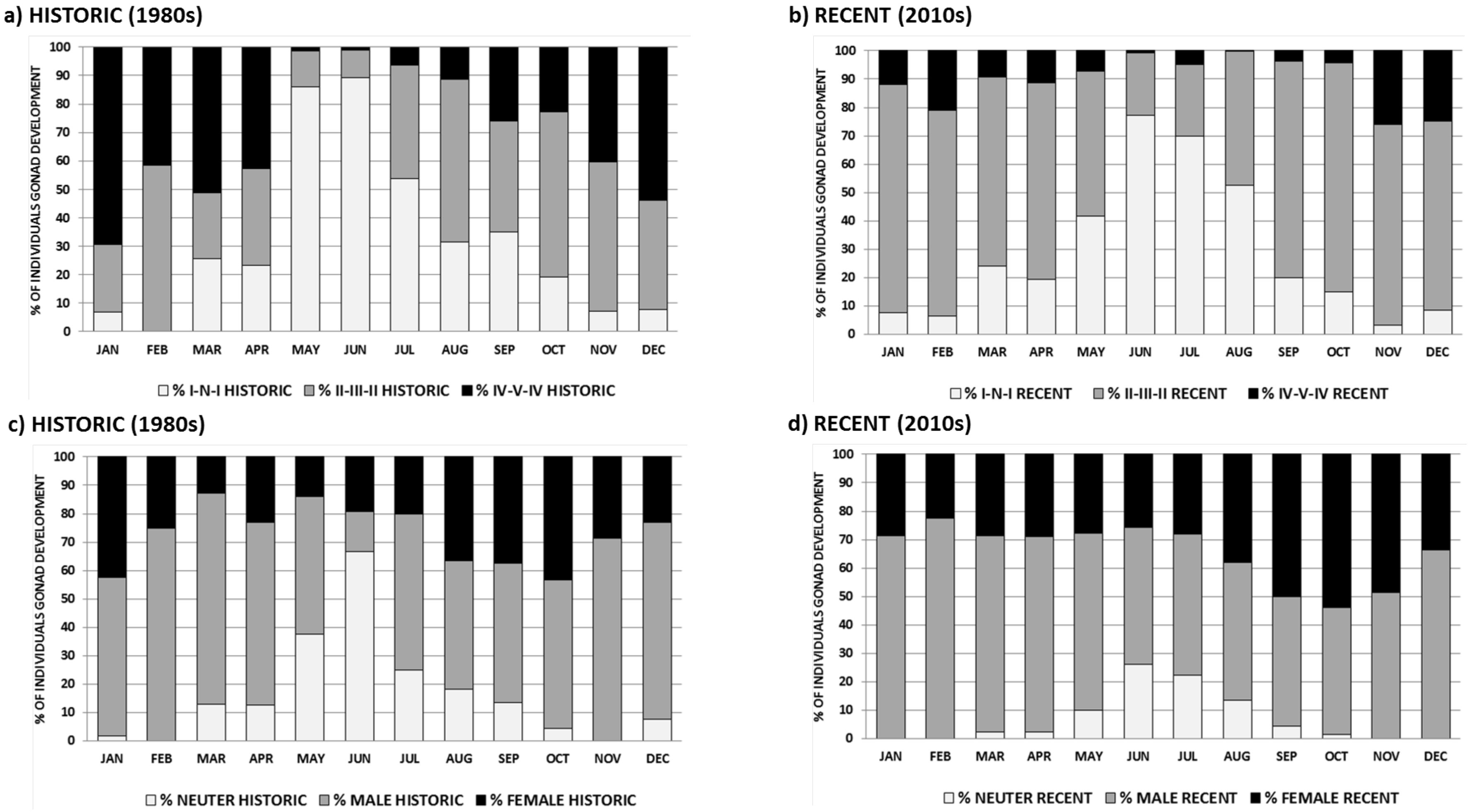


Figure 3.3. Annual pattern of gonad development and sex ratios for *Patella aspera* in São Miguel (+40 mm) historically (1985-1989) and recently (2012-2014): **a)** total historic percentage of immature (%I-N-I), intermediate (%II-III) and mature (%IV-V-IV) gonad stages, **b)** total recent percentage of immature (%I-N-I), intermediate (%II-III) and mature (%IV-V-IV) gonad stages, **c)** historic percentages of sexes (female, male and neuter), and **d)** recent percentages of sexes (female, male and neuter).

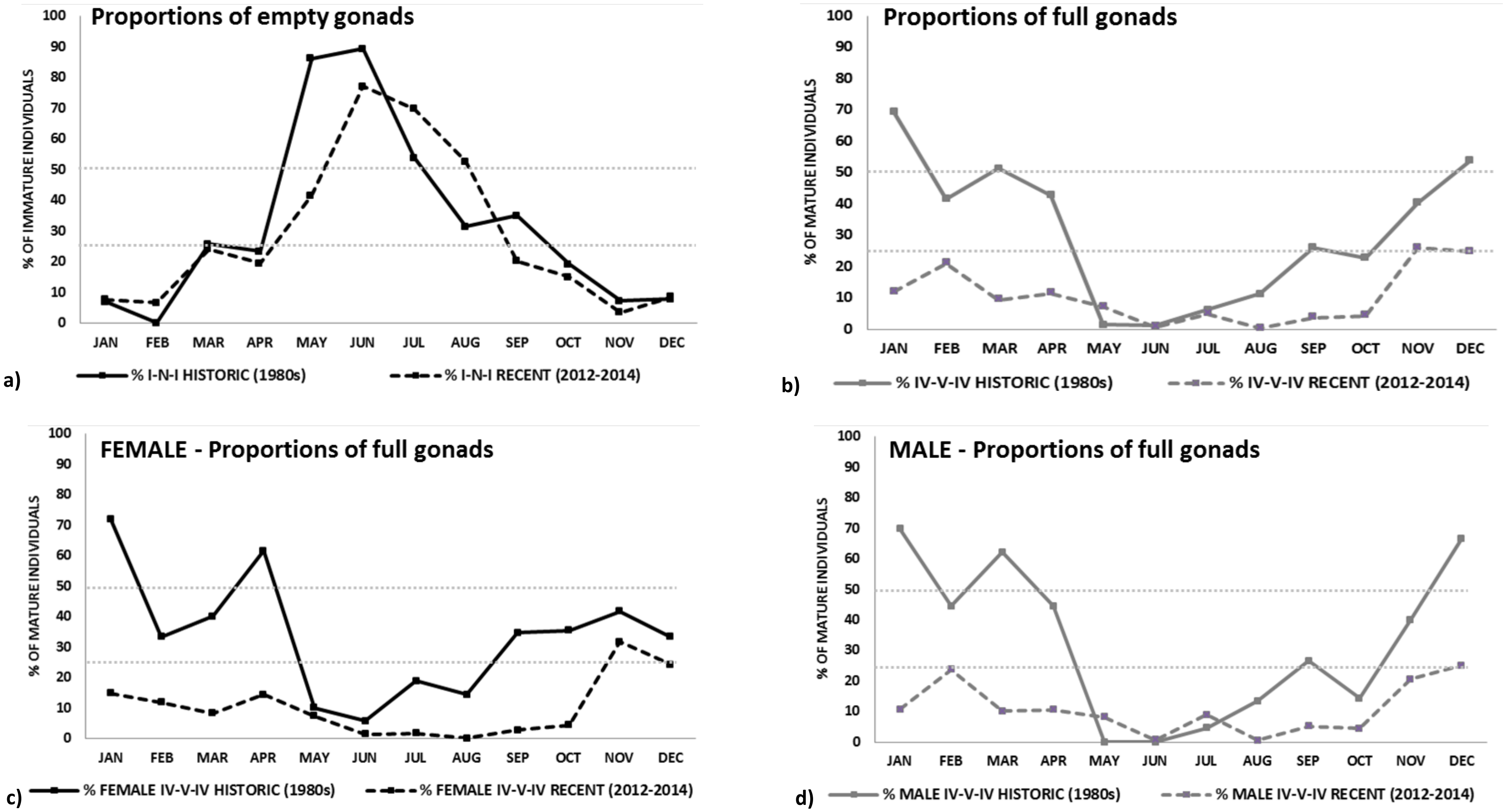


Figure 3.4. Annual pattern of gonad development for *Patella aspera* in São Miguel (+40 mm): **a)** total historic and recent percentage of immature gonad stages (%I-N-I), **b)** total historic and recent percentage of mature gonad stages (%IV-V-IV), **c)** historic and recent female percentage of mature gonad stages (%IV-V-IV), and **d)** historic and recent male percentage of mature gonad stages (%IV-V-IV).

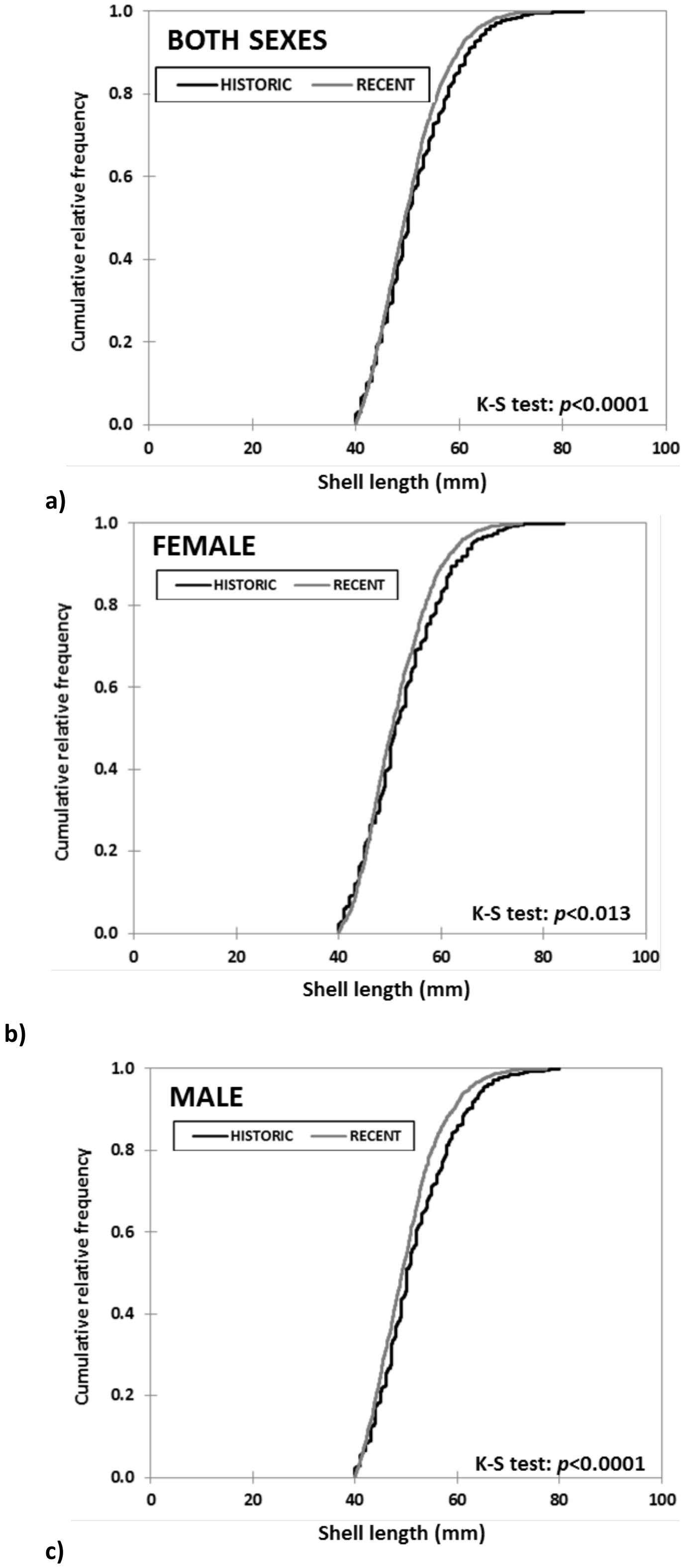


Figure 3.5. Cumulative frequency distributions of shell length for *Patella aspera* in São Miguel (+40 mm): **a)** both sexes shell length (historic N=1293, recent N=2979), **b)** female shell length (historic N=426, recent N=1057), and **c)** male shell length (historic N=655, recent N=1681).

3.3.2.2. Temporal differences in reproductive phenology of *Patella candei gomesii* - Faial Island

Analysis of the available data, showed that, in both historic and recent data, the percentage of immature or neuter individuals (%I-N-I) reached its peak in July (historic - 65%, recent - 70%) indicating a short and incomplete resting season (Figure 3.6.a,b). Reproductive activity, however, was lower over the summer in both periods (Figure 3.6.d). Due to logistical constraints, no winter samples were collected recently for this island. The percentage of individuals at intermediate stage of maturation and emptying (%II-III) ranged between 28-66% (July-November) in the historic data and between 29-66% (July-December) for the recent data (Figure 3.6.a,b). In both periods the higher percentage of individuals reaching the spawning stage (%IV-V-IV) occurred in April (historic - 58%, recent - 42%) (Figure 3.6.a,b). An overlap of the resting season between the historic and the recent data was observed, with perhaps this extending longer more recently (Figure 3.6.c). Despite the low statistical power, due to logistical constraints, there were still significant differences detected in the percentage of immature or empty gonads recently than in the past (Wilcoxon signed-rank test: p=0.047) (Figure 3.6.c). Fewer individuals reached peak ripeness in recent years (Wilcoxon signed-rank test: p=0.016) compared to the past; but the peak of the reproductive season was missed. Therefore these results must be treated with caution (Figure 3.6.d).

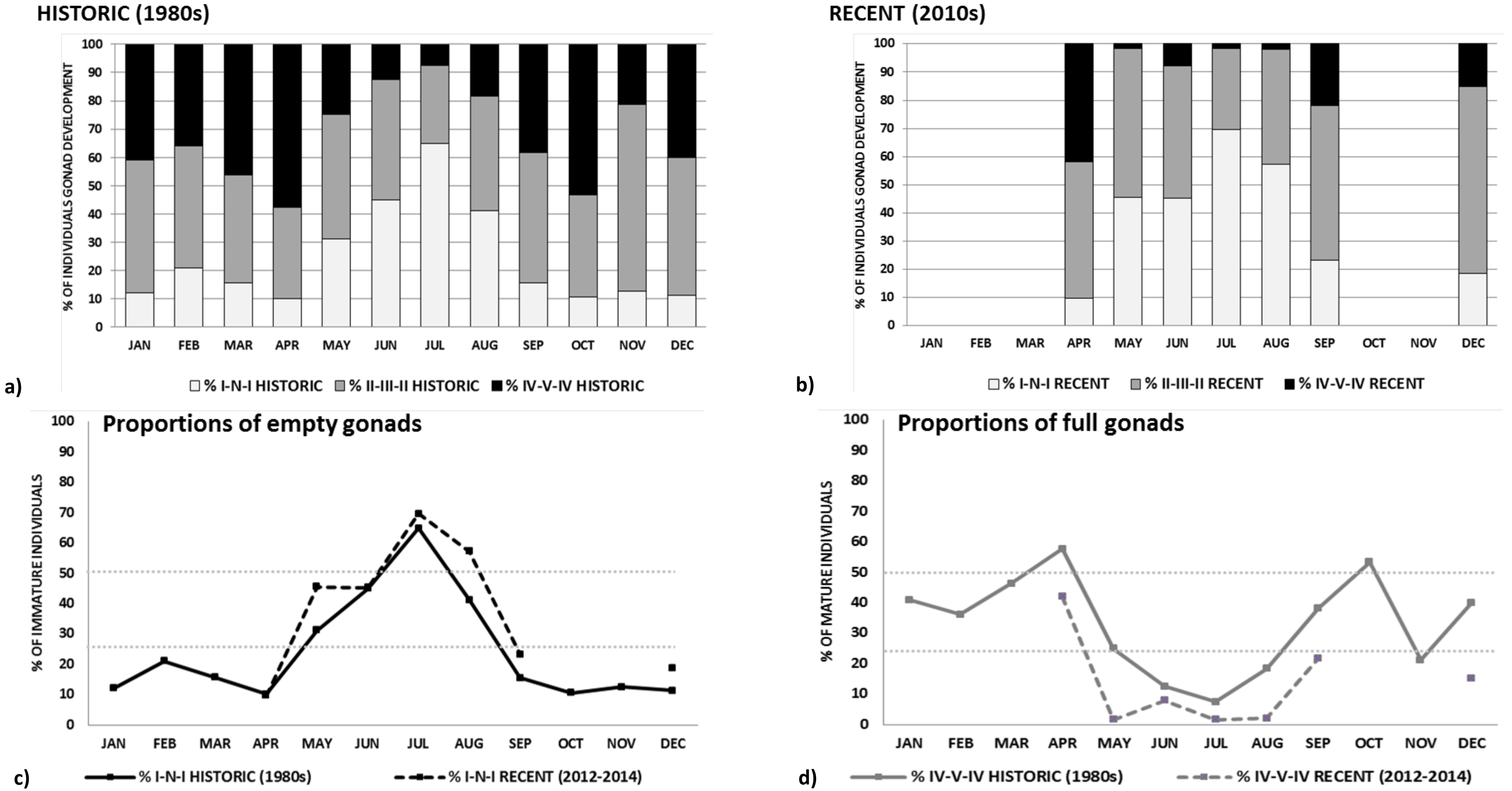


Figure 3.6. Annual pattern of gonad development for *Patella candei gomesii* in Faial (+10 mm) historically (1985-1989) and recently (2012-2014): **a)** total historic percentage of immature (%I-N-I), intermediate (%II-III) and mature (%IV-V-IV) gonad stages, **b)** total recent percentage of immature (%I-N-I), intermediate (%II-III) and mature (%IV-V-IV) gonad stages, **c)** total historic and recent percentage of immature gonad stages (%I-N-I), and **d)** total historic and recent percentage of mature gonad stages (%IV-V-IV).

3.3.3. Spatial patterns in reproductive phenology of *Patella* spp.

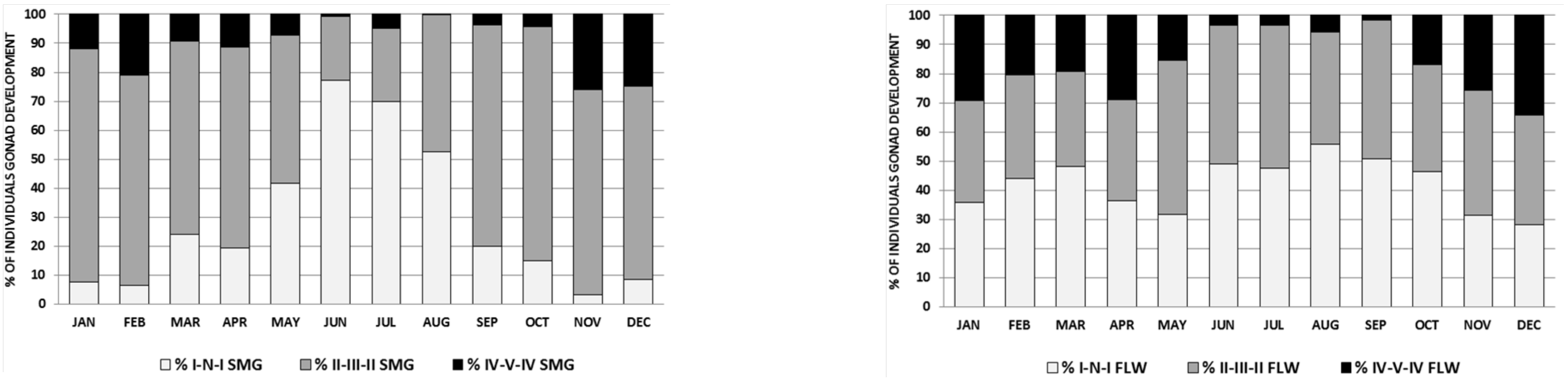
3.3.3.1. Spatial patterns in reproductive phenology of *Patella aspera* - Flores and São Miguel islands

In Flores the percentage of immature and neuter individuals (%I-N-I) reached its maximum (resting season) in August (56%); while in São Miguel this maximum was observed earlier in June (77%) (Figure 3.7.a,b). Through the comparison of the immature gonad stage development (I-N-I) of both islands, a clear resting season was evident for S. Miguel (>50% resting - June, July and August). This was less evident in Flores with over 50% resting only occurring in August, but with more than 40% resting between June and October (Figure 3.8.a). Onset of ripening started earlier in Flores than in S. Miguel. For the most advanced development of gonad stages (%IV-V-IV) the highest percentage of individuals reached the spawning stage in December (34%) in Flores, whereas in S. Miguel this occurred in November (26%) (Figure 3.7.a,b), but the trajectories of ripening were similar. The proportion of ripe individuals (%IV-V-IV) was low in both islands, but ripe individuals were significantly greater in Flores (Wilcoxon sign-rank test: $p=0.021$) (Figure 3.8.a,b).

The largest shell lengths of *P. aspera* were observed in S. Miguel, the differences in shell length being significant between the islands (Kolmogorov-Smirnov test: $p<0.0001$) (averaged shell length: SMG - 50.26 mm (±6.59 mm); FLW - 47.68 mm (±5.70 mm)) (Figure 3.9.a). In S. Miguel there was some variation of the sex ratio in the limpets collected throughout the year (Figure 3.7.c). In contrast the limpets collected in Flores did not show much variation of the sex ratio through the year (Figure 3.7.d). The percentage of females in samples from Flores ranged between 26-42% (respectively December and May); while in S. Miguel they ranged between 22-54% (respectively February and October) (Figure 3.7.c,d). In Flores, the percentage of males ranged between 45-63% (respectively February and November); whereas in S. Miguel they ranged between 45-78% (respectively October and February) (Figure 3.7.c,d). The percentage of neuters in Flores ranged between 7-27% (respectively November and February) while in S. Miguel these ranged between 0-26% (respectively November, December, January, February and June) (Figure 3.7.c,d).

The percentage of females and males was similar between the islands. Both sexes showed a lower percentage of individuals reaching advanced gonad stages (%IV-V-IV) in S. Miguel and Flores, with these percentages being even lower in S. Miguel (Figure 3.8.c,d). A Wilcoxon signed-rank test showed that there were significant differences in the percentage of ripe individuals (%IV-V-IV), both in females and males, between islands (females: $p<0.001$ and males: $p=0.034$). There were also significant differences, for both sexes, in shell length between islands, with the largest individuals collected in S. Miguel (Kolmogorov-Smirnov test: females - $p<0.0001$ and males - $p<0.0001$) (averaged shell length: SMG - female 51.25 mm (±6.65 mm) and male 50.02 mm (±6.48 mm); FLW - female 48.56 mm (±5.90 mm) and male 47.92 mm (±5.73 mm)) (Figure 3.9.b,c).

a) SÃO MIGUEL **b) FLORES**



c) SÃO MIGUEL **d) FLORES**

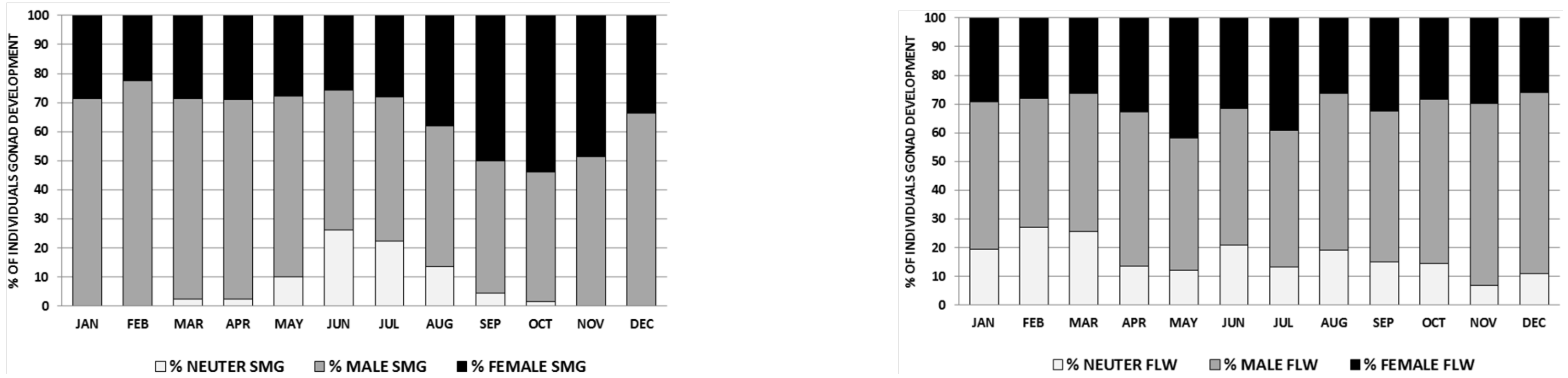


Figure 3.7. Spatial differences in annual pattern of gonad development and sex ratios for *Patella aspera* (+40 mm) recently (2012-2014) across the archipelago (São Miguel (SMG) and Flores (FLW)): **a)** São Miguel percentage of immature (%I-N-I), intermediate (%II-III) and mature (%IV-V-IV) gonad stages, **b)** Flores percentage of immature (%I-N-I), intermediate (%II-III) and mature (%IV-V-IV) gonad stages, **c)** São Miguel percentages of sexes (female, male and neuter), and **d)** Flores percentages of sexes (female, male and neuter).

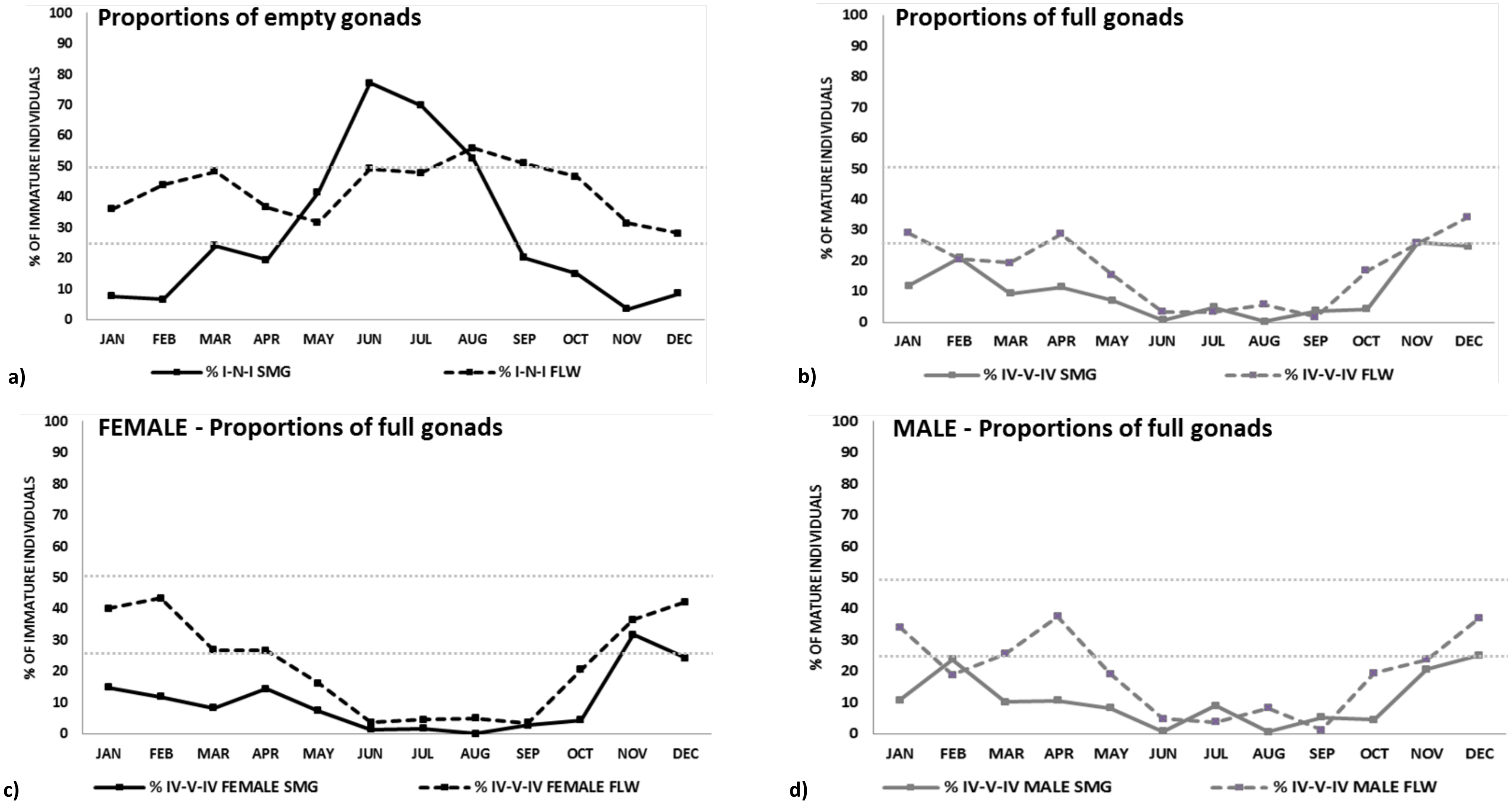


Figure 3.8. Annual pattern of gonad development for *Patella aspera* in S. Miguel (SMG) and Flores (FLW) (+40 mm): **a)** percentage of immature gonad stages (%I-N-I), **b)** percentage of mature gonad stages (%IV-V-IV), **c)** percentage of female mature gonad stages (%IV-V-IV), and **d)** percentage of male mature gonad stages (%IV-V-IV).

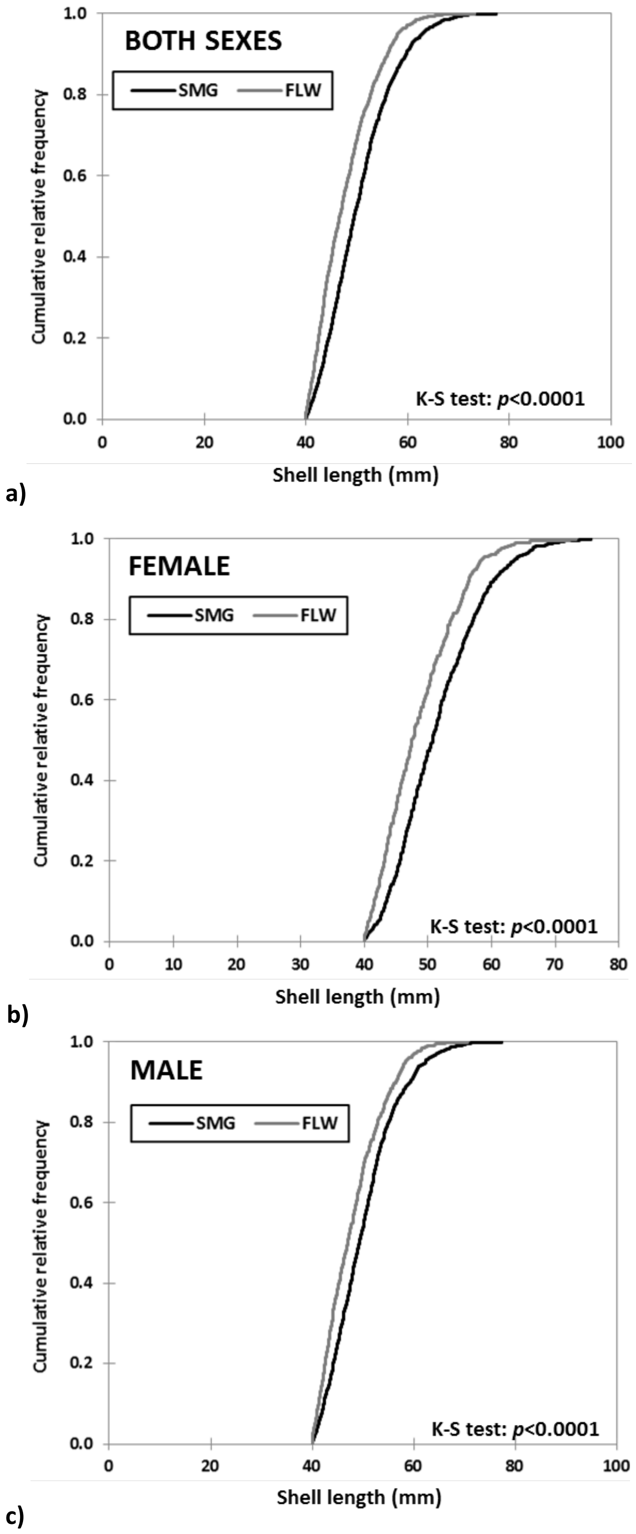


Figure 3.9. Cumulative frequency distributions of shell length for *Patella aspera* in São Miguel and Flores islands (+40 mm): **a)** both sexes shell length (SMG N=2979, FLW N=1773), **b)** female shell length (SMG N=1057, FLW N=559), and **c)** male shell length (SMG N=1681, FLW N=930).

3.3.3.2. Spatial patterns in reproductive phenology of *Patella candei gomesii* - Flores, Santa Maria and São Miguel islands

In all the three islands, the percentage of immature and neuter individuals (%I-N-I) reached its maximum (resting season) in July (Flores - 30%, Santa Maria - 48% and S. Miguel - 62%), with an evident resting season in the Eastern islands (Figure 3.10). In S. Miguel this lasted from June to August, with over 50% resting, while in Santa Maria nearly 50% were resting only in July and August (Figures 3.10 and 3.11). This was less clear in Flores, but over 20% were resting between June and September (Figures 3.10. and 3.11). The percentage of individuals at intermediate levels of gonad maturation (%II-III, filling or emptying) ranged between 43-66% (September-November) in Flores, between 41-82% (November-April) in Santa Maria, and between 30-61% (November-February) in S. Miguel (Figure 3.10). In Flores the highest percentage of individuals reaching the spawning stage (%IV-V-IV) occurred in March (44%); in Santa Maria this occurred in December (54%); whereas in S. Miguel it occurred in November (65%) (Figure 3.10). In all the three islands, a low percentage of individuals (~50% of individuals) reached the maximum ripening stages (IV-V-IV), and subsequently spawned (Figures 3.10 and 3.11). In S. Miguel a clear maximum, indicating spawning, occurred in November (>50% spawning), while in Santa Maria the peak of reproductive activity lasted from December to January (over 50% spawning) (Figures 3.10 and 3.11). In Flores the spawning period was less clear, with over 40% spawning in March and May (Figures 3.10 and 3.11).

A Wilcoxon signed-rank test revealed statistically significant differences in the percentage of individuals at immature stages of gonad development between S. Miguel and Flores islands ($p<0.001$). For the remaining combinations, there were no differences among islands (Table 3.7).

Significant differences were found on the total shell length of *P. candei gomesii* among the islands, with the largest shell lengths recorded in Flores and the lowest in S. Miguel (Kolmogorov-Smirnov test: SMG-FLW - $p<0.0001$, SMG-SMA - $p<0.0001$, and FLW-SMA - $p<0.0001$) (averaged shell length: SMG - 20.54 mm (±4.19 mm), FLW - 35.92 mm (±5.72 mm) and SMA - 27.85 mm (±5.36 mm)) (Figure 3.12).

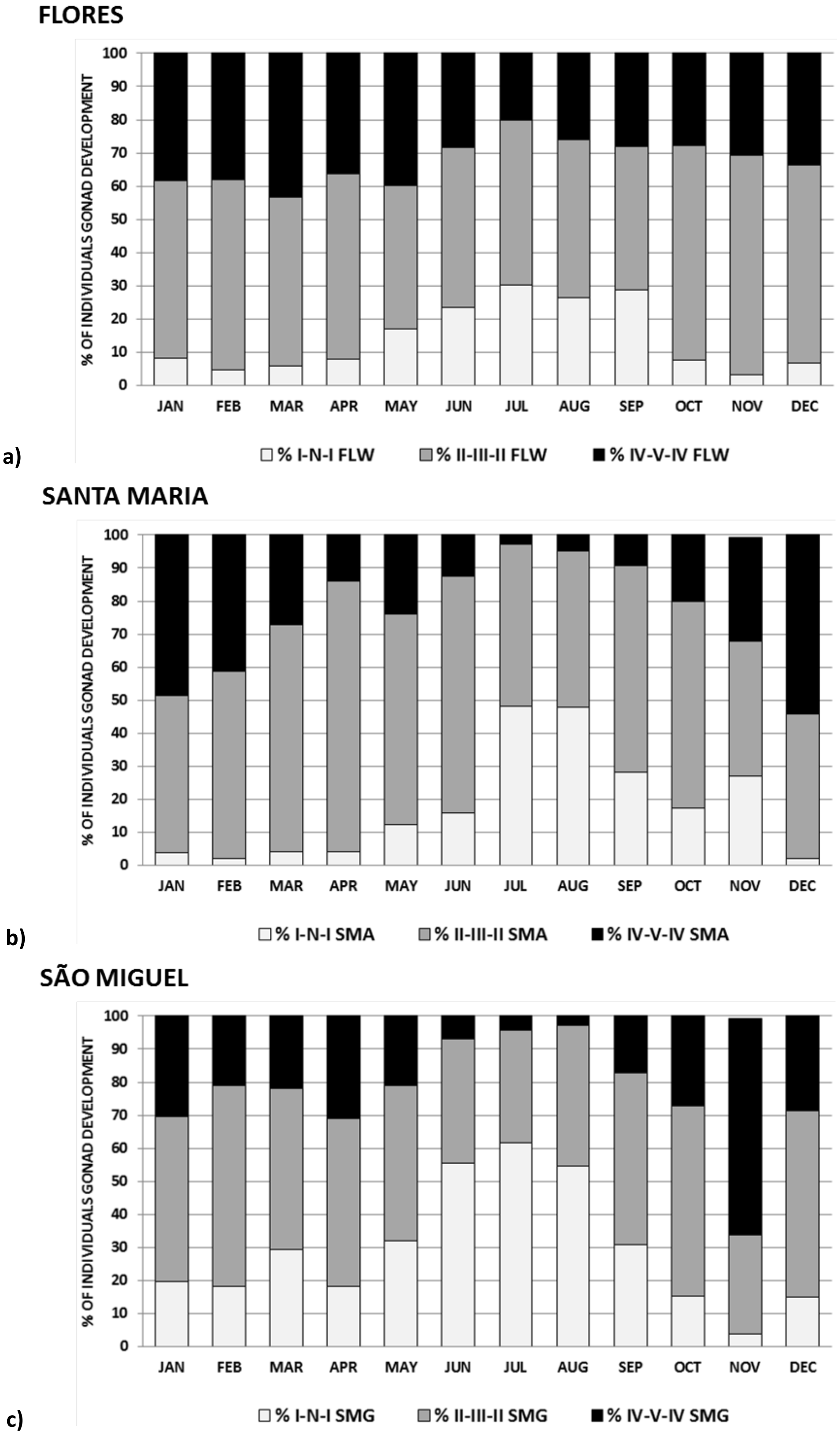


Figure 3.10. Spatial differences in annual pattern of gonad development for *P. candei gomesii* (%I-N-I, %II-III and %IV-V-IV) across the islands (+10 mm) recently (2012-2014): **a)** Flores (FLW), **b)** Santa Maria (SMA), and **c)** São Miguel (SMG).

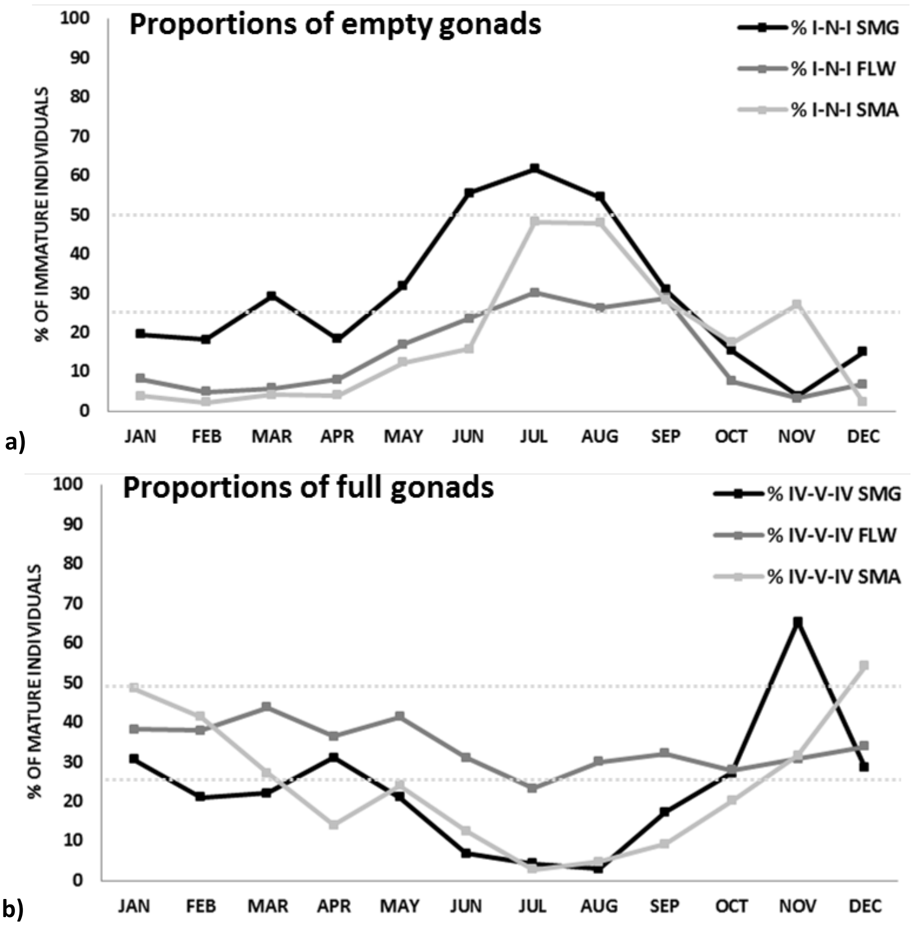


Figure 3.11. Annual pattern of gonad development for *Patella candei gomesii* in São Miguel (SMG), Flores (FLW), and Santa Maria (SMA) islands (+10 mm): **a)** percentage of immature gonad stages (%I-N-I), and **b)** percentage of mature gonad stages (%IV-V-IV).

Table 3.7. Wilcoxon signed-rank test of gonad stage development between islands (%I-N-I and %IV-V-IV) for *Patella candei gomesii* (Bonferroni correction (*p*=0.017); in box - statistically significant).

Wilcoxon signed rank test	% I-N-I			% IV-V-IV		
	SMG v FLW	SMG v SMA	FLW v SMA	SMG v FLW	SMG v SMA	FLW v SMA
W	-78	-56	6	54	10	-48
N	12	12	12	12	12	12
z	-3.059	-2.197	0.235	2.118	0.392	-1.883
P	<0.001	0.027	0.85	0.034	0.733	0.064

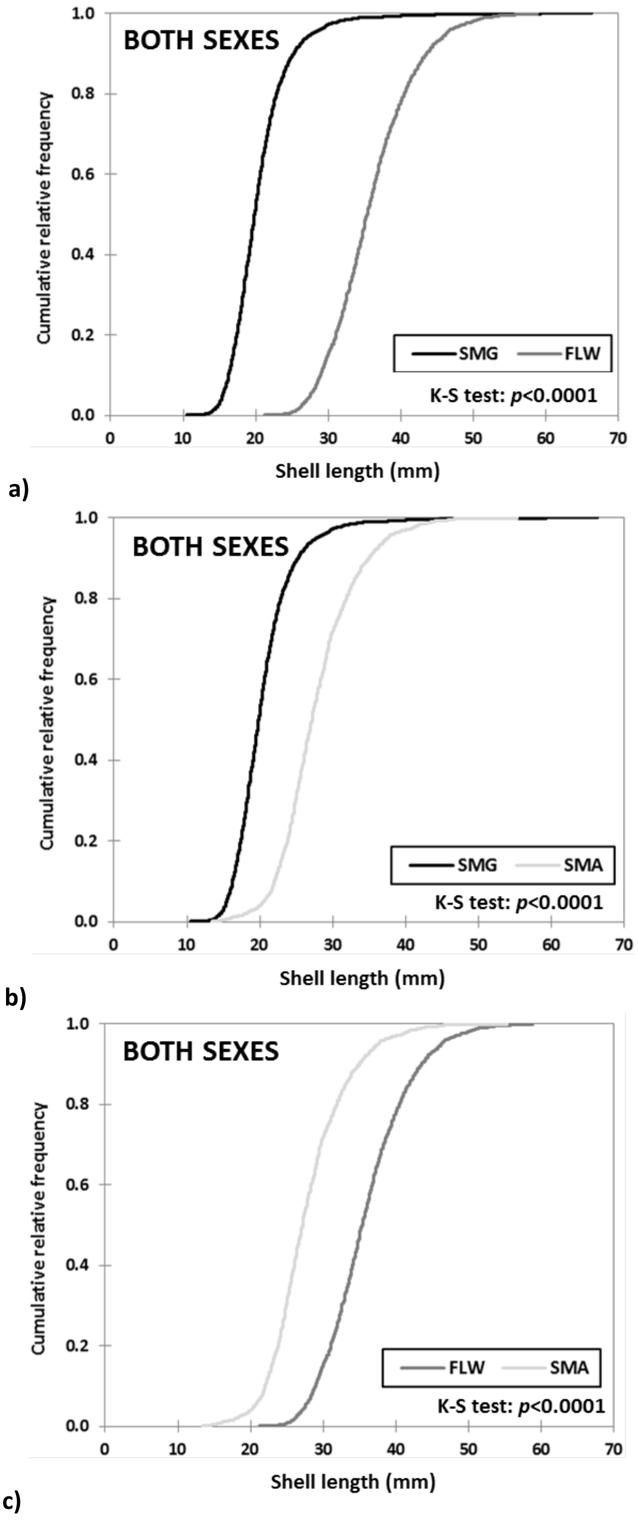


Figure 3.12. Cumulative frequency distributions of shell length for *Patella candei gomesii* between the three islands (+10 mm)*:* **a)** São Miguel - Flores (SMG N=5939, FLW N=2643), **b)** São Miguel - Santa Maria (SMG N=5939, SMA N=1541), and **c)** Flores - Santa Maria (FLW N=2643, SMA N=1541) (Bonferroni correction: *p*=0.017).

3.4. DISCUSSION

3.4.1 Limitations of work

As this work has progressed, several issues have emerged in terms of collection of past data and logistical issues with collection of present day data. Recent collection of the limpets was made on a monthly basis concurrently in several islands; thus several collaborations had to be established. Unfortunately, for Faial Island we were not able to obtain enough data to allow a complete temporal and spatial analysis. Harsh sea conditions, especially in the winter months, also impaired the number of samples collected on several islands. Moreover, intensive exploitation of limpets in the Azores raised some problems for our sampling. For example, the recent collection of *P. aspera* in S. Miguel was made subtidally to ensure specimens matching the established size criteria (+40 mm shell length) for evaluation of gonad development. Historical data for S. Miguel came from market samples collected subtidally, thereby ensuring comparability.

Overall the historical data was scattered in time and space due to past funding limitations and logistical constraints. Despite these problems the overall pattern of reproductive activity of *P. aspera* in S. Miguel could be determined; especially as there was no inter-annual variability in the recent samples. For *P. candei gomesii,* only the duration of the resting period could be determined for recent years. Bad weather and logistical constraints meant samples during peak reproductive activity were missing.

3.4.2. Long-term changes

Investigations into the breeding cycle of the *P. aspera* in Azores in 1985 revealed that this is a protandrous hermaphrodite species that becomes reproductively active between 40-45 mm in shell length (Martins *et al.*, 1987b). According to Martins *et al.* (1987b), *P. aspera* reached the highest gonad state, leading to the spawning, in January (winter spawning), and between May and July specimens were at the lowest gonad state development (summer resting period). In contrast, Martins *et al.* (1987b) were not able to determine a clear breeding cycle in the gonochoristic species - *P. candei gomesii* (sexually mature 10 mm). This species apparently spawned all year round and did not show a synchronized resting period nor a peak of spawning activity.

In my study, the resting period of *P. aspera* appears to be longer, less sharp and with a delay of approximately 1 month (July to August) compared with the data from 30 years ago. These variations could be related with the clear increase of surface air temperature in S. Miguel (see Chapter 2), reflecting the likely increased stress in the summer months; perhaps leading to a longer and delayed resting season. In this study we are comparing the end of a cold period (1980s) with the end of a warm period (2010s) (see Chapter 2). Thus it would be expected that increased global temperatures and higher frequency of extreme warm events would have had a major influence on these populations, perhaps leading to an extended resting period (Moore *et al.*, 2011).

In the recent data, a clear peak of spawning could not be determined for *P. aspera*. However, a statistically significant difference was detected at the onset of reproductive activity, occurring earlier (November and December) compared with the historic data. This could be an indirect consequence of an increase in storminess conditions (extreme events). According to past work (e.g. Orton *et al.*, 1956; Bowman and Lewis, 1977, 1986; Thompson, 1979; Fretter and Graham, 1981) high wave action is a stimulus for the spawning. Guerra and Gaudêncio (1986) also detected a relationship between the spawning peak and stormy conditions for *P. depressa* and *P. ulyssiponensis* in Portugal. Synchrony in the release of the gametes between females and males of *P. aspera* was also observed in my study, which is in agreement with that described for other patellid species (e.g. Branch, 1981). In contrast with historic data, however, a lower proportion of individuals now seem to be reaching mature gonad stages (IV-V-IV less than 25%), suggesting incomplete spawning in this species. This could be due to a lack of synchrony at lower population densities, since according to Ferraz (1998) *P. aspera* is the most exploited of the two exploited patellid species in the Azores. It could also be because limpets were larger in historical samples, thus enabling progress to full maturity; this may not be possible in small recently matured individuals. This lack of full reproductive development and hence output could strongly affect the population dynamics of the species. Moore *et al.* (2011), also recorded a lower proportion of individuals reaching advanced stages of gonad development for *P. vulgata* in Britain and related this with the increase of adverse environmental conditions (increased warming), which could affect the reproductive success of the populations.

The temporal analysis of the reproductive phenology of *P. candei gomesii* has shown significant differences in the breeding cycle of this species. Care is needed, however, in the analyses of these results due to the low number of recent samples. Even so, historical data suggests, this species has multiple spawning peaks (spring and autumn) followed by redevelopment of gonads with some partial resting over the summer months. There appears to be a more defined resting period in recent years than historically, perhaps reflecting greater stress in the summer. These results are partially in agreement with the findings from Cúrdia *et al.* (2005), who stated that this species is an end summer single brood spawners. Their findings, however, were based on observations for one year with sampling once in each season. Moore *et al.* (2011) showed that, in Southwest Britain, the warm water Lusitanian *P. depressa* has multiple broods for much of the year (March-October), as was also shown in warmer conditions of Portugal (Ribeiro *et al.*, 2009). *Patella depressa* is closely related to *P. candei gomesii* (Côrte-Real *et al.*, 1996; Sá-Pinto *et al.*, 2005), suggesting that both species could be multiple spawners.

3.4.3. Spatial patterns

The spatial patterns of the reproductive phenology of *P. aspera* across the Azorean archipelago revealed that populations in West (Flores) had a much less clear resting season than in East (S. Miguel). Moreover, the resting season in the Flores appears to be occurring approximately 2 months after that recorded in S. Miguel. These differences could be related with surface air temperature and sea surface temperature regimes across the archipelago. Sea and air temperatures increased from the West to the East, with the temperatures being highest in S. Miguel (see Chapter 2). Timing of spawning maxima differed across the archipelago, occurring in the West (Flores - December) a month later than in the East (S. Miguel - November). This winter breeding species, however, did not show a clear peak of spawning. It has been suggested that in single brood spawners, such as *P. vulgata*, spawning is triggered by wave activity, resulting in the release of gametes (Orton *et al.*, 1956; Bowman and Lewis, 1977, 1986; Moore *et al.*, 2011). In the Azores, wave action pattern along the archipelago shows an increase of the median wave action from the East to the West (Chapter 2). Also, the Western group appear to have experienced stormier weather conditions in recent years than the Eastern group (Chapter 2). The results for *P. aspera* therefore appear to contradict the suggestion that the increase in stormier events would trigger spawning: earlier peak spawning would be expected in the West; but this was not the case. This could be because lower temperatures result in less rapid gonad development and that there is insufficient ripeness for spawning to be triggered by storms. Low proportions reached maturity in both the East and West; the lowest proportions of individuals reaching mature gonad stages were detected in S. Miguel (less than 25%).

In recent years, *P. candei gomesii* showed a clear summer resting season in all three islands (Flores, S. Miguel and Santa Maria). The resting period started earlier in S. Miguel than in Flores. My results, revealed an evident spawning peak in S. Miguel and Santa Maria (Eastern islands), and suggest that spawning season occurred first in the East (S. Miguel - November and Santa Maria - December) and later in the West (Flores - March). These results follow a similar pattern to that observed for *P. aspera;* both the resting and spawning season in *P. candei gomesii* appear to be occurring earlier in the Eastern than in the Western islands of the Azores archipelago. This perhaps reflects greater stress due to high summer temperatures in the East; this is not alleviated by greater wave action over the summer, leading to an earlier and longer resting phase. The warmer temperatures in the East may allow more rapid ripening and earlier progression to spawning.

3.4.4. Evidence for overexploitation

There was a significant decrease in the shell size of sampled populations of *P. aspera* collected historically and recently in the subtidal. These results reflect the overexploitation of this species in the Azores. According to Ferraz (1998) from the two exploited species of limpets present in the Azores, *P. aspera* is the most harvested. Martins *et al.* (1987b) also shown that the Azorean populations had suffered a decrease in the size of this species in the early 1980s.

There was also a sharp difference in the size of *P. aspera* sampled populations between the East (S. Miguel) and the West (Flores). This may also be related with the different locations were the limpets were collected. It is difficult to find edible and reproductive size *P. aspera* in the intertidal zone, so the collection of this species was made subtidally in S. Miguel. In Flores sufficiently sized individuals could be collected in the low intertidal zone. Côrte-Real *et al.* (1992) observed that subtidal limpets were always larger than those found intertidally, probably related to less stress and greater food availability found in these environments (Hawkins *et al.*, 1990b; Côrte-Real *et al.*, 1996).

The decrease in size, due to harvesting, would have a major impact on the populations, especially on species that are protandrous hermaphrodites (Ribeiro *et al.*, 2009), such as *P. aspera* (Martins et al., 1987b). Continuous overexploitation of this species will have a major effect in these populations, since the size-selective harvesting will alter the sex ratio (Borges *et al.*, 2015), leading to a recruitment failure, due to a decrease in the reproductive output (particularly less eggs) (Ribeiro *et al.*, 2009). At very low population densities lack of synchrony in gamete release often prompted by sperm release acting as a signal (see Levitan, 1988, 1991; Levitan and Petersen, 1995; Levitan and Sewell, 1998; Yund, 2000). These exacerbate this problem increasing Allee effect (Levitan, 1991; McCarthy, 1997; Hawkins *et al.*, 2000; Borges *et al.*, 2015).

In *Patella candei gomesii* limpets were significantly larger in the less populated islands (Flores) than in the highly populated and heavily exploited S. Miguel, confirming previous work (Martins *et al.*, 1987b; Ferraz, 1998; Martins *et al.*, 2008a). *Patella candei gomesii* matures early, does not change sex and shows fast growth; together these traits make this species less susceptible to overexploitation.

3.4.5. Concluding remarks

Some evidence of temporal and spatial shifts in the phenology of the Azorean limpets were identified in this study, probably associated with changes in climate and harvesting. Overall, temperature is an ultimate driver of physiology and hence ripeness of gonads, while storms are a proximate cue for gonad release once ripe. Spatial patterns of phenology did not match predictions; therefore more studies are required in order to determine which environmental factors are important in determining these patterns. In the Azores, the overexploitation of limpets is a major pressure on these populations making these endemic species even more vulnerable to climate change, especially in the case of the protandrous *Patella aspera.*

4. EVIDENCE OF LONG-TERM CHANGES IN THE DISTRIBUTION OF KEY INTERTIDAL SPECIES: CALOURA (PONTA DA GALERA - SÃO MIGUEL ISLAND) AND MONTE DA GUIA (FAIAL ISLAND)

4.1. INTRODUCTION

Global biodiversity is under increasing pressure from human activities driving environmental change. In recent years, there have been major changes in the distribution and abundance of species as a result of complex responses to global environmental changes (Sala *et al.*, 2000; Walther *et al.*, 2002; Helmuth *et al.*, 2006b; Worm *et al.*, 2006; Brook *et al.*, 2008; Cardinale *et al.*, 2012; Garcia *et al.*, 2014). Future scenarios consistently indicate that biodiversity will decline through the 21st century (Pereira *et al.*, 2010). The interaction between regional and local scale impacts (such as habitat loss, habitat degradation, pollution, overexploitation and invasive species) and global climate change represents a great challenge to the biodiversity (Walther *et al.*, 2002; Helmuth *et al.*, 2006b; Brook *et al.*, 2008; Hawkins *et al.*, 2008, 2009; Garcia *et al.*, 2014).

Long-term and broad-scale data are required to distinguish human-induced changes from natural fluctuations (spatial and temporal) in a system (Southward, 1980; Underwood, 1991, 1992, 1994; Southward *et al.*, 1995, 2005; Hawkins *et al.*, 2003, 2008, 2009; Mieszkowska *et al.*, 2006b; Hughes and Heap, 2009; Poloczanska *et al.*, 2011; Wethey *et al.*, 2011). These data sets provide a baseline against which changes can be compared, and provide information to help diagnose the relative importance of global change from regional and local scale impacts (Hawkins *et al.*, 2008, 2015; Mieszkowska *et al.*, 2014b).

Focusing specifically on the effects of recent climate change over the marine ecosystems, several scientific long-term studies have been made; contributing to an increased knowledge and understanding of the current and future potential impacts of climate change (Heip *et al.*, 2011).

Rocky shores are found worldwide, and are typically open systems with sharp environmental gradients, supporting a varied community of plants and animals (Raffaelli and Hawkins, 1996). Their easy accessibility renders them very vulnerable to several human-induced impacts, such as overexploitation, introduction of alien species, coastal urbanization (e.g. addition of coastal defence structures), pollution (e.g. oil spills, eutrophication) as well as responses to global changes (e.g. sea level rise and climate change) (Thompson *et al.*, 2002). These ecosystems are fairly simple which makes them an exceptional model system to study the consequences of climate change and other impacts on communities and ecosystem processes (Helmuth *et al.*, 2006b; Hawkins *et al.*, 2008, 2009). There have been extensive long-term and broad-scale studies providing baselines against which to judge change (e.g. Barry *et al.*, 1995; Herbert *et al.*, 2003; Rivadeneira and Fernández, 2005; Mieszkowska *et al.*, 2006a; Lima *et al.*, 2007; Poloczanska *et al.*, 2011; Wernberg *et al.*, 2013). Moreover, a plethora of experimental studies on these ecosystems (e.g. Connell, 1972; Paine, 1994) has provided good understanding of ecological processes, enabling interpretation of the ecological consequences of climate change and interactions with other impacts (Helmuth *et al.*, 2006b).

The use of rocky shore species as sentinels for the detection of change has advantages over other marine systems that are less accessible and more expensive to survey (Lewis, 1986; Southward *et al.*, 1995, 2005; Hawkins *et al.*, 2008). According to several authors (Lewis, 1996, 1999; Sagarin and Gaines, 2002; Hiscock *et al.*, 2004; Lima *et al.*, 2006) sessile and sedentary rocky shore species are the best candidates to monitor change, since they are visible, simple to identify and slow-moving. Several studies have used intertidal systems to record rapid changes in the abundance and distribution of intertidal species linked with changes in climate (see reviews in Southward *et al.*, 1995; Helmuth *et al.*, 2006b; Hawkins *et al.*, 2009).

The MarClim project investigated the effects of climate change on marine biodiversity in the UK and Ireland using previously well-studied rocky shores species as biological indicators. Results provided evidence of recent climate change leading to changes in the abundance, population structure and biogeographic ranges in some intertidal species (Hawkins *et al.*, 2003, 2008, 2009; Southward *et al.*, 2005; Mieszkowska *et al.*, 2006a,b, 2007, 2014a). Examples of northward shifts of the northern limits of several warm-water species and small retractions of some cold-water species at their southern distributional limits were also provided (Southward, 1991; Lima *et al.*, 2006; Mieszkowska *et al.*, 2006a; Wethey and Woodin, 2008). Changes have also been observed in the annual reproductive cycles of several species (Mieszkowska *et al.*, 2007; Moore *et al.*, 2011).

The overall aim of this chapter was to make long-term comparisons (late 1980s to 2012-2014) in two marine protected areas (MPAs) in the Azores for which baseline data were available: Caloura in São Miguel (see Hawkins *et al.*, 1990a) and Monte da Guia in Faial Island (unpublished data from Expedition Azores 1989 and Martins *et al.*, 1992). For both Caloura and Monte da Guia, patterns of vertical distribution and abundance of key species in the Azorean rocky intertidal zone were compared. Comparisons were made between 1988 and 2012-2014 in the case of Caloura, and between 1989 and 2013-2014 in the case of Monte da Guia. The recent surveys were done annually for three (Caloura) and two (Monte da Guia) years respectively to measure inter-annual variability.

The observed changes were discussed in light of the knowledge of the factors affecting the Azorean rocky intertidal in these areas. In addition to possible climate change responses, Azorean rocky shores are heavily exploited for limpets (Martins *et al.*, 1987a,b; Hawkins *et al.*, 1990a, 2000; Santos *et al.*, 1990) a keystone grazer that has a major influence on rocky shore communities (Martins *et al.*, 2008a, 2009, 2010).

4.2. MATERIAL AND METHODS

4.2.1. Study Areas, data collection and sampling design

4.2.1.1. Caloura - Ponta da Galera (São Miguel Island)

On São Miguel, the study site was at Ponta da Galera, Caloura (Figure 4.1). This is a Site of Conservation Interest (SCI) and a Limpet Protection Zone (LPZ) where the extraction of biota is completely forbidden; nevertheless, there is a lack of complete enforcement precluding its full function as a marine protected area (Martins *et al.*, 2011). Three basaltic rock areas separated by at least 40 m were surveyed, with different levels of wave exposure ranging from exposed (a small headland - A), to moderately exposed (the side of a gully - B) and moderately sheltered (a small embayment - C) (Figure 4.2).

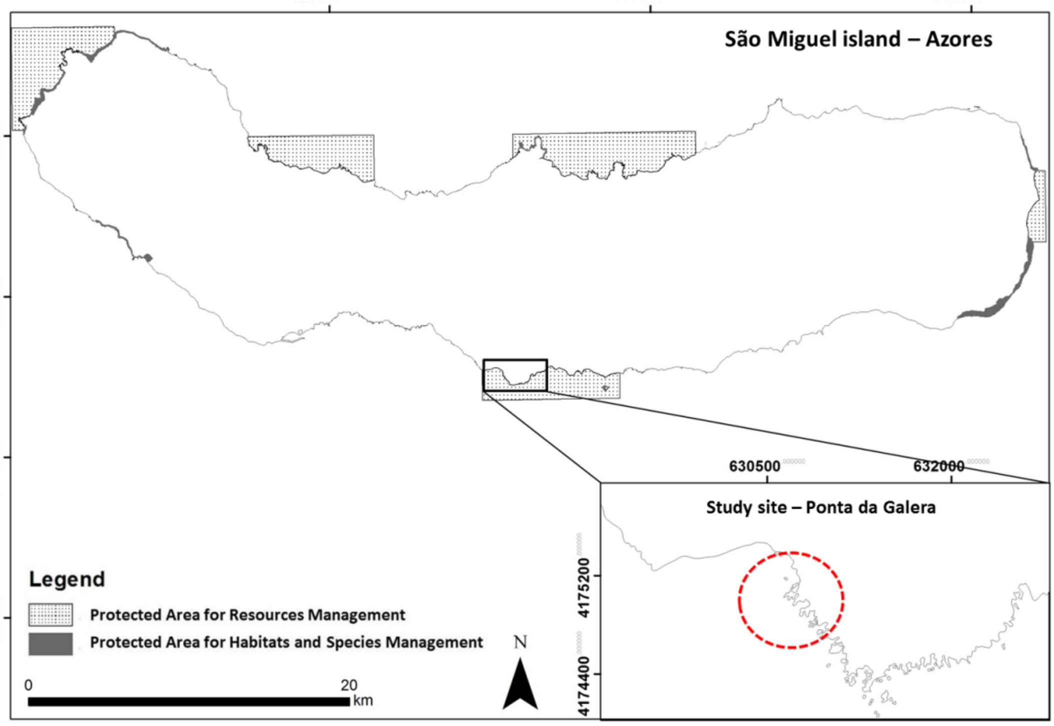


Figure 4.1. São Miguel Island showing location studied - Ponta da Galera (Caloura).

Figure 4.2. Transects studied: **A)** Exposed; **B)** Moderately Exposed; **C)** Moderately Sheltered.

Data were collected in two distinct periods, the 1980s (in 1988 by S. J. Hawkins, A. I. Neto and their colleagues (Hawkins *et al.*, 1990a)) and the 2010s (2012-2014) under the present study. Historic data was extracted directly from Hawkins *et al.* (1990a) using the program *ImageJ v.1.46e* and compared with recent data, since, unfortunately the raw data could not be relocated. The same transects were used in both the historic survey (Hawkins *et al.*, 1990a) and the new surveys. The exact survey areas from 1988 survey were easily located due to marks left on the rock and the memory of S. J. Hawkins who participated in two of the re-surveys.

The recent survey was replicated annually over three years: July-August 2012, July 2013 and July 2014. Although only a single survey was made historically (Hawkins *et al.*, 1990a), using data from three replicated years was necessary to reduce the likelihood that results are influenced by chance or stochastic events preceding the sampling time (e.g. storms) or particularly abnormal years in terms of environmental conditions that could affect the interpretation of results. This approach is often used in environmental impact studies where only a single impacted site is available and compared to multiple control sites (ACI and BACI designs) (Underwood, 1991, 1992, 1994). Surveys were made during low-water spring tides, using the same sampling methods as the 1988 surveys, as described in Hawkins *et al.* (1990a) to ensure comparability.

Two graduated poles were used to determine the elevations along each transect relative to low water. Elevations were related to chart datum for the Azores, using the level of the sea at the time of predicted low-water (± 0.10 m above Chart Datum). On each sampling date and in each of the three areas, non-destructive samples were made at several vertical intervals, determined by the shore topography and the upper and lower limits of vertical distribution of taxa and functional groups. At each area and shore level, the abundance of mobile organisms (e.g. patellid limpets) was estimated by counting all individuals inside replicate quadrats. The abundance of sessile organisms was estimated as percent cover using the relative abundance of taxa in each of the quadrats. Five replicate quadrats (0.50 x 0.50 m on the lower algal dominated shore; 0.25 x 0.25 m quadrats from the barnacle-dominated shore upwards) were sampled at each level on the shore. Taxa were identified to the lowest taxonomic resolution possible in the field.

4.2.1.2. Monte da Guia (Faial Island)

Monte da Guia (Faial Island) is a fully-enforced no-entry marine reserve (Figure 4.3). At this location, four soft volcanic tuff areas were selected and surveyed (Figure 4.4): two inner (T1 and T5) and two outer areas (T2 and T6). The surveyed areas were exposed to different levels of wave action from relatively sheltered to exposed sites (inside to outside of Monte da Guia). Areas outside were more accessible and hence protection was less enforced, but was still greater than non-protected sites.

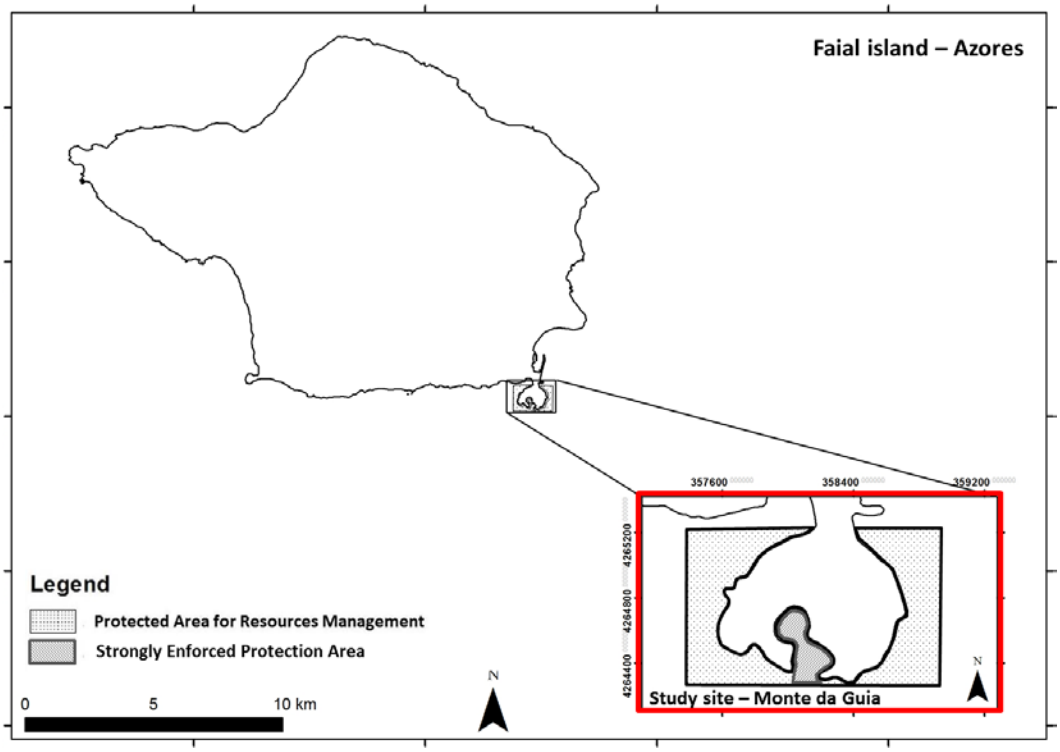


Figure 4.3. Faial Island showing location studied - Monte da Guia.

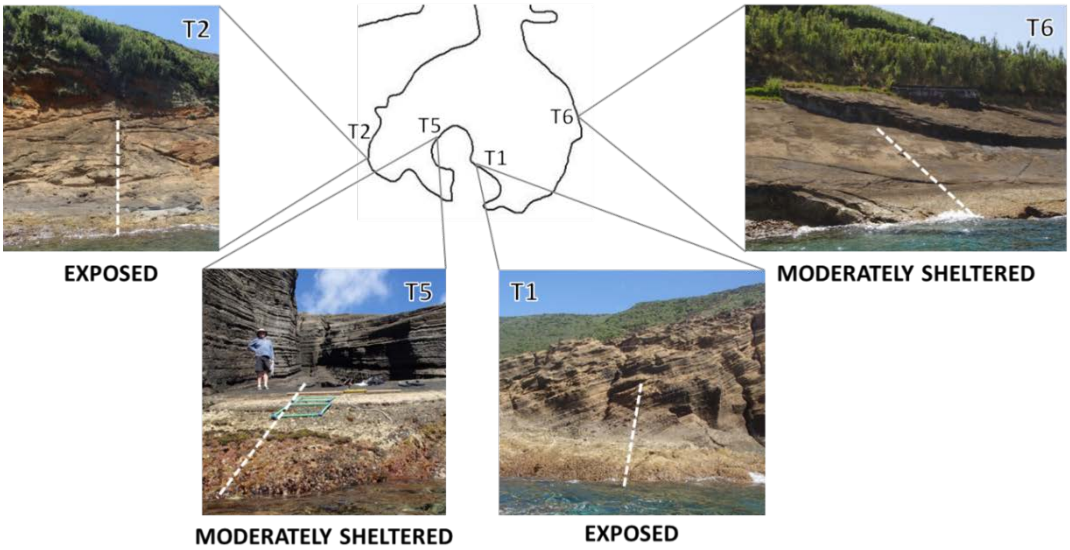


Figure 4.4. Transects studied: T2 and T6 - outside; T5 and T1 inside of Monte da Guia.

The data were collected in two distinct periods: 1989 and in 2013-2014. From the ten areas surveyed in the summer of 1989 by S. J. Hawkins and his colleagues (Martins *et al.*, 1992), four were selected to resurvey (T1, T2, T5 and T6). The same exact transects were located by marks left on the rock and the memory of S. J. Hawkins.

T1, T2, T5 and T6 surveys were made in July 2013 and 2014. Data collection and sampling design followed the same approach as in Caloura.

4.2.2. Data analysis

For analysis in Caloura, organisms were grouped to match the categories used by Hawkins *et al.* (1990a). In Monte da Guia the organisms were grouped to match the categories used in 1989 by S. J. Hawkins and colleagues (unpublished data). These were broadly similar.

4.2.2.1. Changes in the structure of assemblages at key shore levels

At both locations, for each area (Caloura - A (Exposed), B (Moderately Exposed) and C (Moderately Sheltered); Monte da Guia - T1, T2, T5 and T6), historic (Caloura - 1988; Monte da Guia - 1989) and recent (Caloura - 2012 to 2014; Monte da Guia - 2013 and 2014) data on the abundance of key organisms was compared at each of three distinct functional shore levels: (i) the lower eulittoral or sublittoral fringe - low shore (Caloura (0.55-0.76m); Monte da Guia (0.50-0.74m)); (ii) the upper eulittoral - mid shore (Caloura (1.46-1.83m); Monte da Guia (1.95-2.02m)); and (iii) the supralittoral or upper littoral fringe - high shore (Caloura (2.66-2.75m); Monte da Guia (2.25-2.52m)). This was done by comparing the abundance of organisms between the historic data and each of the recent surveys respectively and also against the pooled average of the recent surveys. For each taxon, the relative variation in the abundance between periods was estimated by dividing the abundance of the taxa extracted from the historic data (Caloura - Hawkins *et al.* (1990a); Monte da Guia - unpublished data), for the corresponding shore level, from the relative abundance of the taxa for each of the 5 replicate quadrats recently surveyed. These were then averaged (n=5 for each year, n=15 pooled data for Caloura, n=10 pooled data for Monte da Guia) to provide a standardized measure of change in the abundance of taxa, where values greater than 1 indicate that the taxa increased in abundance, values smaller than 1 indicate that the taxa decreased in abundance and values around 1 indicate that abundance of taxa has remained similar relative to sampling in 1988 (Caloura) or 1989 (Monte da Guia). The overlap of 95% confidence intervals was used to assess whether changes in abundance were significant.

4.2.2.2. Changes in the overall abundance of taxa

To investigate if there were significant differences in the overall abundance of the taxa between 1988 (Caloura) or 1989 (Monte da Guia) and the recent pooled data (Caloura - 2012 to 2014 and Monte da Guia - 2013 and 2014), a Wilcoxon matched-pairs signed-rank test was used where data were sufficient (at least 6 pairs) (W critical value α=0.05). This rank-based non-parametric statistical test uses the relative size of the scores of the same or matched subjects under two experimental conditions by comparing the distributions for positive and negative differences of the ranks of their absolute values (Lowry, 1998). This test allows testing, for paired samples, the null hypothesis (H_0) that the two sets of observations come from the same population against the hypothesis (H_1) that the populations differ in each location (mean or median) (Quinn and Keough, 2002). This was done separately for each location and area with the pooled recent data (Caloura - A, B and C; Monte da Guia - T1, T2, T5 and T6).

4.2.2.3. Changes in the vertical distribution of taxa

For each location and area surveyed (Caloura - A, B and C; Monte da Guia - T1, T2, T5 and T6), the mean abundance of each taxon in both historic and recent surveys (Caloura - 1988, 2012, 2013 and 2014; Monte da Guia - 1989, 2013 and 2014) was plotted against shore height to visually inspect any change in vertical distribution of the organisms over time. It must be noted that for Caloura only the taxa that were plotted in Hawkins *et al.* (1990a) were considered.

4.3. RESULTS

4.3.1. Caloura - Ponta da Galera (São Miguel Island)

4.3.1.1. Changes in the structure of assemblages at key shore levels

Whilst most taxa sampled in 1988 were still present in 2012-2014, some changes in abundance and assemblage composition were recorded.

In the exposed transect (A), taxa such as *Verrucaria* sp., sponges and *Mitra nigra* (Gmelin 1791), which were present in 1988, were never found during the 3 recent surveys. In contrast, *Halopteris scoparia* was consistently present in all 3 recent surveys but was not recorded in 1988. This could have been due to lack of taxonomic expertise of S. J. Hawkins and A. I. Neto in 1988. A few other species were sporadically absent, but not consistently so during the 3 surveyed years (Table 4.1).

In the moderately exposed area (B), *Fucus spiralis*, *Verrucaria* sp., higher plants, sponges, *Mitra nigra* and *Pachygrapsus marmoratus* were regularly absent (over the three years) during the recent surveys. In contrast, *Rivularia* sp. and *Halopteris scoparia* were consistently present in the recent surveys but were not recorded in 1988 (Table 4.1).

In the moderately sheltered transect (C), higher plants, sponges and *M. nigra* were the only 3 taxa present in 1988 that were now consistently absent in all the recent surveys. Unlike these, green algae, *Asparagopsis armata* (Harvey 1855) and *Dictyota* sp. were constantly present in all the recent surveys but were absent from 1988 records (Table 4.1).

Despite the conspicuous changes in the presence or absence of taxa between the two periods, these represent local, not regional extinctions, and are all still relatively common elsewhere. In fact, a few taxa (e.g. *Verrucaria* sp., sponges and higher plants) were not recorded in the recent surveys, although they were present nearby. A few species might also have been overlooked or misidentified during surveys. For instance, the dark colour of *Verrucaria* sp. makes it difficult to distinguish within a black basalt background and it also could be confused with cyanobacteria.

Table 4.1. Caloura taxa absent (-) and new taxa (+) in recent surveys (2012-2014) compared with 1988 survey.

Taxa	A - EXPOSED			B - MODERATELY EXPOSED			C – MODERATELY SHELTERED		
	2012	2013	2014	2012	2013	2014	2012	2013	2014
Gelidium sp.		-	-			-	-		
Nemalion helminthoides				-					
Codium adherens	-								
Green algae							+	+	+
Fucus spiralis			+	-	-	-			
Verrucaria sp.	-	-	-	-	-	-		-	-
Lichina pygmaea				+					-
Rivularia sp.				+	+	+		-	-
Higher plants		-	-	-	-	-	-	-	-
Sponges	-	-	-	-	-	-	-	-	-
Mitra nigra	-	-	-	-	-	-	-	-	-
Pachygrapsus marmoratus		+		-	-	-		-	-
Stramonita haemastoma		-	-		-	-	-		
Patella candei gomesii		-							
Patella aspera			-						-
Lomentaria articulata	+	+							
Halopteris scoparia	+	+	+	+	+	+	+		+
Osmundea sp./*Laurencia* sp.		+	+		+				+
Laurencia marilsae		+						+	+
Laurencia viridis			+		+				+
Caulacanthus ustulatus		+	+					+	+
Chondracanthus acicularis			+						
Asparagopsis armata		+	+		+	+	+	+	+
Pterocladiella capillacea			+		+	+			+
Dyctiota sp.		+	+		+		+	+	+
Colpomenia sinuosa		+	+		+	+			
Leathesia sp.				+					
Codium adherens							+		+
Codium elisabethe			+						
Valonia macrophysa							+		
Chondria sp.									+
Drachiella sp.									+
Ceramium sp.			+						
Cladophora sp.			+		+	+		+	
Chaetomorpha linum			+						+
Liagora sp.			+						
Polysiphonia sp.			+						
Bryopsis sp.					+				
Rhodymenia sp.			+						
Placamium cartilagineum					+			+	+
Blue/green cyanobacteria		+			+				
Eulalia viridis			+						
Ligia sp.		+					+		
Pomatoceros		+							
TOTAL	-(9)/+(24)			-(9)/+(14)			-(10)/+(17)		

In all transects and shore levels, the majority of the taxa showed a significant decrease in abundance between 1988 and the recent surveys (Table 4.2).

On the lower shore, compared to 1988, there was a significant increase in the abundance of total algal turfs both in the exposed and moderately sheltered transects (Table 4.2). In the moderately exposed transect, there was a significant, albeit small, decrease in abundance of total algal turfs. Where present, non-calcareous crusts, calcareous crusts, the macroalgae *Codium adhaerens* (Agardh 1822) and the whelk *Stramonita haemastoma*, all showed a significant reduction in abundance compared to

1988 (Table 4.2). The abundance of the sea-urchin *P. lividus* increased significantly in the exposed transect, but decreased significantly in the other two transects (moderately exposed and sheltered) (Table 4.2). These changes were generally consistent when comparing each year separately and when data were pooled together.

At mid shore levels, and where present, there was a significant reduction in the abundance of the barnacle *C. stellatus*, the grazing gastropods *P. aspera* and *M. neritoides*, calcareous crusts, green algae and *N. helminthoides* ((Velley) Batters 1902) (Table 4.2). In contrast, the abundance of non-calcareous crusts and *G. microdon* increased, although this was not significant for the later. The abundance of the littorinid *T. striatus* decreased significantly in the exposed and moderately exposed transects but increased significantly in the moderately sheltered transect (although this was only significant in one of the three years) (Table 4.2).

At upper levels on the shore, the abundance of both littorinids *T. striatus* and *M. neritoides* decreased significantly across all the range of wave exposure (Table 4.2). The barnacle *C. stellatus* was absent from the moderately sheltered transect. In the remaining transects, its abundance increased significantly in the exposed transect, but decreased significantly in the moderately exposed transect (Table 4.2).

Overall, there appears to have been a functional change in the community, especially at mid shore levels, where the abundance of key perennial primary producers increased, while the abundance of the dominant space occupier, the filter-feeder barnacle *C. stellatus*, and grazing gastropods (*P. aspera* and *M. neritoides*) tended to decrease.

Table 4.2. Caloura: relative changes in mean abundance of taxa (recent versus historic data) for 3 shore heights (low, mid and high) at the Exposed, Moderately Exposed and Moderately Sheltered areas (±CI - interval of confidence (95% confidence), (*) significant difference in the abundance between 1988 and 2012-14, POL - data pooled).

SHORE LEVEL	TAXA (% cover / nos.m^{-2})	A - EXPOSED								B - MODERATELY EXPOSED								C - MODERATELY SHELTERED							
		2012/1989	±CI	2013/1989	±CI	2014/1989	±CI	POL/1989	±CI	2012/1989	±CI	2013/1989	±CI	2014/1989	±CI	POL/1989	±CI	2012/1989	±CI	2013/1989	±CI	2014/1989	±CI	POL/1989	±CI
LOW	Total algal turf	-	-	1.150	**0.017***	-	-	1.150	**0.017***	0.810	**0.099***	0.990	0.068	-	-	0.900	**0.080***	1.150	0.278	1.440	**0.034***	1.460	**0.001***	1.350	**0.115***
	Codium adherens	-	-	0.020	**0.039***	-	-	0.020	**0.039***	0.640	0.535	0.020	**0.036***	-	-	0.330	**0.323***	-	-	-	-	-	-	-	-
	Non-calcareous crust	-	-	0.150	**0.180***	-	-	0.150	**0.180***	-	-	-	-	-	-	-	-	0.750	0.723	-	-	0.040	**0.052***	0.260	**0.287***
	Calcareous crust	-	-	0.010	**0.028***	-	-	0.010	**0.028***	-	-	-	-	-	-	-	-	-	-	0.600	1.176	0.700	0.854	0.430	**0.477***
	Paracentrotus lividus	-	-	3.090	**1.448***	-	-	3.090	**1.448***	0.020	**0.025***	0.000	**0.003***	-	-	0.010	**0.014***	0.310	**0.369***	-	-	0.010	**0.012***	0.100	**0.136***
	Stramonita haemastoma	-	-	-	-	-	-	-	-	0.800	0.733	-	-	-	-	0.400	**0.433***	-	-	-	-	0.200	**0.392***	0.070	**0.131***
MID	*Gelidium* sp.	-	-	-	-	-	-	-	-	7.670	**4.209***	-	-	-	-	3.830	3.195	-	-	-	-	-	-	-	-
	Green algae	0.300	**0.256***	0.050	**0.033***	0.050	**0.080***	0.130	**0.103***	0.030	**0.052***	-	-	-	-	0.010	**0.026***	-	-	-	-	-	-	-	-
	Nemalion helminthoides	-	-	-	-	0.020	**0.039***	0.000	**0.013***	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	Non-calcareous crust	-	-	-	-	-	-	-	-	6.800	6.857	11.600	**7.270***	-	-	9.200	**4.965***	-	-	-	-	-	-	-	-
	Calcareous crust	-	-	0.060	**0.048***	-	-	0.020	**0.021***	0.030	**0.052***	0.050	**0.064***	-	-	0.040	**0.040***	-	-	-	-	-	-	-	-
	Chthamalus stellatus	0.010	**0.005***	0.010	**0.005***	-	-	0.000	**0.003***	0.140	**0.067***	0.020	**0.006***	-	-	0.080	**0.052***	-	-	0.090	**0.030***	0.090	**0.111***	0.090	**0.054***
	Patella aspera	-	-	-	-	-	-	-	-	0.200	**0.392***	0.100	**0.196***	-	-	0.150	**0.209***	-	-	-	-	-	-	-	-
	Patella candei gomesii	-	-	-	-	-	-	-	-	2.240	**1.159***	-	-	-	-	1.120	0.913	-	-	-	-	-	-	-	-
	Tectarius striatus	0.000	**0.002***	-	-	-	-	0.000	**0.001***	0.000	**0.005***	-	-	-	-	0.000	**0.003***	-	-	3.330	**0.900***	-	-	1.660	1.167
	Melarhaphe neritoides	-	-	-	-	-	-	-	-	0.060	**0.044***	-	-	-	-	0.030	**0.028***	-	-	0.220	**0.438***	-	-	0.110	**0.219***
HIGH	*Chthamalus stellatus*	3.500	**0.831***	2.750	**1.429***	0.800	0.750	2.350	**0.818***	0.070	**0.065***	0.530	0.556	-	-	0.300	**0.303***	-	-	-	-	-	-	-	-
	Tectarius striatus	0.100	**0.036***	0.590	**0.376***	0.020	**0.018***	0.240	**0.176***	1.490	1.097	0.560	**0.283***	-	-	1.030	0.614	0.870	0.837	0.550	0.631	0.870	0.602	0.760	0.381
	Melarhaphe neritoides	0.090	**0.065***	0.040	**0.087***	-	-	0.040	**0.038***	0.230	**0.212***	0.550	0.455	-	-	0.390	**0.259***	0.170	**0.134***	0.260	**0.358***	0.170	**0.067***	0.200	**0.122***

4.3.1.2. Changes in the overall abundance of taxa

When considering the entire vertical range of species distribution, there was generally a reduction in the abundance of seven taxa: the gastropods *M. neritoides* and *P. aspera*, the barnacle *C. stellatus*, the calcareous crusts, *N. helminthoides*, and the lichens *Lichina pygmaea* ((Müller) Agardh 1820) and *Verrucaria* sp. (Table 4.3). In contrast, there was generally an increase in abundance of the gastropod *P. candei gomesii*, total algal turf, non-calcareous crusts, *H. scoparia*, *Osmundea* sp./*Laurencia* sp., coarsely-branched algae and blue/green cyanobacteria. Unlike the above, the littorinid *T. striatus*, the semi-terrestrial crab *P. marmoratus*, green algae and *F. spiralis* had variable changes in abundance depending on the level of wave exposure (Table 4.3).

Wilcoxon matched-pairs signed-rank test (Table 4.4) showed that overall, some of these changes were significant although the ability of this test to detect significant changes largely depend on the number of pairs which was limited in most cases.

Table 4.3. Caloura overall mean abundance of taxa in 1988 and recent surveys (2012-2014 pooled (POL); difference between 1988 and recent data (≠)).

Taxa		A - EXPOSED		B - MODERATELY EXPOSED		C - MODERATELY SHELTERED	
		Abundance	≠	Abundance	≠	Abundance	≠
Melarhaphe neritoides (nos.m^{-2})	88	143.640	-82.090	331.740	-221.720	102.300	-70.730
	POL	61.550		110.020		31.570	
Tectarius striatus (nos.m^{-2})	88	261.310	42.410	77.410	20.800	46.500	-7.500
	POL	303.720		98.210		39.000	
Patella candei gomesii (nos.m^{-2})	88	5.880	3.300	3.440	3.850	1.600	0.000
	POL	9.180		7.290		1.600	
Patella aspera (nos.m^{-2})	88	2.450	-1.690	2.880	-2.600	2.470	-1.940
	POL	0.760		0.280		0.530	
Pachygrapsus marmoratus (nos.m^{-2})	88	0.000	0.020	0.180	-0.180	0.530	-0.480
	POL	0.020		0.000		0.050	
Chthamalus stellatus (% cover)	88	14.570	-10.130	12.000	-8.910	2.470	-1.640
	POL	4.440		3.090		0.830	
Total algal turf (% cover)	88	4.380	19.290	16.350	7.430	0.070	27.940
	POL	23.670		23.780		28.010	
Calcareous crusts (% cover)	88	4.930	-0.900	1.410	-1.020	1.730	-1.140
	POL	4.030		0.390		0.590	
Non-calcareous crusts (% cover)	88	0.600	0.020	0.180	2.460	6.600	2.690
	POL	0.620		2.640		9.290	
Green algae (% cover)	88	2.520	-2.250	2.590	-2.510	0.000	0.150
	POL	0.270		0.080		0.150	
Halopteris scoparia (% cover)	88	0.000	0.140	0.000	0.460	0.000	0.050
	POL	0.140		0.460		0.050	
Fucus spiralis (% cover)	88	0.000	0.010	0.530	-0.530	-	
	POL	0.010		0.000			
Nemalion helminthoides (% cover)	88	1.690	-1.630	1.680	-1.640	-	
	POL	0.060		0.040			
Osmundea sp./*Laurencia* sp. (% cover)	88	0.000	1.300	0.000	0.010	0.000	0.010
	POL	1.300		0.010		0.010	
Coarsely branch algae (% cover)	88	0.000	5.130	0.000	6.120	0.000	6.800
	POL	5.130		6.120		6.800	
Lichina pygmaea (% cover)	88	-		0.010	0.000	3.170	-2.910
	POL			0.010		0.260	
Blue/green cyanobacteria (% cover)	88	0.000	4.610	0.000	1.340	-	
	POL	4.610		1.340			
Verrucaria sp. (% cover)	88	0.480	-0.480	0.470	-0.470	0.400	-0.400
	POL	0.000		0.000		0.000	

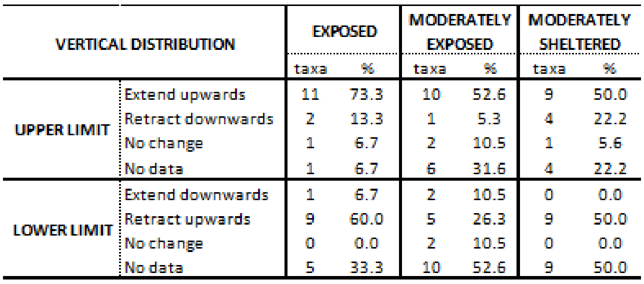
Table 4.4. Wilcoxon matched-pairs signed-rank test comparing changes in abundance between 1988 and recent pooled data (2012-14) in the three studied areas at Caloura (NA - not enough match pairs; in box - statistically significant).

Wilcoxon signed-rank test	A - EXPOSED			B - MODERATELY EXPOSED			C - MODERATELY SHELTERED		
	W	Z	p	W	Z	p	W	Z	p
Melarhaphe neritoides (nos.m^{-2})	-144	-2.897	**0.002**	-77	-2.417	**0.013**	-64	-2.845	**0.002**
Tectarius striatus (nos.m^{-2})	13	0.308	0.782	34	0.879	0.404	-48	-1.364	0.188
Patella candei gomesii (nos.m^{-2})	3	0.314	0.844	4	0.730	NA	-1	-0.105	1.000
Patella aspera (nos.m^{-2})	-9	-0.943	0.438	-15	-2.023	NA	-9	-1.214	NA
Pachygrapsus marmoratus (nos.m^{-2})	1	1.000	NA	-6	-1.732	NA	-43	-2.758	**0.008**
Chthamalus stellatus (%)	-32	-1.255	0.233	-39	-2.312	**0.020**	-16	-1.352	0.219
Total algal turf (%)	45	2.668	**0.004**	18	1.260	0.250	28	2.366	**0.016**
Calcareous crusts (%)	-5	-0.255	0.850	-9	-0.943	0.440	2	0.169	0.940
Non-calcareous crusts (%)	27	1.605	0.129	10	1.826	NA	5	0.524	0.688
Green algae (%)	-19	-1.992	0.060	-22	-1.859	0.080	15	2.060	0.060
Halopteris scoparia (%)	15	2.121	NA	6	1.604	NA	6 (NA)	1.604	NA
Fucus spiralis (%)	1	1.000	NA	-45	-3.000	**0.004**	-	-	-
Nemalion helminthoides (%)	-15	-1.572	0.156	-10	-1.826	NA	-	-	-
Osmundea sp./*Laurencia* sp. (%)	10	1.826	0.125	1	1.000	NA	1	1.000	NA
Coarsely branch algae (%)	10	1.826	NA	6	1.604	NA	21	2.201	**0.031**
Lichina pygmaea (%)	-	-	-	-1	-0.447	NA	-25	-1.482	0.164
Blue/green cyanobacteria (%)	10	1.826	0.125	3	1.340	NA	-	-	-
Verrucaria sp. (%)	-55	-3.162	**0.002**	-36	-2.828	**0.008**	-21	-2.333	**0.031**

4.3.1.3. Changes in the vertical distribution of taxa

Compared to 1988, the recent surveys showed that across the gradient in wave exposure there was a substantial number of taxa (50-73%) whose upper vertical limits of distribution extended upshore; this being most pronounced on the exposed transect (Table 4.5 and Figures 4.5 to 4.10). These included taxa such as *T. striatus*, *P. candei gomesii*, *P. aspera*, total algal turf, *Gelidium* sp., *Codium adhaerens*, non-calcareous crusts, *N. helminthoides*, calcareous crusts, *Lichina pygmaea* and *Rivularia* sp.. In contrast, on the moderately sheltered transect, a few taxa (22% - *M. neritoides, C. stellatus, Verrucaria* sp. and *S. haemastoma*) showed contraction of their upper limits compared 1988 (see Table 4.5 and Figures 4.5 to 4.10). Across the range of exposure to wave action, the lower limits of a substantial proportion of taxa (26-60%) also rose to higher levels on the shore compared to 1988 (Table 4.5 and Figures 4.5 to 4.10). These included taxa such as *M. neritoides, T. striatus*, *C. stellatus*, *P. candei gomesii*, *P. aspera, Gelidium* sp., *N. helminthoides, Verrucaria* sp., *Lichina pygmaea* and *Rivularia* sp.. Compared to 1988, most species moved up on the shore as a block with extensions of both the upper limit of vertical distribution and by disappearing from lower levels on the shore (retraction of the lower limit). In general, patterns of vertical distribution were consistent between the recent years (2012-2014), not showing inter-annual variability. Exceptions were the high shore snails (*M. neritoides* and *T. striatus*) where peaks of abundance varied between years, although overall vertical range changed little.

Table 4.5. Numbers of taxa that changed their upper and lower limits of vertical distribution compared to 1988 at Caloura.



VERTICAL DISTRIBUTION		EXPOSED		MODERATELY EXPOSED		MODERATELY SHELTERED	
		taxa	%	taxa	%	taxa	%
UPPER LIMIT	Extend upwards	11	73.3	10	52.6	9	50.0
	Retract downwards	2	13.3	1	5.3	4	22.2
	No change	1	6.7	2	10.5	1	5.6
	No data	1	6.7	6	31.6	4	22.2
LOWER LIMIT	Extend downwards	1	6.7	2	10.5	0	0.0
	Retract upwards	9	60.0	5	26.3	9	50.0
	No change	0	0.0	2	10.5	0	0.0
	No data	5	33.3	10	52.6	9	50.0

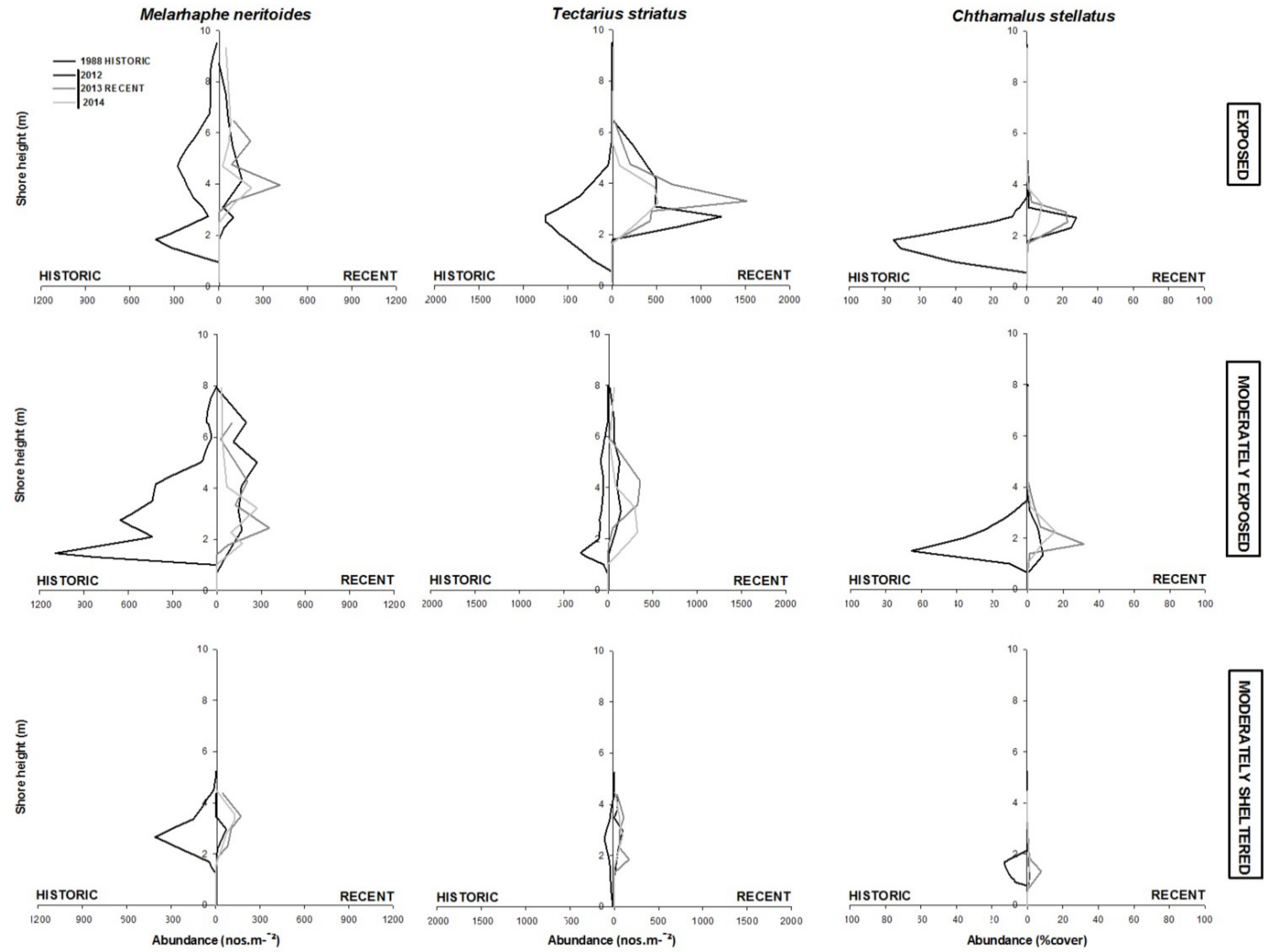


Figure 4.5. Caloura vertical distribution of *Melarhaphe neritoides*, *Tectarius striatus* and *Chthamalus stellatus* in the studied transects A, B and C (Exposed, Moderately Exposed and Moderately Sheltered) for historic (1988) and recent surveys (2012, 2013 and 2014) in relation to shore height (MSLW - Maximum Spring Low Water level (0.16m)).

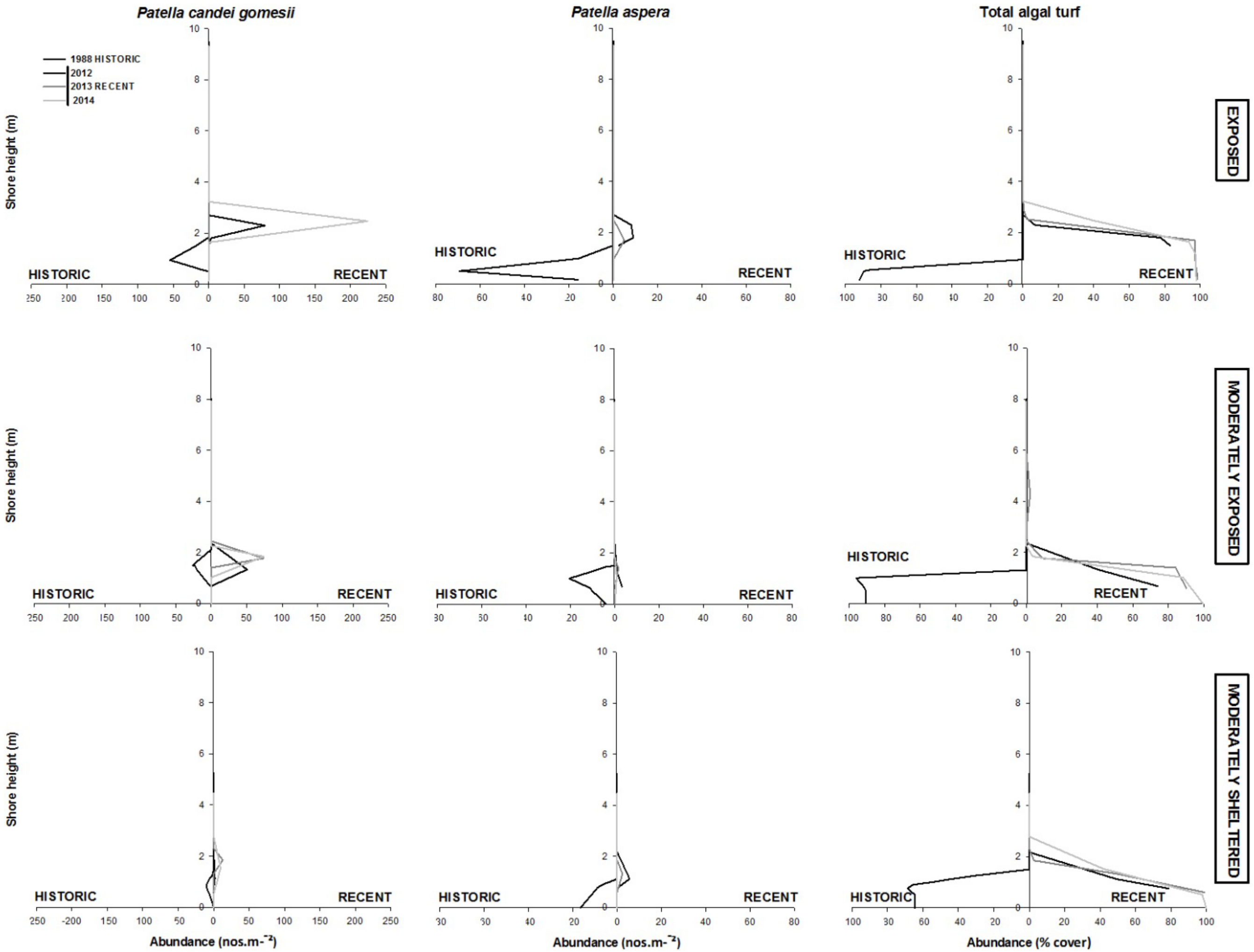


Figure 4.6. Caloura vertical distribution of *Patella candei gomesii*, *Patella aspera* and total algal turf in the studied transects A, B and C (Exposed, Moderately Exposed and Moderately Sheltered) for historic (1988) and recent surveys (2012, 2013 and 2014) in relation to shore height (MSLW - Maximum Spring Low Water level (0.16m)).

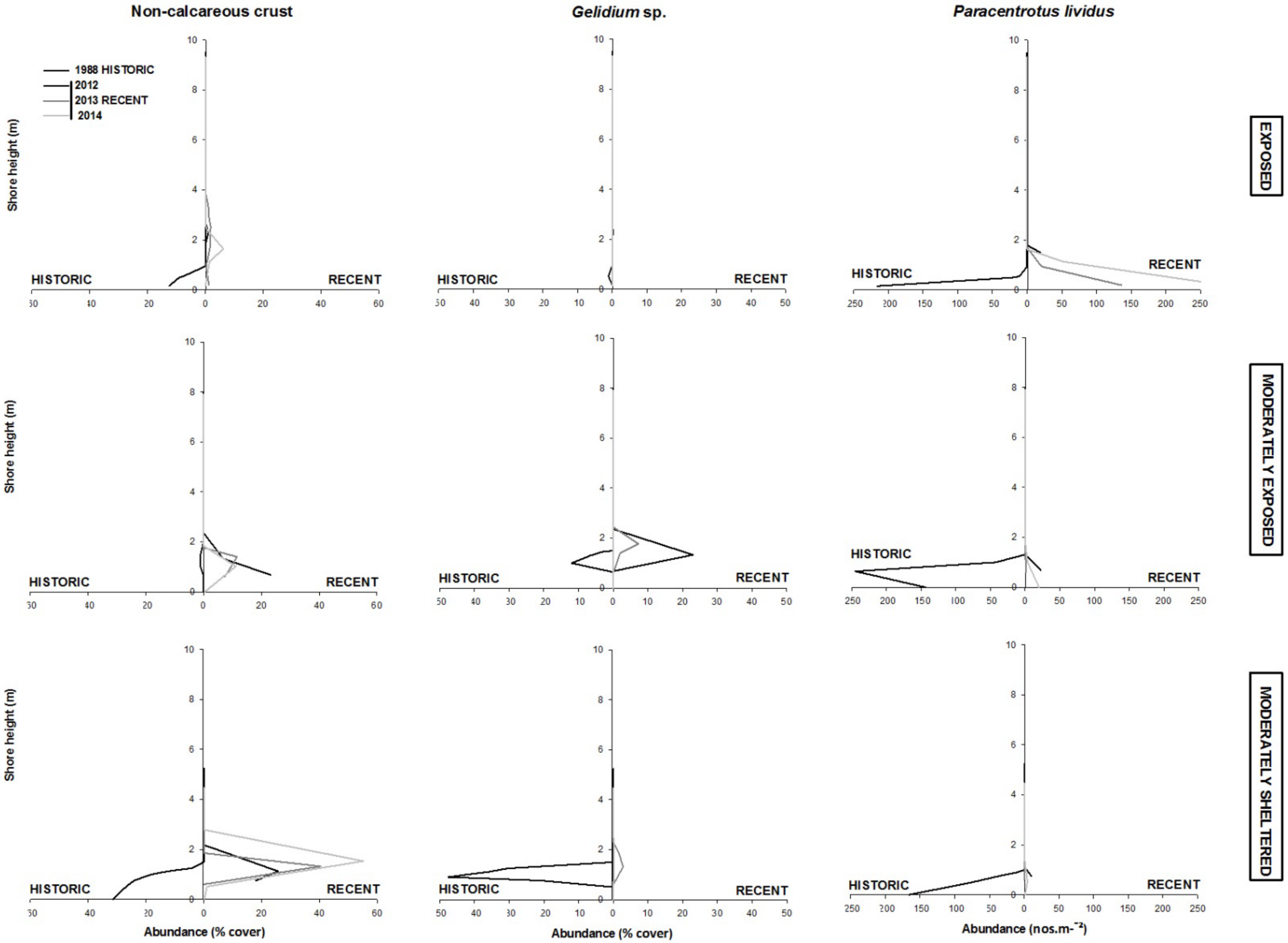


Figure 4.7. Caloura vertical distribution of non-calcareous crusts, *Gelidium* sp. and *Paracentrotus lividus* in the studied transects A, B and C (Exposed, Moderately Exposed and Moderately Sheltered) for historic (1988) and recent surveys (2012, 2013 and 2014) in relation to shore height (MSLW - Maximum Spring Low Water level (0.16m)).

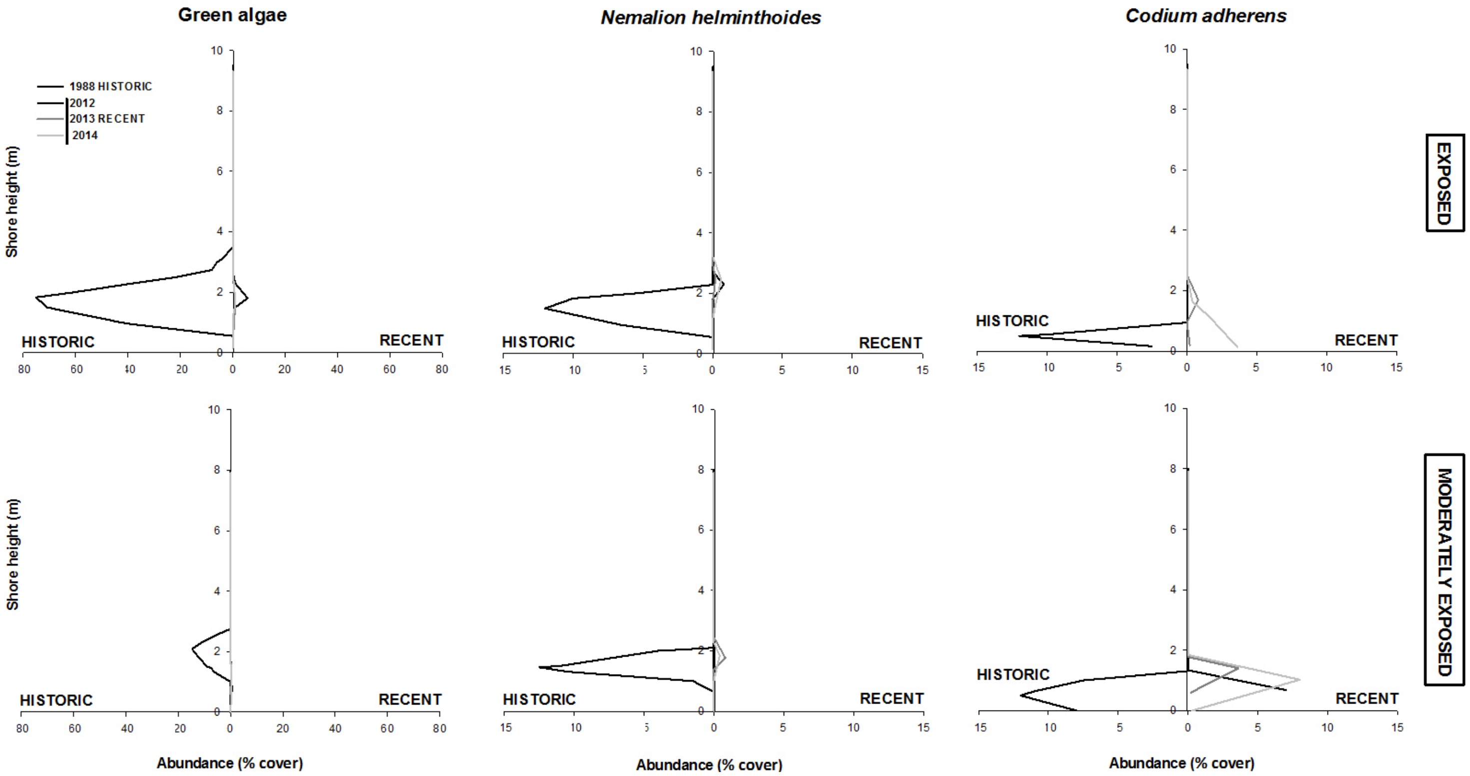


Figure 4.8. Caloura vertical distribution of green algae, *Nemalion helminthoides* and *Codium adhaerens* in the studied transects A and B (Exposed and Moderately Exposed) for historic (1988) and recent surveys (2012, 2013 and 2014) in relation to shore height (MSLW - Maximum Spring Low Water level (0.16m)).

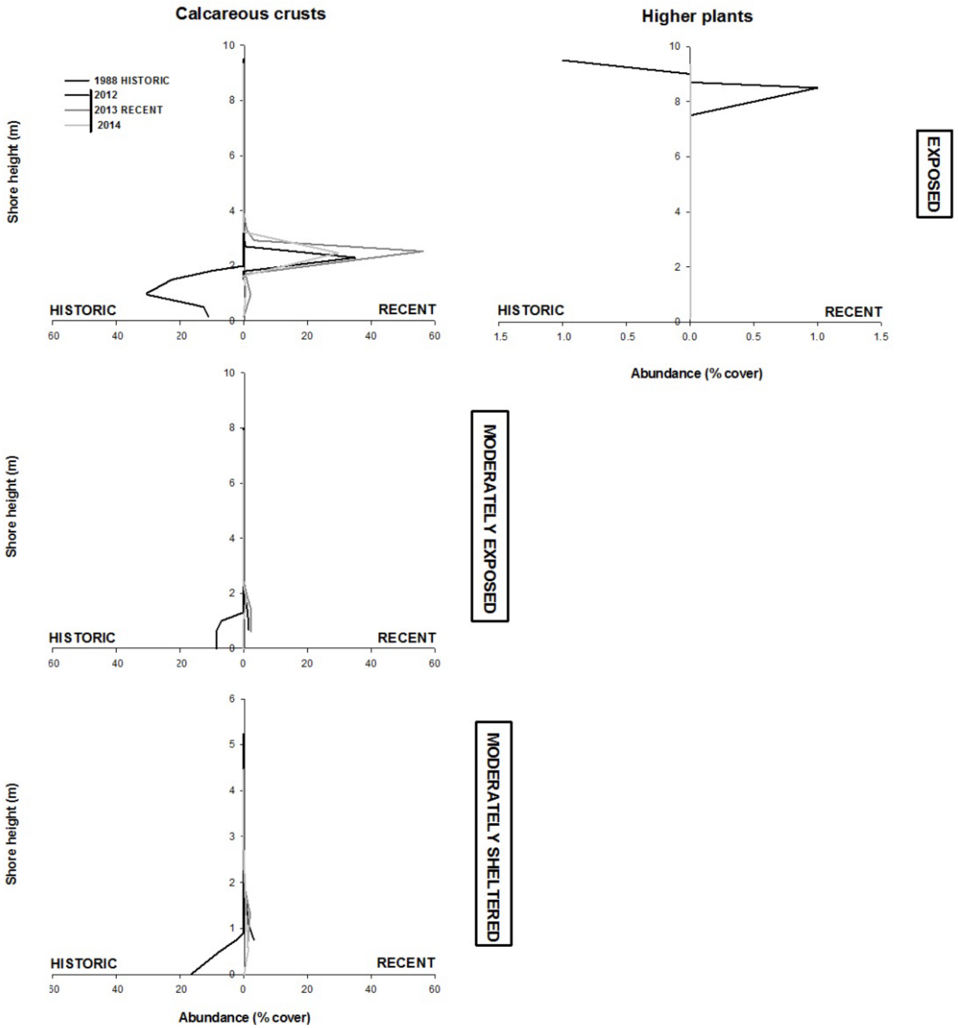


Figure 4.9. Caloura vertical distribution of calcareous crusts in the studied transects A, B and C (Exposed, Moderately Exposed and Moderately Sheltered) and higher plants in transect A (Exposed) for historic (1988) and recent surveys (2012, 2013 and 2014) in relation to shore height (MSLW - Maximum Spring Low Water level (0.16m)).

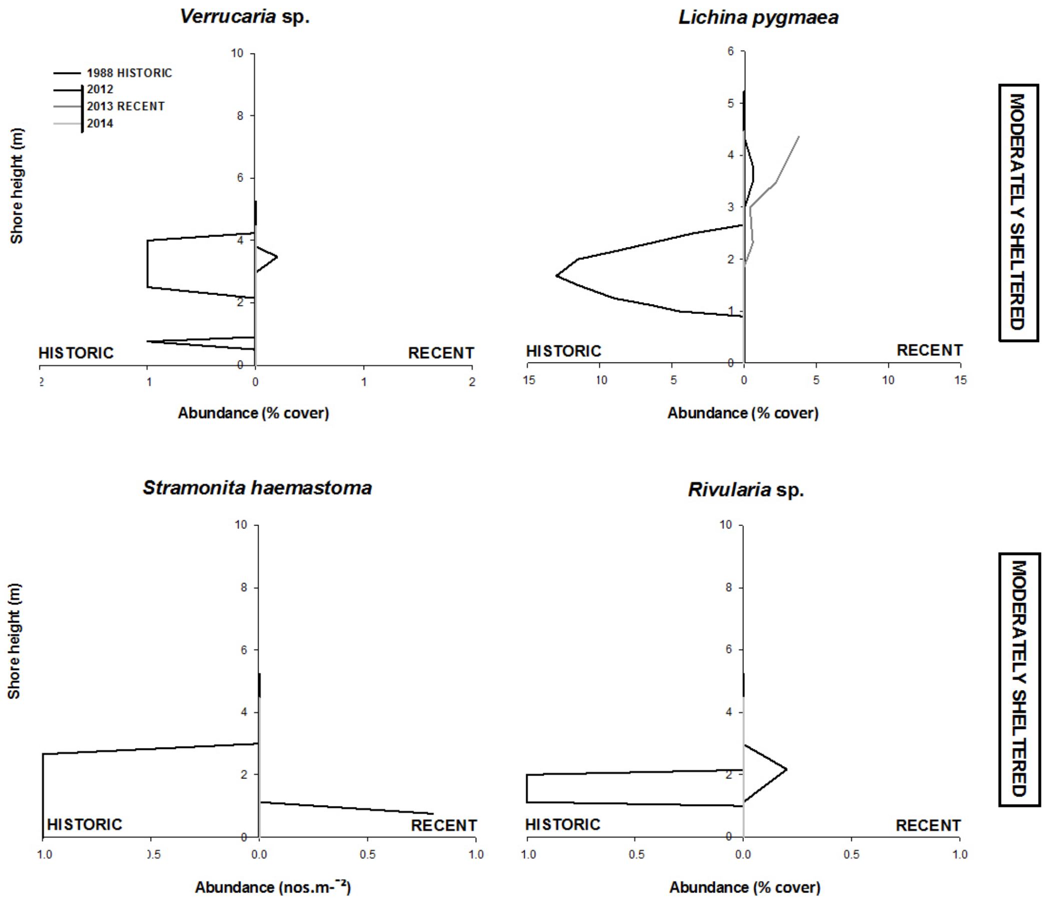


Figure 4.10. Caloura vertical distribution of *Verrucaria* sp., *Lichina pygmaea, Stramonita haemastoma* and *Rivularia* sp. in the studied transect C (Moderately Sheltered) for historic (1988) and recent surveys (2012, 2013 and 2014) in relation to shore height (MSLW - Maximum Spring Low Water level (0.16m)).

4.3.2. Monte da Guia (Faial Island)

4.3.2.1. Changes in the structure of assemblages at key shore levels

In general, most taxa sampled in 1989 were still present in 2013-2014. There were, however, some recorded changes in abundance and assemblage composition. In the relatively sheltered transect T1, taxa such as *Gelidium* sp., *Cladophora* sp. and *Plocamium cartilagenium* ((Linnaeus) Dixon 1967) were consistently (over two years) absent during the recent surveys. In contrast, *Rivularia* sp., *Pachygrapsus marmoratus*, *Melarhaphe neritoides*, *Cardita calyculata* (Linnaeus 1758), *Halopteris scoparia, Colpomenia sinuosa* ((Mertens ex Roth) Derbès and Solier 1851)*, Chaetomorpha linum* ((Müller) Kützing 1845)*,* sponges and anemones were consistently present in the recent surveys but not recorded in 1989 (Table 4.6).

For the exposed transect T2, taxa such as *Gelidium* sp., *Megabalanus* sp., *Arbacia lixula* and serpulidae polychaetes that were present in 1989 were not found during the two recent surveys. In contrast, *Littorina saxatilis*, blue/green cyanobacteria and pomatoceros were consistently found in the two recent surveys but were absent from 1989 records (Table 4.6).

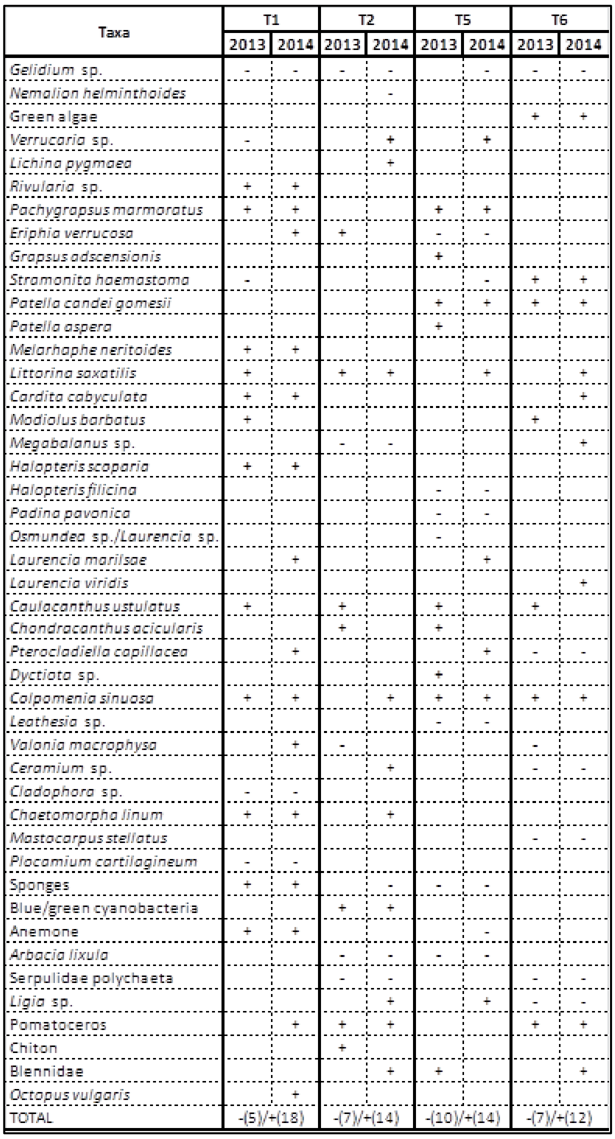
In the relatively sheltered transect T5, *Eriphia verrucosa* (Forskål 1775)*, Halopteris filicina* ((Grateloup) Kützing 1843)*, Padina pavonica* ((Linnaeus) Thivy 1960)*, Leathesia* sp. and *Arbacia lixula* were the only 5 taxa present in 1989 that were absent in the recent surveys. Unlike these, *Pachygrapsus marmoratus*, *Patella candei gomesii* and *Colpomenia sinuosa* were consistently present in all the recent surveys but were absent from the 1989 survey (Table 4.6).

For the relatively sheltered transect T6, taxa such as, *Gelidium* sp., *Pterocladiella capillacea* ((Gmelin) Santelices and Hommersand 1997)*, Ceramium* sp., *Mastocarpus stellatus* ((Stackhouse) Guiry 1984), serpulidae polychaete and *Ligia* sp., were recorded in 1989, but were never found during the two recent surveys. In contrast, *Stramonita haemastoma*, *Patella candei gomesii, Colpomenia sinuosa,* green algae and pomatoceros were consistently present in both the recent surveys but were not recorded in 1989 survey (Table 4.6).

Regardless of the changes in the presence or absence of taxa between 1989 and 2013-2014 surveys, all these taxa continue to be common in the intertidal rocky shores of the

Azores. A few species might also have been overlooked or misidentified during the surveys (e.g. cyanobacteria or *Verrucaria* sp.).

Table 4.6. Monte da Guia taxa absent (-) and taxa addition (+) in recent surveys (2013-2014) compared with 1989 survey.



Taxa	T1		T2		T5		T6	
	2013	2014	2013	2014	2013	2014	2013	2014
Gelidium sp.	-	-	-	-		-	-	-
Nemalion helminthoides				-				
Green algae							+	+
Verrucaria sp.	-			+		+		
Lichina pygmaea				+				
Rivularia sp.	+	+						
Pachygrapsus marmoratus	+	+			+	+		
Eriphia verrucosa		+	+		-	-		
Grapsus adscensionis					+			
Stramonita haemastoma	-					-	+	+
Patella candei gomesii					+	+	+	+
Patella aspera					+			
Melarhaphe neritoides	+	+						
Littorina saxatilis	+		+	+		+		+
Cardita cabyculata	+	+						+
Modiolus barbatus	+						+	
Megabalanus sp.			-	-				+
Halopteris scoparia	+	+						
Halopteris filicina					-	-		
Padina pavonica					-	-		
Osmundea sp./*Laurencia* sp.					-			
Laurencia marilsae		+				+		
Laurencia viridis								+
Caulacanthus ustulatus	+		+		+		+	
Chondracanthus acicularis			+		+			
Pterocladiella capillacea		+				+	-	-
Dyctiota sp.					+			
Colpomenia sinuosa	+	+		+	+	+	+	+
Leathesia sp.					-	-		
Valonia macrophysa		+	-				-	
Ceramium sp.				+			-	-
Cladophora sp.	-	-						
Chaetomorpha linum	+	+		+				
Mastocarpus stellatus							-	-
Plocamium cartilagineum	-	-						
Sponges	+	+		-	-	-		
Blue/green cyanobacteria			+	+				
Anemone	+	+				-		
Arbacia lixula			-	-	-	-		
Serpulidae polychaeta			-	-			-	-
Ligia sp.				+		+	-	-
Pomatoceros		+	+	+			+	+
Chiton			+					
Blennidae				+	+			+
Octopus vulgaris		+						
TOTAL	-(5)/+(18)		-(7)/+(14)		-(10)/+(14)		-(7)/+(12)	

In all transects and shore levels, the majority of the taxa showed a significant decrease in abundance between 1989 and the recent surveys (Table 4.7).

On the lower shore, compared to 1989, there was a significant increase in the abundance of total algal turfs, coralline turfs and the filter-feeder *Megabalanus azoricus* in T1. In contrast the abundance of these taxa decreased significantly in T6. Coralline turfs also decreased significantly in T5 and T2. Abundance of the macroalga

Asparagopsis armata decreased significantly in T1 and T6. Where present, *Osmundea* sp./*Laurencia* sp., *Halopteris scoparia*, bare rock, calcareous crusts and *Eriphia verrucosa*, all showed a significant reduction in abundance compared to 1989. The abundance of the sea-urchin *P. lividus* increased significantly on T6, but decreased significantly in the other three transects (T1, T2 and T5). The whelk *Stramonita haemastoma* decreased significantly in T2. The abundance of the alga *Codium adhaerens*, where present, increased significantly in T2, but decreased significantly in transects T1 and T5. The algae *Chondracanthus acicularis* ((Roth) Fredericq 1993) and *Chaetomorpha pachynema* ((Montagne) Kützing 1847), where present, showed a significant increase in abundance. Non-calcareous crusts, present only in T2 and T5, showed significant but opposite results, since in T5 their abundance has increased while in T2 it had decreased. The limpet *P. aspera* was present in T2 and T5, showing an overall increase of abundance in both transects, yet these increases were not significant. However, in 2013 the abundance of this grazer in T5 showed a significant decrease. The remaining taxa (sponges and anemones), did not show significant differences in abundance. The majority of the above changes, were generally consistent both when comparing each year separately and when data were pooled together, the exception being for the grazer *P. aspera* in T5 (Table 4.7).

At mid shore levels, where present, there was a significant reduction in the abundance of the grazing gastropods *P. candei gomesii* (T1) and *P. aspera* (T6), the non-calcareous crusts (T1 and T6), *Lithophyllum tortuosum* ((Esper) Foslie 1900) (T6) and *Rivularia* sp. (T6). In contrast, where present, the abundance of littorinid *T. striatus* increased significantly (T2). The barnacle *C. stellatus*, showed a significant decrease of abundance in T1 and T2, in contrast with T6 where its abundance was greater. Calcareous crusts, showed significant but variable results, increasing abundance in T1 and T2 but decreasing in T6. In general the total algal turf and the coralline turfs, where present, increased significantly in abundance. The alga *N. helminthoides* and green algae did not show a significant difference in the abundance. These changes were generally consistent both when comparing each year separately and when data were pooled together, the exception being for total algal turf (T6) and bare rock (T2) (Table 4.7).

At upper levels on the shore, the abundance of the barnacle *C. stellatus*, the littorinid *M. neritoides*, calcareous crusts and *Rivularia* sp. decreased significantly in all the studied areas. In contrast, the abundance of total algal turf and cyanobacteria increased significantly in transects T1 and T5, respectively. Bare rock in T2 showed a significant increase, while in the remaining transects decreased (T1, T5 and T6). The littorinid *T. striatus* showed a significant decrease in abundance in T1 and T5, while in T2 and T6 it increased significantly in abundance. The algae *N. helminthoides* showed a non-significant increase in abundance. These changes were generally consistent both when comparing each year separately and when data were pooled together, the exception being for the littorinid *T. striatus* in T2 (Table 4.7).

Overall, there appears to have been a functional change in the community at mid shore level, through a decrease of abundance in the dominant space occupier *C. stellatus* and an increase of algal turf. The remaining two shore levels do not appear to have suffered a functional change in community. However, it must be noted that at low shore levels, especially in T6 there was a significant reduction in the abundance of total algal turf and an increase in the number of sea-urchin *P. lividus*. Worth considering also, that in the high shore levels all transects showed a reduction in the littorinid *M. neritoides* and the filter-feeder barnacle *C. stellatus*.

Table 4.7. Monte da Guia: relative changes in mean abundance of taxa (recent versus historic data) for 3 shore heights (low, mid and high) at the T1, T2, T5 and T6 areas (Note: no data for T5 at mid shore level in 1989 survey) (±CI - interval of confidence (95% confidence), (*) significant difference in the abundance between 1989 and 2013-14, POL - data pooled).

SHORE LEVEL	TAXA (% cover/nos.m^{-2})	T1						T2						T5						T6					
		2013/1989	±CI	2014/1989	±CI	POL/1989	±CI	2013/1989	±CI	2014/1989	±CI	POL/1989	±CI	2013/1989	±CI	2014/1989	±CI	POL/1989	±CI	2013/1989	±CI	2014/1989	±CI	POL/1989	±CI
LOW	Total algal turf	1.682	**0.007***	1.229	0.377	1.455	**0.231***	1.156	**0.018***	0.983	0.153	1.070	0.092	0.925	0.643	1.451	0.370	1.188	0.395	0.988	**0.005***	0.094	**0.123***	0.541	**0.298***
	Coralline turf	7.821	**1.704***	4.872	**2.010***	6.346	**1.572***	0.814	**0.151***	0.971	0.206	0.893	0.131	0.642	**0.232***	0.835	0.478	0.739	**0.256***	0.925	**0.060***	0.040	**0.072***	0.483	**0.292***
	Asparagopsis armata	0.115	**0.092***	0.731	0.646	0.423	**0.368***	-	-	-	-	-	-	1.000	1.379	1.407	1.539	1.204	0.968	0.105	**0.206***	0.158	**0.309***	0.132	**0.176***
	Codium adherens	0.067	**0.131***	0.467	**0.160***	0.267	**0.163***	2.000	3.167	3.000	**1.222***	2.500	1.633	-	-	0.346	**0.582***	0.173	**0.298***	-	-	-	-	-	-
	Non-calcareous crust	-	-	-	-	-	-	-	-	1.020	0.039	0.510	**0.334***	5.395	**2.929***	2.763	**1.594***	4.079	**1.826***	-	-	-	-	-	-
	Calcareous crust	0.150	**0.033***	0.700	**0.122***	0.425	**0.189***	0.086	**0.052***	0.614	0.751	0.350	**0.395***	-	-	-	-	-	-	-	-	-	-	-	-
	Osmundea sp./*Laurencia* sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.116	**0.000***	-	-	0.058	**0.038***
	Chondracanthus acicularis	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	10.667	**3.947***	-	-	5.333	**3.950***
	Chaetomorpha pachynema	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2.000	**0.653***	-	-	1.000	0.722
	Halopteris scoparia	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.185	**0.199***	-	-	0.093	**0.112***
	Bare rock	-	-	0.655	0.690	0.328	**0.389***	-	-	-	-	-	-	0.222	**0.308***	1.000	1.960	0.611	0.963	-	-	-	-	-	-
	Patella aspera	-	-	-	-	-	-	2.000	3.920	4.000	3.667	3.000	2.613	0.125	**0.245***	2.250	1.855	1.188	1.170	-	-	-	-	-	-
	Paracentrotus lividus	0.779	**0.171***	0.706	**0.052***	0.742	**0.088***	0.573	**0.240***	0.568	**0.320***	0.571	**0.189***	0.235	**0.075***	0.232	**0.063***	0.234	**0.045***	0.250	**0.490***	49.000	**15.771***	24.625	**17.576***
	Sponges	-	-	-	-	-	-	-	-	-	-	-	-	1.000	1.960	-	-	0.500	0.980	-	-	-	-	-	-
	Anemonie	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1.333	1.905	-	-	0.667	0.998
	Megabalanus azoricus	3.000	**1.123***	6.625	**1.998***	4.813	**1.603***	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	Eriphia verrucosa	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.500	0.980	-	-	0.250	**0.490***
	Stramonita haemastoma	-	-	2.000	2.400	1.000	1.307	0.100	**0.196***	0.100	**0.196***	0.100	**0.131***	-	-	-	-	-	-	-	-	-	-	-	-
MID	Total algal turf	98.600	**1.176***	89.800	**3.062***	94.200	**3.264***	4.500	**0.980***	5.500	**1.833***	5.000	**1.033***	-	-	-	-	-	-	0.158	**0.108***	2.032	**0.578***	1.095	0.672
	Coralline turf	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1.771	**0.543***	0.886	0.633
	Lithophyllum tortuosum	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.065	**0.067***	0.032	**0.038***
	Non-calcareous crust	0.077	**0.092***	-	-	0.038	**0.050***	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.167	**0.200***	0.083	**0.109***
	Calcareous crust	0.600	0.784	6.200	**1.999***	3.400	**2.091***	11.000	**5.045***	95.500	**11.637***	53.250	**28.243***	-	-	-	-	-	-	0.077	**0.000***	0.923	0.384	0.500	**0.331***
	Green algae	3.000	2.400	-	-	1.500	1.497	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	Nemalion helminthoides	-	-	-	-	-	-	-	-	1.000	1.200	0.500	0.653	-	-	-	-	-	-	-	-	-	-	-	-
	Rivularia sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1.020	0.039	-	-	0.510	**0.334***
	Chthamalus stellatus	0.006	**0.007***	0.009	**0.007***	0.007	**0.005***	0.672	**0.166***	0.545	**0.079***	0.609	**0.096***	-	-	-	-	-	-	5.833	**1.334***	11.111	**2.982***	8.472	**2.312***
	Bare rock	-	-	0.194	**0.233***	0.097	**0.127***	6.522	**3.078***	0.391	**0.341***	3.457	2.478	-	-	-	-	-	-	2.704	**0.200***	0.252	**0.149***	1.478	0.810
	Patella candei gomesii	-	-	0.010	**0.020***	0.005	**0.010***	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	Patella aspera	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.208	**0.112***	0.104	**0.086***
	Tectarius striatus	-	-	-	-	-	-	3.341	**1.198***	1.246	0.977	2.293	**0.999***	-	-	-	-	-	-	-	-	-	-	-	-
HIGH	Total algal turf	480.000	**5.368***	475.000	**16.688***	477.500	**8.424***	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	Nemalion helminthoides	3.000	2.400	-	-	1.500	1.497	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	Rivularia sp.	-	-	-	-	-	-	-	-	1.000	1.960	0.500	0.980	0.018	**0.036***	0.091	**0.036***	0.055	**0.036***	-	-	0.500	**0.400***	0.250	**0.249***
	Calcareous crust	-	-	-	-	-	-	-	-	0.167	**0.327***	0.083	**0.163***	-	-	-	-	-	-	-	-	-	-	-	-
	Blue/green cyanobacteria	-	-	-	-	-	-	-	-	-	-	-	-	5.778	**1.125***	7.556	**0.503***	6.667	**0.871***	-	-	-	-	-	-
	Chthamalus stellatus	0.023	**0.007***	0.008	**0.007***	0.015	**0.006***	0.008	**0.006***	0.662	**0.102***	0.335	**0.219***	0.009	**0.018***	0.037	**0.002***	0.023	**0.013***	-	-	0.305	**0.137***	0.153	**0.119***
	Bare rock	0.024	**0.019***	0.039	**0.042***	0.031	**0.022***	4.471	**0.519***	2.308	**0.385***	3.389	**0.770***	0.726	0.283	0.268	**0.125***	0.497	**0.222***	0.129	**0.037***	1.163	0.278	0.646	0.363
	Tectarius striatus	0.001	**0.001***	-	-	0.000	**0.001***	0.023	**0.029***	3.098	**1.585***	1.560	1.252	0.002	**0.003***	0.020	**0.019***	0.011	**0.011***	-	-	3.086	**0.675***	1.543	1.057
	Melarhaphe neritoides	-	-	-	-	-	-	0.227	**0.133***	0.924	0.509	0.576	**0.337***	0.012	**0.020***	0.035	**0.036***	0.023	**0.021***	-	-	-	-	-	-

4.3.2.2. Changes in the overall abundance of taxa

When considering the entire vertical distribution of the 15 species studied as a whole, there were variable changes in abundance depending on the level of wave exposure. From these, some taxa can be highlighted, such as the littorinids (*T. striatus* and *M. neritoides*), the gastropod grazers (*P. candei gomesii* and *P. aspera*), the filter-feeders (*C. stellatus*), the sea-urchin (*P. lividus*), the turfs and the blue/green cyanobacteria. The abundance of *M. neritoides* and the turfs (total algal and coralline turfs) increased in T1, T2 and T6, and decreased in T5. The abundance of *P. candei gomesii* and the blue/green cyanobacteria decreased in T1, and increased in T2, T5 and T6. *Patella aspera* decreased in abundance in T6, but increased in all the remaining transects (T1, T2 and T5). *Tectarius striatus* decreased in T1 and T5, whereas in T2 and T6 it increased in abundance. *Chthamalus stellatus* increased in abundance in T5 and T6 and decreased in the remaining two transects (T1 and T2). The sea-urchin *P. lividus* increased in abundance in T1 and T6, whereas in T2 and T5 it decreased (Table 4.8).

Overall, the Wilcoxon matched-pairs signed-rank test did not detect significant changes, since its ability to detect significant changes largely depends on the number of pairs, which was limited in most cases (Table 4.9).

Table 4.8. Monte da Guia overall mean abundance of taxa in 1989 and recent surveys (2013-2014 pooled (POL); difference between 1989 and recent data (≠)).

Taxa		A - EXPOSED		B - MODERATELY EXPOSED		C - MODERATELY SHELTERED	
		Abundance	≠	Abundance	≠	Abundance	≠
Melarhaphe neritoides (nos.m^{-2})	88	143.640	-82.090	331.740	-221.720	102.300	-70.730
	POL	61.550		110.020		31.570	
Tectarius striatus (nos.m^{-2})	88	261.310	42.410	77.410	20.800	46.500	-7.500
	POL	303.720		98.210		39.000	
Patella candei gomesii (nos.m^{-2})	88	5.880	3.300	3.440	3.850	1.600	0.000
	POL	9.180		7.290		1.600	
Patella aspera (nos.m^{-2})	88	2.450	-1.690	2.880	-2.600	2.470	-1.940
	POL	0.760		0.280		0.530	
Pachygrapsus marmoratus (nos.m^{-2})	88	0.000	0.020	0.180	-0.180	0.530	-0.480
	POL	0.020		0.000		0.050	
Chthamalus stellatus (% cover)	88	14.570	-10.130	12.000	-8.910	2.470	-1.640
	POL	4.440		3.090		0.830	
Total algal turf (% cover)	88	4.380	19.290	16.350	7.430	0.070	27.940
	POL	23.670		23.780		28.010	
Calcareous crusts (% cover)	88	4.930	-0.900	1.410	-1.020	1.730	-1.140
	POL	4.030		0.390		0.590	
Non-calcareous crusts (% cover)	88	0.600	0.020	0.180	2.460	6.600	2.690
	POL	0.620		2.640		9.290	
Green algae (% cover)	88	2.520	-2.250	2.590	-2.510	0.000	0.150
	POL	0.270		0.080		0.150	
Halopteris scoparia (% cover)	88	0.000	0.140	0.000	0.460	0.000	0.050
	POL	0.140		0.460		0.050	
Fucus spiralis (% cover)	88	0.000	0.010	0.530	-0.530	-	
	POL	0.010		0.000			
Nemalion helminthoides (% cover)	88	1.690	-1.630	1.680	-1.640	-	
	POL	0.060		0.040			
Osmundea sp./*Laurencia* sp. (% cover)	88	0.000	1.300	0.000	0.010	0.000	0.010
	POL	1.300		0.010		0.010	
Coarsely branch algae (% cover)	88	0.000	5.130	0.000	6.120	0.000	6.800
	POL	5.130		6.120		6.800	
Lichina pygmaea (% cover)	88	-		0.010	0.000	3.170	-2.910
	POL			0.010		0.260	
Blue/green cyanobacteria (% cover)	88	0.000	4.610	0.000	1.340	-	
	POL	4.610		1.340			
Verrucaria sp. (% cover)	88	0.480	-0.480	0.470	-0.470	0.400	-0.400
	POL	0.000		0.000		0.000	

Table 4.9. Wilcoxon matched-pairs signed-rank test comparing changes in abundance between 1989 and recent pooled data (2013-14) in the four studied areas at Monte da Guia (NA - not enough match pairs; in box - statistically significant).

Wilcoxon signed-rank test	T1			T2			T5			T6		
	W	Z	p	W	Z	p	W	Z	p	W	Z	p
Melarhaphe neritoides (nos.m^{-2})	6	1.604	NA	9	1.214	NA	9	0.943	0.438	6	1.105	NA
Tectarius striatus (nos.m^{-2})	-5	-0.524	0.688	28	2.371	$\boxed{0.020}$	5	0.674	NA	15	2.023	0.063
Patella candei gomesii (nos.m^{-2})	-2	-0.365	NA	-2	-0.170	0.940	10	1.826	NA	15	2.032	NA
Patella aspera (nos.m^{-2})	21	2.207	$\boxed{0.030}$	7	0.944	NA	10	1.826	NA	0	0.000	1.000
Chthamalus stellatus (%)	-2	-0.169	0.938	-7	-0.415	0.734	18	1.521	0.156	8	0.676	0.578
Paracentrotus sp. (nos.m^{-2})	3	0.405	0.810	-4	-0.730	NA	-6	-1.604	NA	3	1.342	NA
Total algal turf (%)	28	1.960	0.055	35	2.073	$\boxed{0.040}$	-5	-0.674	NA	16	1.352	0.219
Coralline turf (%)	15	1.572	0.156	7	0.734	0.563	-8	-1.461	NA	2	0.365	NA
Coarsely branch algae (%)	21	2.201	$\boxed{0.030}$	6	1.095	NA	10	1.826	NA	10	1.826	NA
Green algae (%)	20	1.400	0.200	36	2.520	$\boxed{0.008}$	5	0.670	NA	15	2.020	0.060
Osmundea sp./*Laurencia* sp. (%)	9	0.943	0.438	-5	-0.921	NA	-1	-0.447	NA	0	0.000	NA
Bare rock (%)	-20	-1.400	0.195	43	2.191	$\boxed{0.030}$	29	1.718	0.098	6	0.507	0.688
Calcareous crust (%)	10	0.850	0.470	-28	-1.960	0.060	7	0.940	NA	13	1.360	0.220
Non calcareous crust (%)	16	1.360	0.220	-7	-0.593	0.578	10	1.826	NA	0	0.000	NA
Rivularia sp. (%)	3	1.342	NA	11	1.511	NA	5	0.674	NA	-3	-0.552	NA
Blue/greens cyanobacteria (%)	-3	-1.342	NA	6	1.604	NA	28	2.366	$\boxed{0.020}$	15	2.023	NA

4.3.2.3. Changes in the vertical distribution of taxa

The recent surveys, compared to 1989, showed that across the wave exposure gradient there were differences in the vertical distribution of the taxa. In the more exposed transects (T1 and T2) there were a considerable number of taxa (72-95%) with higher upper vertical limits of distribution (Table 4.10 and Figures 4.11 to 4.18). These included taxa such as *M. neritoides, T. striatus*, *C. stellatus,* total algal turf, *Osmundea* sp./*Laurencia* sp., *Asparagopsis armata, P. candei gomesii*, *P. aspera*, *P. lividus*, non-calcareous crusts, green algae, calcareous crusts, *Megabalanus azoricus, S. haemastoma* and *Codium adhaerens*. In the less exposed transects (relatively sheltered T5 and T6), a substantial number of taxa (46-62%) also showed a retraction in their upper limit of distribution compared to that recorded in 1989 (Table 4.10 and Figures 4.11 to 4.18). These included taxa such as *P. lividus*, coralline turfs, *Asparagopsis armata* and *Halopteris scoparia*.

Across the range of exposure to wave action, a substantial proportion of taxa (18-38%) also showed a rise in their lower limit of vertical distribution on the shore compared to 1989 (Table 4.10 and Figures 4.11 to 4.18). This suggests that compared to 1989 many species effectively moved up on the shore as a block with extension of their upper limit of vertical distribution and by disappearing from lower levels on the shore (contraction of the lower limit), especially on more exposed transects. Despite some differences in abundance, in general, the patterns of vertical distribution were consistent between recent years (2013-2014), not showing an inter-annual variability. Exceptions were the high shore snail *T. striatus* and the filter feeder *C. stellatus* where overall the peaks of abundance varied between years, even though generally the vertical range changed little.

Table 4.10. Numbers of taxa that changed their upper and lower limits of vertical distribution compared to 1989 at Monte da Guia.

VERTICAL DISTRIBUTION		T1		T2		T5		T6	
		taxa	%	taxa	%	taxa	%	taxa	%
UPPER LIMIT	Extend upwards	20	95.2	18	72.0	7	31.8	3	14.3
	Retract downwards	0	0.0	0	0.0	10	45.5	13	61.9
	No change	0	0.0	2	8.0	0	0.0	2	9.5
	No data	1	4.8	5	20.0	5	22.7	3	14.3
LOWER LIMIT	Extend downwards	1	4.8	2	8.0	2	9.1	4	19.0
	Retract upwards	8	38.1	6	24.0	4	18.2	6	28.6
	No change	0	0.0	2	8.0	1	4.5	0	0.0
	No data	12	57.1	15	60.0	15	68.2	11	52.4

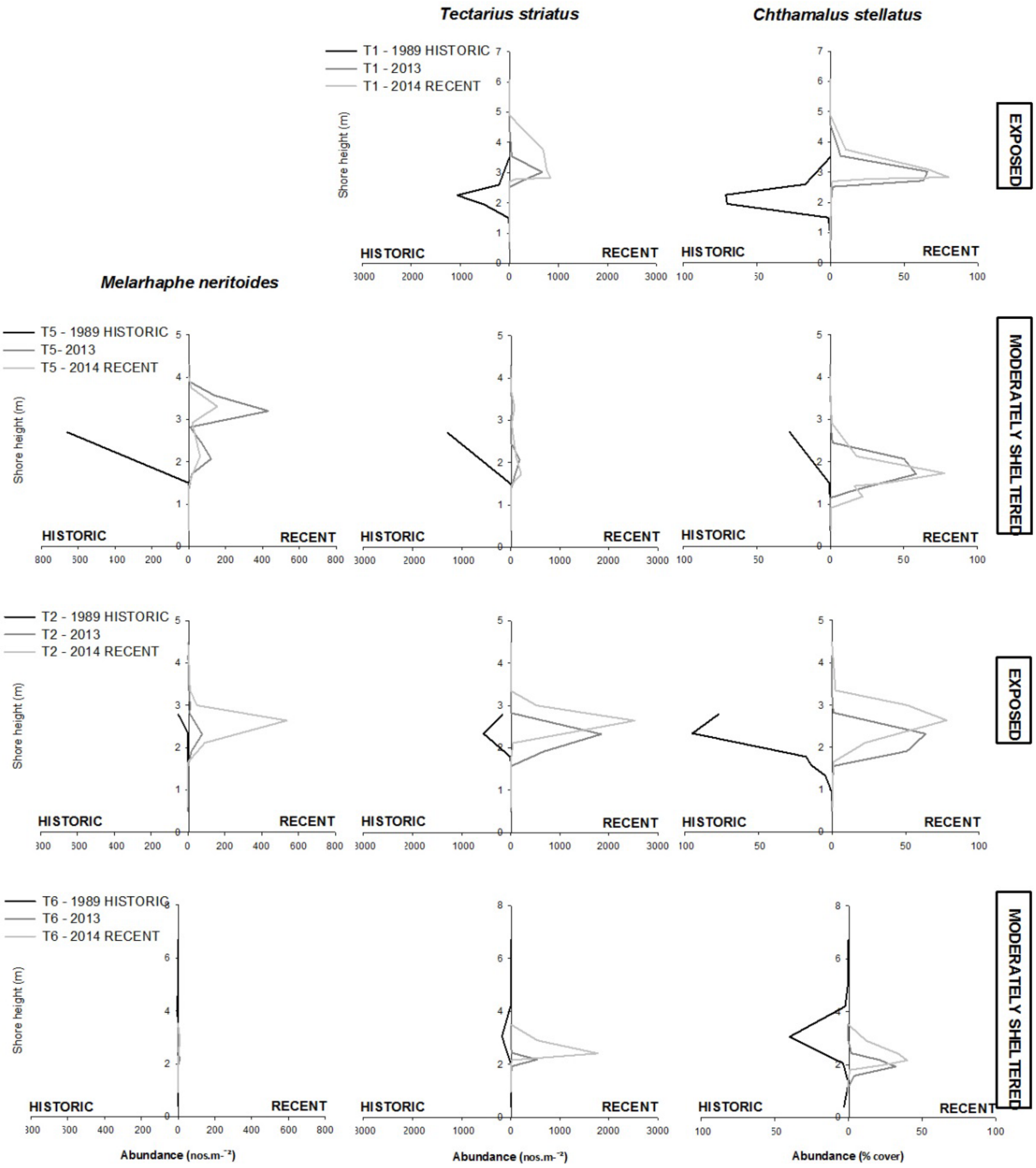


Figure 4.11. Monte da Guia vertical distribution of *Melarhaphe neritoides*, *Tectarius striatus* and *Chthamalus stellatus* in the studied transects (T1, T5, T2 and T6) for historic (1989) and recent surveys (2013 and 2014) in relation to shore height (MSLW - Maximum Spring Low Water level (0.16m)).

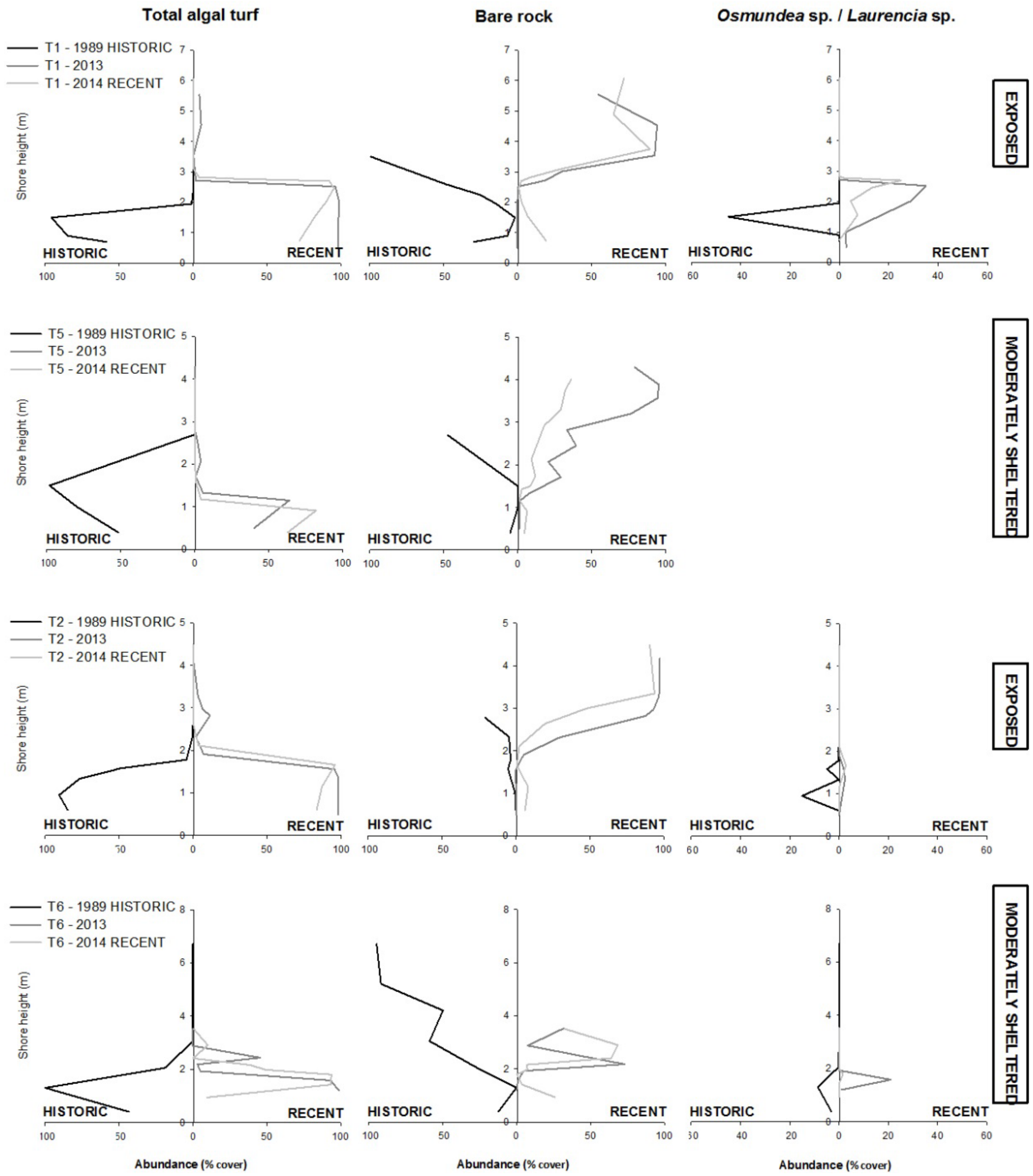


Figure 4.12. Monte da Guia vertical distribution of total algal turf, bare rock and *Osmundea* sp./*Laurencia* sp. in the studied transects (T1, T5, T2 and T6) for historic (1989) and recent surveys (2013 and 2014) in relation to shore height (MSLW - Maximum Spring Low Water level (0.16m)).

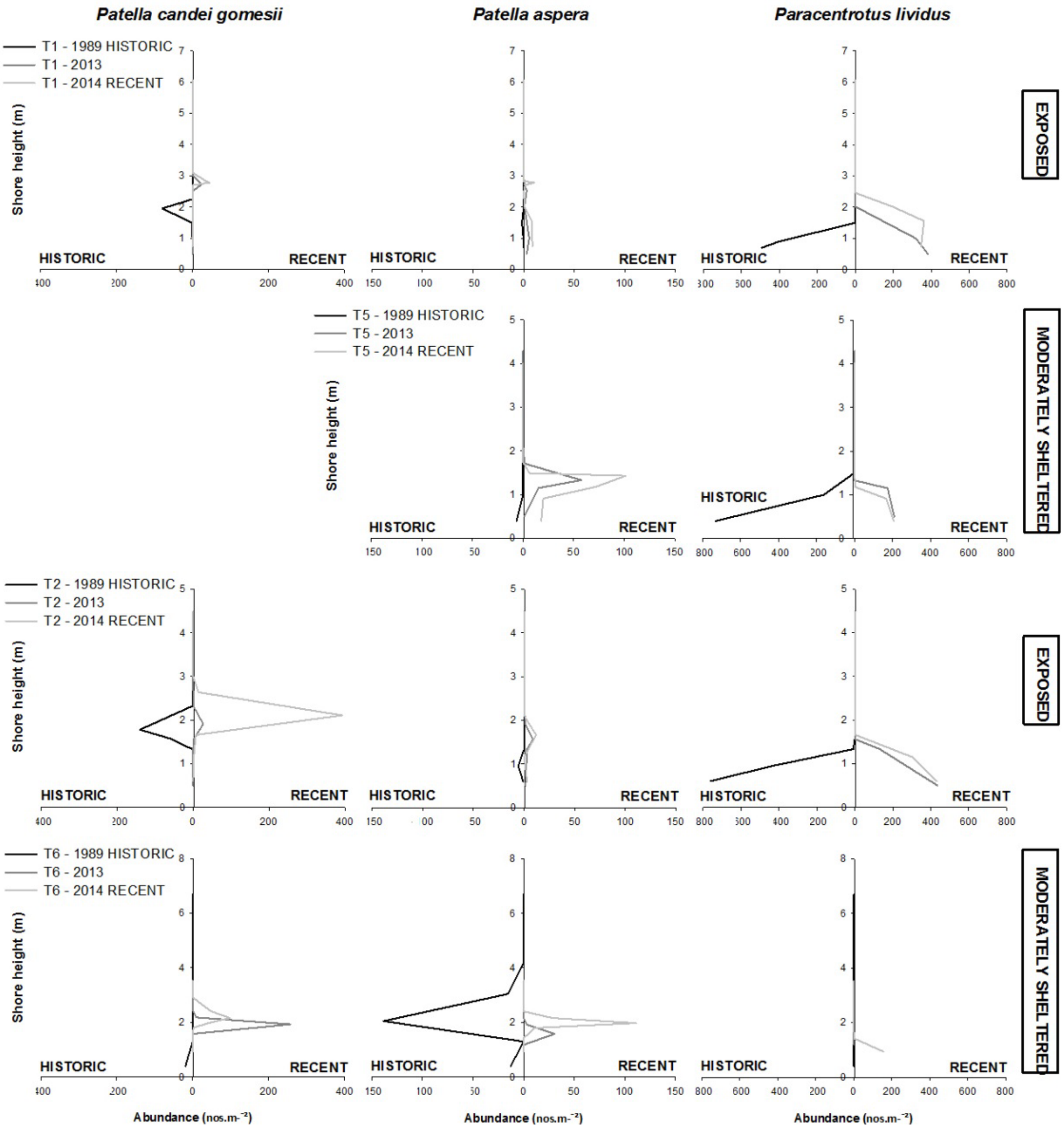


Figure 4.13. Monte da Guia vertical distribution of *Patella candei gomesii*, *Patella aspera* and *Paracentrotus lividus* in the studied transects (T1, T5, T2 and T6) for historic (1989) and recent surveys (2013 and 2014) in relation to shore height (MSLW - Maximum Spring Low Water level (0.16m)).

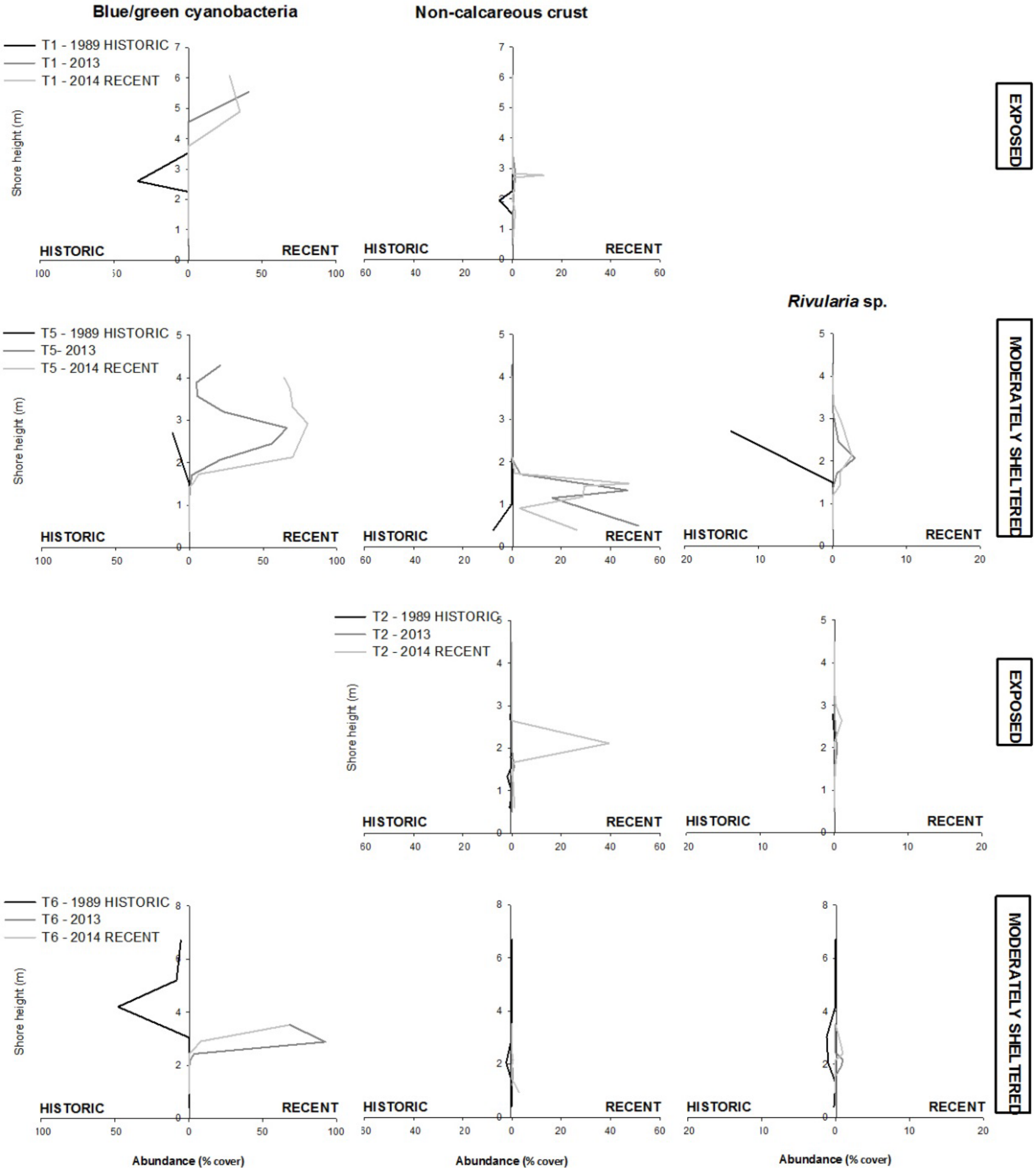


Figure 4.14. Monte da Guia vertical distribution of blue/green cyanobacteria, non-calcareous crusts and *Rivularia* sp. in the studied transects (T1, T5, T2 and T6) for historic (1989) and recent surveys (2013 and 2014) in relation to shore height (MSLW - Maximum Spring Low Water level (0.16m)).

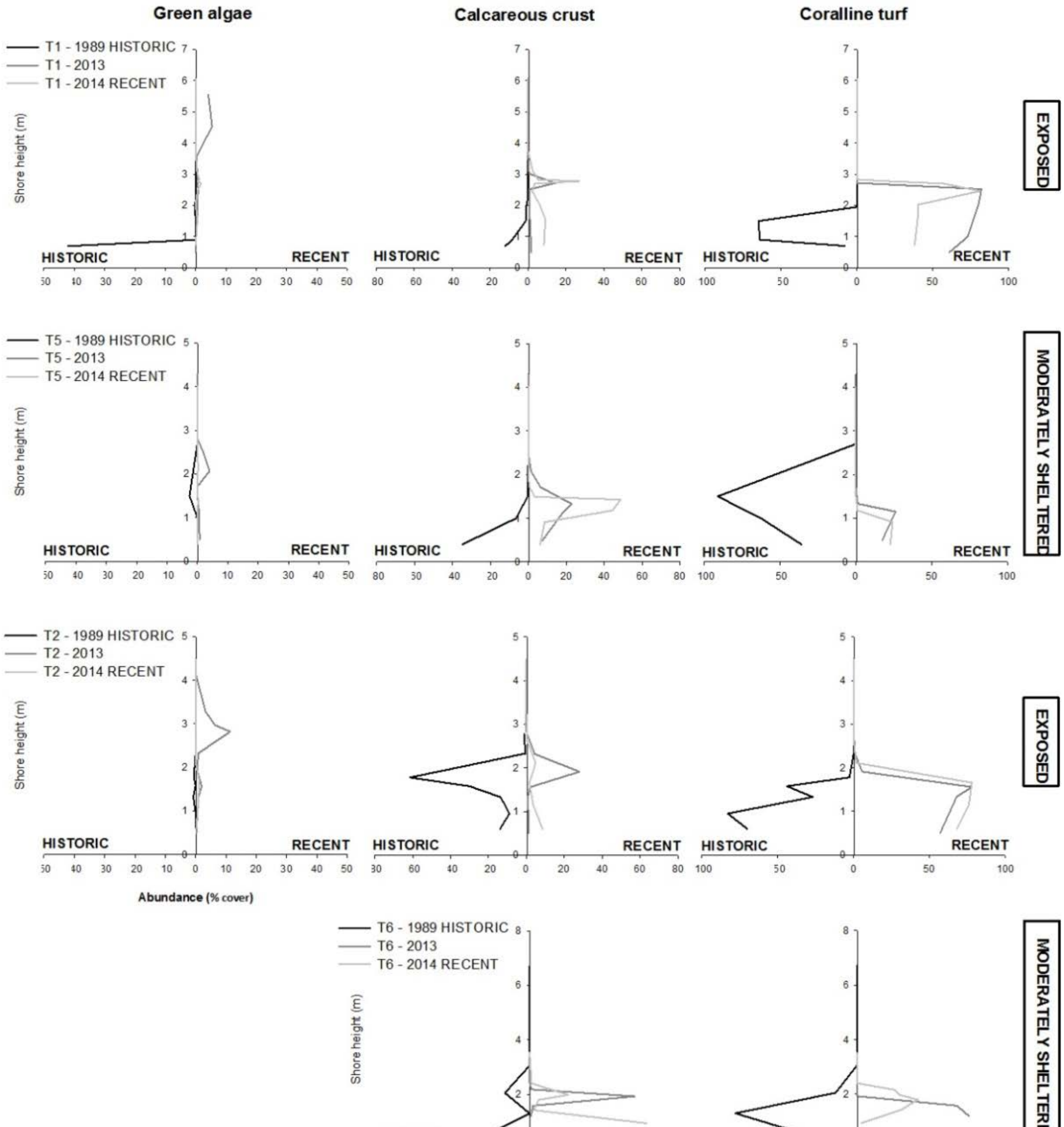


Figure 4.15. Monte da Guia vertical distribution of green algae, calcareous crusts and coralline turfs in the studied transects (T1, T5, T2 and T6) for historic (1989) and recent surveys (2013 and 2014) in relation to shore height (MSLW - Maximum Spring Low Water level (0.16m)).

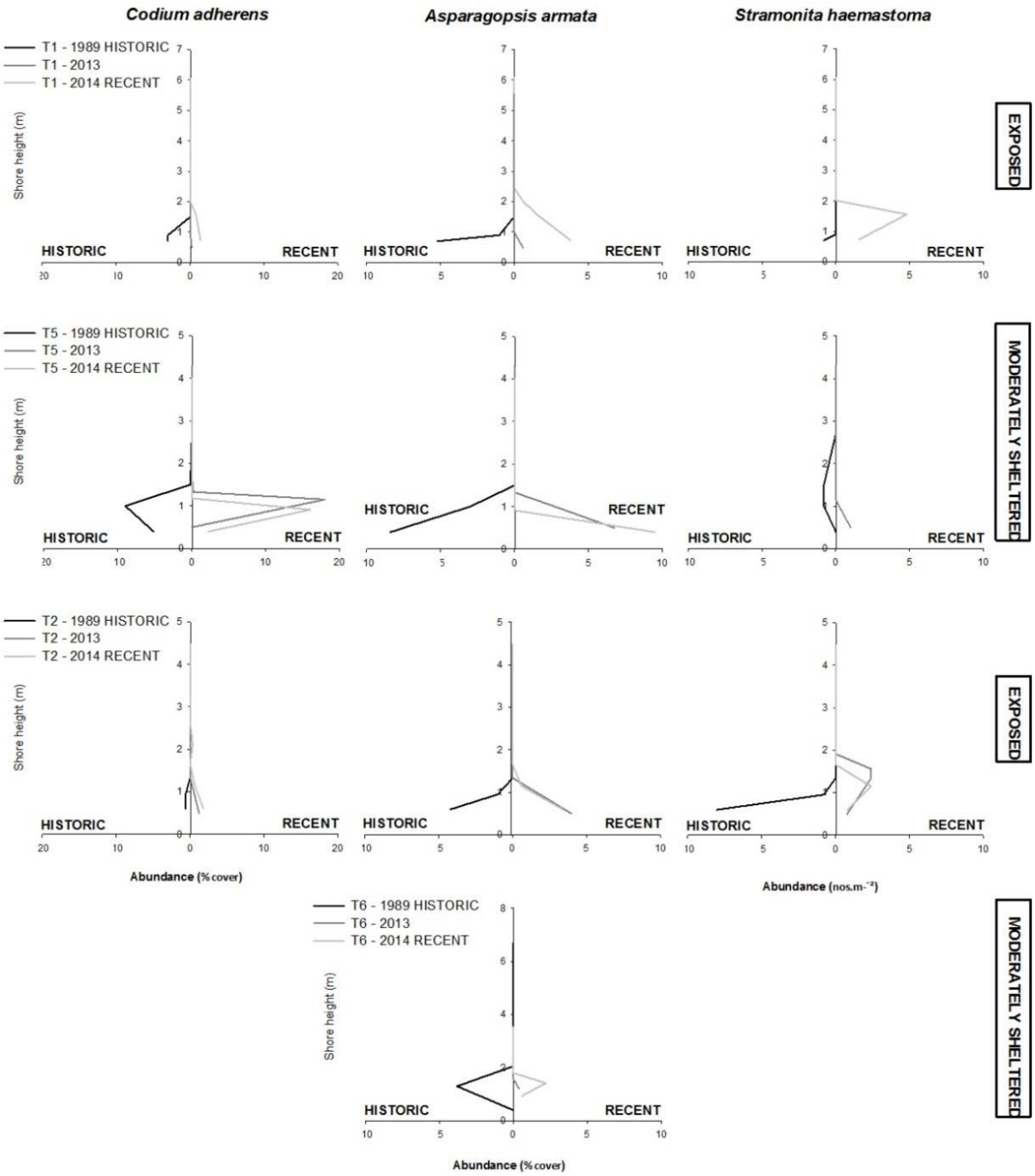


Figure 4.16. Monte da Guia vertical distribution of *Codium adhaerens*, *Asparagopsis armata* and *Stramonita haemastoma* in the studied transects (T1, T5, T2 and T6) for historic (1989) and recent surveys (2013 and 2014) in relation to shore height (MSLW - Maximum Spring Low Water level (0.16m)).

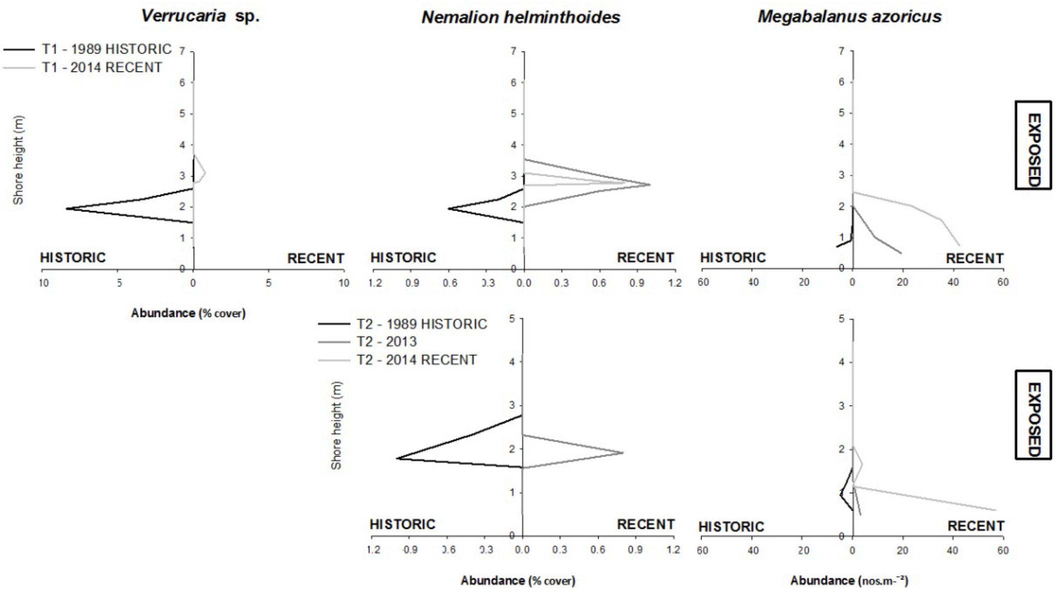


Figure 4.17. Monte da Guia vertical distribution of *Verrucaria* sp., *Nemalion helminthoides* and *Megabalanus azoricus* in the studied transects (T1 and T2) for historic (1989) and recent surveys (2013 and 2014) in relation to shore height (MSLW - Maximum Spring Low Water level (0.16m)).

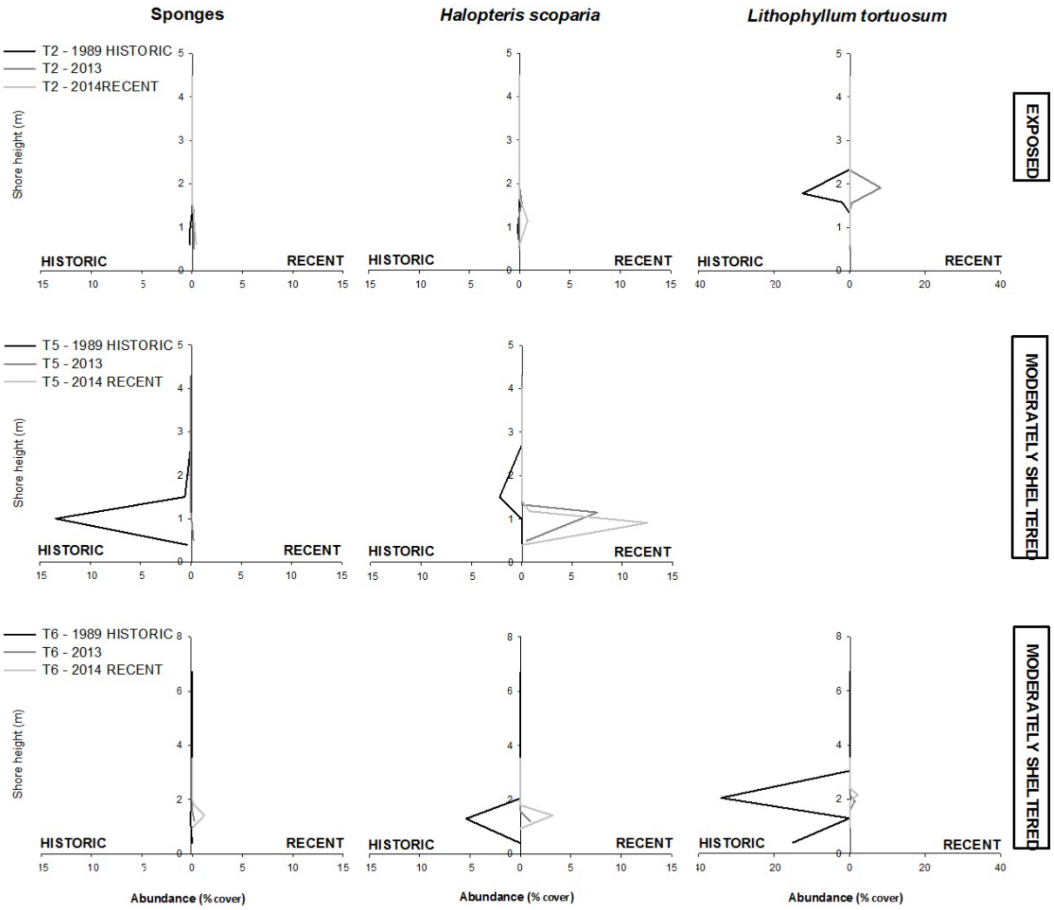


Figure 4.18. Monte da Guia vertical distribution of sponges, *Halopteris scoparia* and *Lithophyllum tortuosum* in the studied transects (T2, T5, and T6) for historic (1989) and recent surveys (2013 and 2014) in relation to shore height (MSLW - Maximum Spring Low Water level (0.16m)).

4.4. DISCUSSION

Long-term research is essential to discriminate global climate signals from the background noise of natural variability plus the effects of regional and local scale human impacts (Mieszkowska *et al.*, 2014b). Such studies thus provide an excellent baseline against which we can compare changes. The robustness of the data, however, depends on the quality and frequency of the sampling (Schiel, 2011). Through a combination of available historical data and contemporary recently collected data, I was able to describe long-term changes in the abundance and distribution of intertidal species, in relation to recent climate change.

The major limitations in this study were the comparability between the two sets of data (historic versus recent), since only a single historic survey was available for comparison. There were also no intermediate data collected between the historic and the recently collected data. Details regarding the methods used in the historical data were scarce, at least for the Monte da Guia location. Also, some of the historic data was collected by researchers with different backgrounds and different fields of expertise, which could have led to misidentifications (e.g. *Verrucaria* sp. and cyanobacteria). In order to guarantee quality long-term research, a methodology has to be previously planned and set up, then being applied by staff with proper training, avoiding subsequent errors. Despite the above, some inferences can still be made from the available data.

4.4.1. Changes in the abundance of taxa and structure of assemblages

In general, differences in the presence or absence of some taxa were recorded for both Caloura and Monte da Guia. Most of these taxa, however, continue to be common on the rocky shores of the Azores. Absences recorded may represent local, not regional, fluctuations and absences. These changes could reflect small-scale changes in the distribution of organisms (Martins *et al.*, 2008b), combined with a relatively poor level of replication (5 per transect). Also the presence or absence of motile animals (e.g. *Mitra nigra*, *Pachygrapsus marmoratus*) may be related to short-term changes in behaviour, and hence not related to variations in environmental conditions.

Overall, there has been a substantial increase in the abundance of algal turfs on the lower shore (lower eulittoral zone and sublittoral fringe), whereas at mid and high shore levels, the abundance of the dominant space occupier *C. stellatus* and grazing gastropods (limpets and littorinids) has decreased concomitantly with increasing abundance of algal turf. These results suggest that there has been a functional change in community structure over time with consumers being replaced by primary producers; especially at mid shore levels. This occurred on all transects in both Monte da Guia and Caloura - the notable exception was T5 in the inner Caldeira of Monte da Guia, which was a properly enforced no-take and no-entry area

These observed changes could be related with the overexploitation of limpets within the Azores archipelago (Martins *et al.*, 2009, 2010). At the transition between low and mid shore levels there is an interaction between 3 key taxa - algae, limpets and barnacles, all competing for space (Hawkins and Hartnoll, 1983b, 1985; Boaventura *et al.*, 2002a,c). Due to the human consumption of limpets in the Azores, that equilibrium has been disrupted, which has led to a major increase in the abundance of algal turf, and as a consequence a reduction in free space available for recruitment of limpets and settlement of barnacle larvae (Martins *et al.*, 2008a, 2010). The removal of top-down herbivores can lead to an increase of algal abundance (Lubchenco, 1978; Hawkins and Hartnoll, 1983b). Herbivores directly control the distribution and abundance of macroalgae through the grazing of post settlement stages or on mature plants (Jones, 1946; Hawkins, 1981; Lubchenco and Gaines, 1981; Hawkins and Hartnoll, 1983b; Hawkins *et al.*, 1989; Jenkins and Hartnoll, 2001; Boaventura *et al.*, 2002b; Jenkins *et al.*, 2005; Coleman *et al.*, 2006; Jonsson *et al.*, 2006; Davies *et al.*, 2007). Removal of grazers can lead to increased primary production, disrupting communities and ecosystem functioning (Lubchenco, 1978; Lubchenco and Gaines, 1981). Overall, an increase in the abundance of taxa appears to occur between the historic and the recent data, especially at mid and high shore levels, at more exposed locations.

4.4.2. Changes in the vertical distribution of taxa

Generally there was an upward shift of both lower and upper vertical limits of distribution of the taxa recorded in comparison to the historic data. These results suggest that species have moved up the shore as a block via extensions of the upper limit of vertical distribution, and by disappearing from lower levels on the shore. Yet, there were some notable differences in behaviour among transects differing in the exposure to wave action. Expansion of the upper limits of taxa was more evident in exposed transects and less so in the more sheltered transects. In contrast, some contraction of the upper limit of vertical distribution was evident in more moderately sheltered transects, but was not apparent in more exposed transects. The lower limits of vertical distribution also tended to retract in more exposed transects. Such difference in species responses between transects may be related to an interaction between global warming and wave action. The trimming of upper limits of some species on relatively sheltered transects could be related to the increase of heat stress during extreme warm events. Without the amelioration due to wave splash that occurs in more exposed conditions, the organisms present at sheltered shores are more vulnerable to these impacts (Schonbeck and Norton, 1978; Hawkins and Hartnoll, 1985). In contrast, on the more exposed transects, heat stress may be alleviated or overridden by the continuous wetting due to increased wave action. As warming increases, mobile animals will became constrained to microhabitats where climatic extremes are ameliorated by topographic features (Seabra *et al.*, 2011) or biota such as algal canopies (Moore *et al.*, 2007a).

According to climate change predictions, there will be an increase in mean temperature and wave action (Schneider, 2001; Trenberth *et al.*, 2007). Increasing wave action seems to be a more logical explanation for the overall uplifting of assemblages towards upper levels on the shore, suggesting that increase wave action may actually mitigate the effects of increasing temperature in more exposed conditions. The increasing abundance of total algal turf observed at the low shore levels, however, is most likely the result of overexploitation of limpets (Martins *et al.*, 2009, 2010). The removal of grazers after oil spills (Southward and Southward, 1978) and experimentally (Underwood and Jernakoff, 1984; Boaventura *et al.*, 2002a) has been shown to lead to algal turf occurring higher on the shore. Lower shore species would be expected to out-compete those higher in the turf zone if conditions are favourable (Hawkins and Hartnoll, 1985).

Our results are consistent with the predicted response to increased wave action (stormier seas) in the Azores over the last ~30 years. These changes might have the largest influence over the community structure of the intertidal rocky shore in the Azores, where exposed shores are the dominant feature of the coastline. The biological data collected in this study are consistent with the expected increase in wave action (stormier seas) having occurred. The oceanographic analysis (Chapter 2) suggests, however, that mean monthly values of wave action over the last ~30 years in São Miguel and Faial islands have not increased. According to Young *et al.* (2011), over the past two decades there was a non-significant trend for mean monthly values of wave height. When considering the extreme conditions, however, a significant trend of increasing wave height was detected especially at higher latitudes. Thus more frequent return time of extreme events may be more important than average conditions (Benedetti-Cecchi *et al.*, 2006, 2015).

Wave action affects organisms directly and indirectly, by changing behaviour, the relative importance of biotic interactions and via modifying thermal and desiccation stress (Connell, 1972; Menge, 1976; Lindegarth and Gamfeldt, 2005). Physical variables, such as wave exposure and desiccation have an important effect on the distribution and abundance of sessile species (Dayton, 1971). According to Connell (1972), the upper limit of many rocky intertidal organisms, particularly higher shore species (Schonbeck and Norton, 1978; Hawkins and Hartnoll, 1985) is thought to be established by thermal or desiccation stress related to aerial exposure at low tide. This explains the upward expansion and the increase of abundance of *Tectarius striatus*, since desiccation is reduced at the upper levels of exposed shores by wave spray (Lewis, 1964), allowing organisms to spread higher, up the shore on exposed coasts. Upper limits can also, however, be set by competition and grazing, particularly on the mid and lower shore (Underwood, 1980; Hawkins and Hartnoll, 1985; Boaventura *et al.*, 2002a). Organisms living on the shore have been shown to occur at or near the edge of their limit of thermal tolerance (Wolcott, 1973; Davenport and Davenport, 2005). *Chthamalus stellatus* also showed a decrease in abundance at higher shore levels, which is also probably related to increasing cover of algal turfs as a consequence of the low abundance of limpets (Martins *et al.*, 2008b, 2010). Martins *et al.* (2010) showed that barnacles are out-competed by turf-forming algae in the absence of limpets in the Azores. When this occurs, algae extend higher on the shore until they have reached their ability to deal with desiccation, which prevents further extension. This leads to a decrease of space available for barnacles to settle.

4.4.3. Changes in the intertidal due to other factors

According to Martins *et al.* (2010) the Azorean upper eulittoral is dominated by algal turf, which is not a stable condition and only persists due to the low levels of limpet abundance caused by chronic overexploitation of this resource. Although in Caloura, the abundance of *Patella candei gomesii* recorded was slightly greater (albeit not significant) than that of 1988, these were mostly very small individuals. In addition, the larger *Patella aspera* showed a decrease (albeit not significant) compared to 1988. On a more extensive survey Martins *et al.* (2010), found a substantial decline in limpet abundance on this same area. Although Caloura is within a marine protected area, which should confer the area some protection, Martins *et al.* (2011) found that enforcement levels were low and did not prevent the illegal harvesting of limpets. The above may suggest that limpets have decreased in abundance through time (due to overharvesting), which may be driving the increasing abundance of algal turfs recorded (Underwood, 1980; Hawkins and Hartnoll, 1983b; Underwood and Jernakoff, 1984; Boaventura *et al.*, 2002a; Martins *et al.*, 2008a).

Monte da Guia is within a marine protected area with a higher level of enforcement (no-take and no-entry area). Despite this, scars of recently collected limpets were seen in transects on the outer side of Monte da Guia. This suggests that real enforcement only takes place inside the inner Caldeira of Monte da Guia. The only transect where algal turf did not spread upwards was inside Monte da Guia (T5) where a dense population of larger limpets was also present (Figure 4.19). Also, this was the only transect where an increase in the range of the vertical distribution of *C. stellatus* both upwards and downwards was detected. Moreover, T5 showed an increase in numbers of *P. aspera* on lower shore in recent surveys compared to 1989. Although this increase in numbers was non-significant, limpets were much larger than previously recorded. Limpets are important grazers in most temperate ecosystems, influencing patterns of relative dominance by macroalgae or barnacles (Southward, 1964; Hawkins, 1981; Hawkins and Hartnoll, 1985) and modifying community dynamics (Jones, 1946, 1948; Raffaelli and Hawkins, 1996; Jenkins *et al.*, 1999b; a; Jenkins and Hartnoll, 2001; Coleman *et al.*, 2006). Thus, factors affecting the performance or distribution of limpets will likely have cascading community-level effects (Seabra *et al.*, 2011).

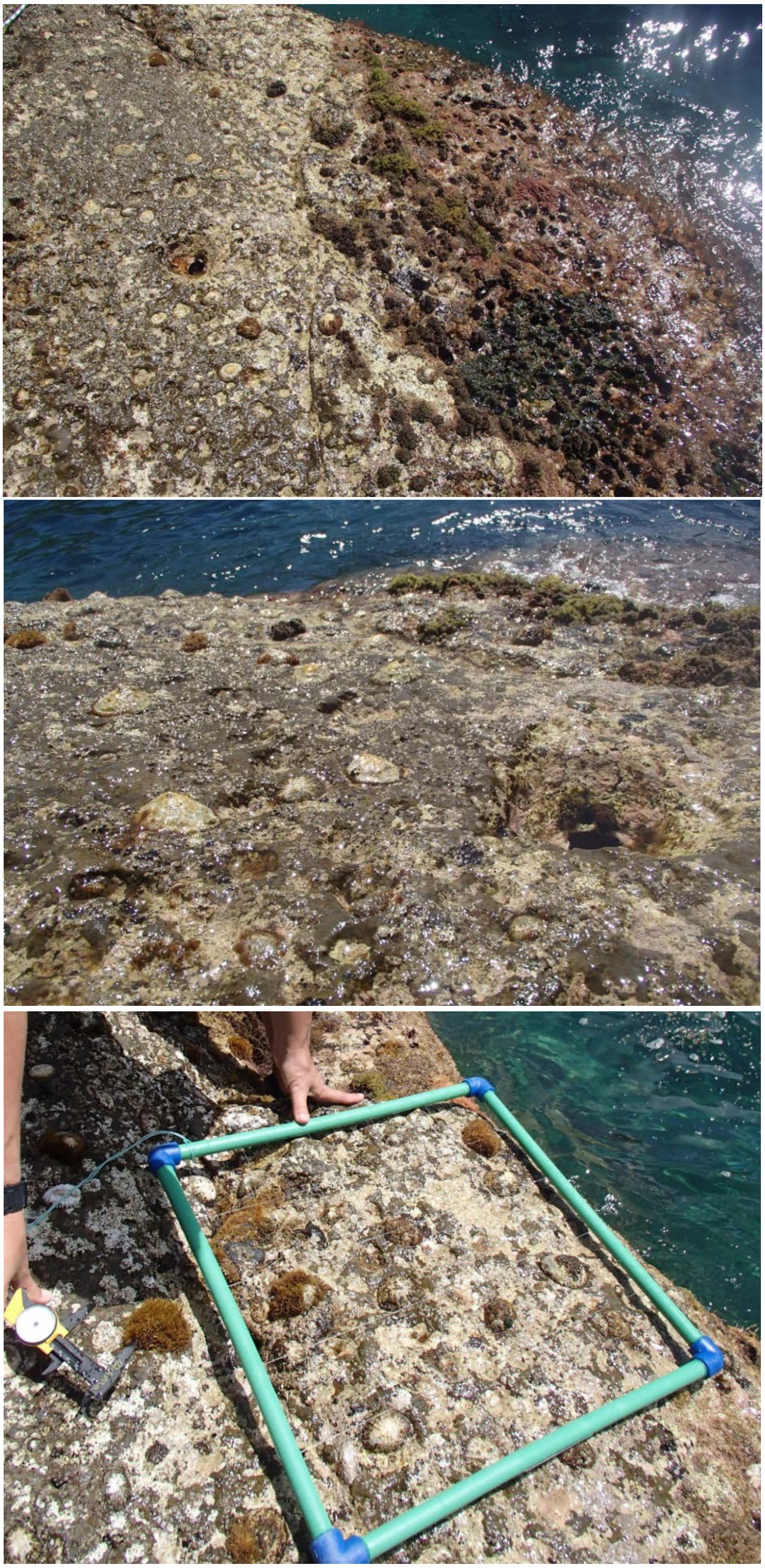


Figure 4.19. Limpets on the lower shore inside the Caldeira of Monte da Guia (transect 5) (quadrat size: 50 x 50 cm).

4.4.4. Concluding remarks

There are some indications of the possible influence of climate change on the intertidal communities in the Azores. Possible trimming back of upper limits, consistent with higher frequency of extreme warm events, is only apparent in more sheltered locations and restricted to upper shore species (e.g. *M. neritoides* and *T. striatus*). There has been an uplifting of the zones of several species in more exposed shores, perhaps attributable to more upward wetting due to stormier conditions; although the available averaged physical data for the Azores is not consistent with increased storminess reported by others (e.g. Wang *et al.*, 2004; Wolf and Woolf, 2006). In the absence of limpet grazing due to overexploitation, low shore algal species can extend upshore aided by more upward wetting. This in turn leads to less barnacle cover, even on moderately sheltered shores such as at Caloura. On most of the shores of the Azores any influence of extreme warm events are likely to be overridden by upward wetting due to storminess. Transect 5 in the heavily limpet repopulated inner Caldeira of Monte da Guia is a tantalising indication of what rocky shores would be if limpets were not heavily exploited. Thus human exploitation of limpets is probably having a greater effect than climate on Azorean shores; but both factors probably interact to enable rising of low shore algae in more exposed locations. Overall, long-term observations are vital for an accurate knowledge of the state of our seas and shorelines (Hawkins *et al.*, 2008, 2009). It is crucial to incorporate current patterns and future forecasts into marine conservation and management plans (Mieszkowska *et al.*, 2006a; Firth and Hawkins, 2011; Hawkins *et al.*, 2013b).

5. EXPERIMENTAL SIMULATION OF HOW AZOREAN INTERTIDAL COMMUNITIES MIGHT RESPOND TO CHANGES IN ENVIRONMENTAL CONDITIONS?

5.1. INTRODUCTION

Recent rapid climate change, such as increases in temperature and changes in the magnitude and frequency of extreme climatic events (Trenberth *et al.*, 2007; Lima and Wethey, 2012; IPCC, 2013) will influence the distribution of species, community structure and hence ecosystem functioning (Harley *et al.*, 2006; Helmuth *et al.*, 2006b; Smale *et al.*, 2013). Changes in disturbance regimes as a consequence of climate change may lead to ecosystem disruption if they influence keystone consumers or habitat forming species (Hawkins *et al.*, 2009; Smale *et al.*, 2013; Smale and Vance, 2015).

Climate change scenarios forecast increasing sea temperatures and storminess (physical factors) (IPCC, 2013). Predictions and observations also support the idea that many warm temperate, sub-tropical and tropical organisms such as algae (e.g. Beaugrand *et al.*, 2002b; Hays *et al.*, 2005; Lima *et al.*, 2007), invertebrates (e.g. Parker and Dixon, 1998; Sagarin *et al.*, 1999; Mieszkowska *et al.*, 2006a, 2007) and fish (e.g. Parker and Dixon, 1998; Perry *et al.*, 2005; Fodrie *et al.*, 2010; Sala *et al.*, 2011; Nakamura *et al.*, 2013) will continue shifting northwards. Species range shifts will probably lead to new species interactions between warmer and colder water (Cheung *et al.*, 2013; Poloczanska *et al.*, 2013; Vergés *et al.*, 2014a). Temperate canopy algae may be particularly vulnerable to predicted increases in physical stresses such as extreme temperatures and greater wave action, as well as intensified biological stresses (Hawkins *et al.*, 2008, 2009; Jenkins *et al.*, 2008; Ferreira *et al.*, 2014; Smale and Vance, 2015).

Canopy algae are considered ecosystem engineers (*sensu* Jones *et al.*, 1994) in coastal environments. They modify habitat conditions and thus promote the survival or the presence of other organisms, increase mortality in some contexts due to sweeping increasing spatial complexity, enhancing biodiversity and thus influencing the structure and functioning of coastal ecosystems (Hawkins, 1983; Reed and Foster, 1984; Hawkins and Hartnoll, 1985; Thompson *et al.*, 1996; Jenkins *et al.*, 1999b, 2008; Bruno and Bertness, 2001; Castilla *et al.*, 2004; Jonsson *et al.*, 2006; Borthagaray and Carranza, 2007; Bouma *et al.*, 2009; Cavieres and Badano, 2009 ; Altieri *et al.*, 2010; Sueiro *et al.*, 2011; Bulleri *et al.*, 2012; Nicastro *et al.*, 2013; Watt and Scrosati, 2013).

Canopy-forming macroalgae are key elements of intertidal and shallow subtidal communities in many temperate regions (Lewis, 1964; Stephenson and Stephenson, 1972; Jonsson *et al.*, 2006; Ferreira *et al.*, 2014). In the rocky intertidal, algal canopies can have direct and indirect positive and negative effects on other species (Chapman and Johnson, 1990; Steneck *et al.*, 2002; Eriksson *et al.*, 2007; Jenkins *et al.*, 2008), for instance, among direct effects, algal canopies negatively affect the amount of light reaching the substratum and that is available for understorey organisms (Arenas *et al.*, 2006). They may also, reduce the settlement of algal propagules and larvae via the sweeping of their fronds (Hawkins, 1983; Hawkins and Hartnoll, 1983b; 1985; Jenkins *et al.*, 1999c), whilst they may positively influence understorey organisms by retaining moisture, reducing temperature stress and protecting organisms from the solar radiance (Hawkins, 1983; Bertness *et al.*, 1999; Jenkins *et al.*, 1999b; Figueiredo *et al.*, 2000; Lilley and Schiel, 2006; Moore *et al.*, 2007b; Hawkins *et al.*, 2008). These direct effects may in turn lead to indirect effects such as via changes in the abundance of key organisms. For instance, by negatively affecting the settlement of limpets and barnacles, canopy algae may indirectly promote the establishment of macroalga turfs (Jenkins *et al.*, 2005).

There has been a global decline or loss of habitat-forming species in many temperate rocky shores (e.g. North Atlantic: Jenkins *et al.*, 1999a,b; Yesson *et al.*, 2015; Mediterranean: Benedetti-Cecchi *et al.*, 2001a; Airoldi and Beck, 2007; New Zealand: Lilley and Schiel, 2006; California: Thom and Widdowson, 1978; Baltic Sea: Vogt and Schramm, 1991; Wikström and Kautsky, 2007; Nicastro *et al.*, 2013). These key habitat-forming species have been exposed to several impacts of human origin at local scales, such as coastal urbanization (Airoldi and Beck, 2007), harvesting (Airoldi *et al.*, 2008), invasive species (Mangialajo *et al.*, 2008), as well as global climate change (Schiel and Lilley, 2011). The loss of such key habitat-forming canopy algae may lead to changes in the biodiversity with potentially community-wide cascading effects (Nicastro *et al.*, 2013).

Fucoid canopy algae are dominant on sheltered conditions on North-East Atlantic rocky shores (Lewis, 1964; Hawkins and Hartnoll, 1985; Thompson *et al.*, 1996; Jonsson *et al.*, 2006), tending to decline in abundance with decreasing latitude along the coasts of the North-East Atlantic (Ballantine, 1961; Hawkins and Hartnoll, 1983a; Southward *et al.*, 1995; Jenkins *et al.*, 2008; Ferreira *et al.*, 2014). Many fucoid species reach their southern range limit along the Portuguese coastline (Ballantine, 1961; Ribera *et al.*, 1992; Lima *et al.*, 2007; Ferreira, 2012; Nicastro *et al.*, 2013; Ferreira *et al.*, 2014). *Fucus spiralis* and the recently described *Fucus giuryi* are the exceptions extending South down to Morocco and Canaries. Here, they are edge populations, which may be particularly vulnerable to global changes (Lima and Wethey, 2012).

In the Azores, the northern species *F. spiralis* is present at the mid shore zone of moderate exposed conditions. It forms scattered patches and is commonly associated with the turf-forming *Gelidium microdon* (Martins, 2009). According to Neto (1997), *F. spiralis* has a prolonged reproductive period being fertile all year around in the Azores.

The overall aim of my study was to investigate the community-level consequences of the loss of the northern ecosystem engineer species *Fucus spiralis* from Azorean rocky shores. *Fucus spiralis,* in the Azores, is an edge population and it is at risk from both extreme hot events and general warming at the upper limit of its distribution. Moreover, it is potentially exposed to intense herbivory at the lower limit of distribution on the shore. Here, I simulated the complete and partial loss of *Fucus spiralis*, mimicking macroalgae loss both due to increased storminess that rips off the entire plant, as well as the thinning of macroalgae cover as a result of heat stress (Schonbeck and Norton, 1978; Hawkins and Hartnoll, 1985) or increased grazing levels due to northward migration of herbivorous fish (e.g. *Sarpa salpa*). It was hypothesised that the loss of *F. spiralis* might affect the structure of the understorey assemblage and that the effects will vary according to the intensity of the treatment (complete versus partial loss). The experiment started at two different seasons: (1) at the end of the summer, to simulate reduction in canopy cover as a consequence of increased temperature stress and grazing; and (2) at the end of winter, to simulate loss of canopy due to extreme wave action. This was important as timing of disturbance may mediate the response of the understorey assemblage to the loss of the canopy macroalgae. The damage caused by fish grazing was also quantified and the suspected grazer identified as *Sarpa salpa* (M. Vale *personal observation*).

Note that during the course of my thesis, the taxonomy of *F. spiralis* was reviewed (Zardi *et al.*, 2011, 2015). The fucoid species present in the Azores is now thought to probably be the recently described *Fucus giuryi* and not *Fucus spiralis* as previously thought (K. R. Nicastro and G. I. Zardi *personal communication*). Since, both fucoid species (*F. guiryi* and *F. spiralis*) show the same distribution and are considered northern species (Zardi *et* *al.*, 2011, 2015; Guiry and Guiry, 2015); the underlining logic of the work has not changed. For simplicity, and until further confirmation, I have retained the initial name *Fucus spiralis*.

5.2. MATERIAL AND METHODS

5.2.1. Study Area

Two study locations were selected on the South coast of São Miguel: A) Lotacor - adjacent to Lotaçor at Santa Clara in Ponta Delgada, and B) ETAR - adjacent to the sewage treatment station at Pranchinha in Ponta Delgada (Figure 5.1). These two locations were selected because they support extensive patches of *Fucus spiralis*; they are both gentle sloping shores and similarly exposed to wave action (moderately exposed). At these locations *F. spiralis* forms conspicuous patches in the upper eulittoral zone and is commonly associated with the corticated *Gelidium microdon* and the foliose algae *Ulva rigida*. Barnacles and limpets are generally not as abundant amongst *F. spiralis*, unlike elsewhere. No influence of effluent from the sewage treatment station was anticipated as this was dispersed offshore (~50m) via a pipe. Some problems were later encountered due to leakage during the course of the experiment (see below).

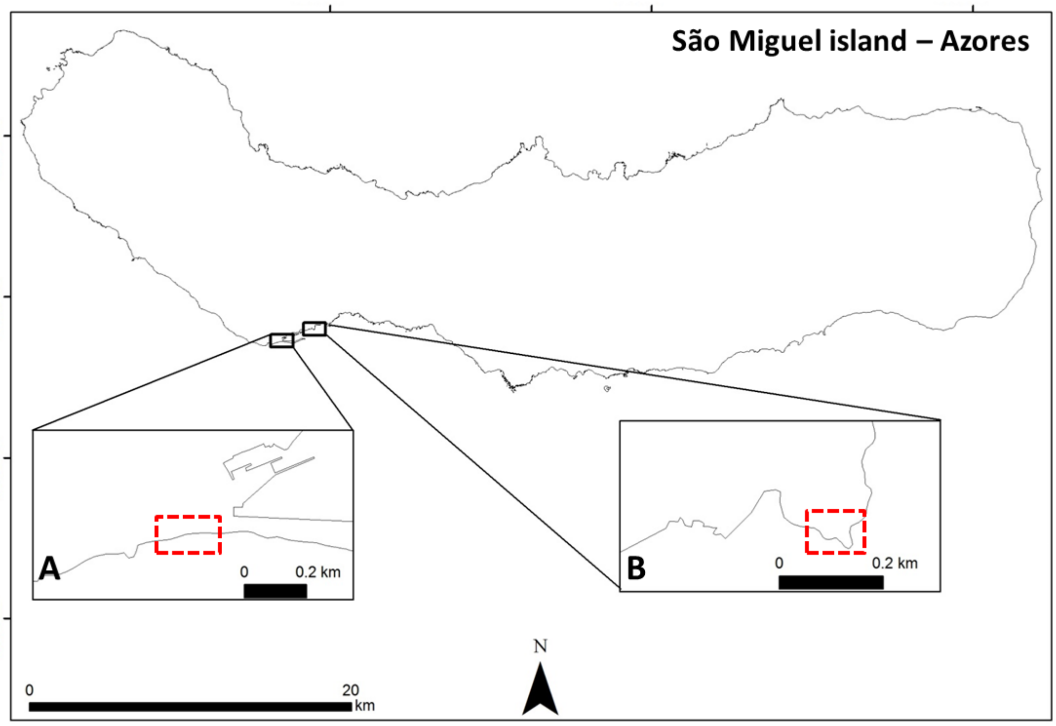


Figure 5.1. Study locations on the South coast of São Miguel island: **A)** Lotacor and **B)** ETAR.

5.2.2. Experimental design

For each experiment (end of summer and end of winter initiation) and at each location, 20 x 20 cm plots with >70% cover of *F. spiralis* were selected and marked in the corners with screws and a coloured label. The plots (patches of habitat) were then randomly assigned into one of three treatments (n=5 per treatment): 1) Control (C) - no removal of *F. spiralis*; 2) 100% Complete Removal (R) of *F. spiralis* achieved by scraping off plants holdfast with a scalpel; and 3) Partial Removal (PR) of *F. spiralis* plants achieved by cutting algal fronds with scissors leaving only the stipe and holdfast mimicking the effects of grazing by *Sarpa salpa*. There were thus a total of 60 experimental plots (2 locations (Lotacor and ETAR) x 2 experiments (end of summer and end of winter initiation) x 3 treatments (C, R and PR) x 5 replicates). Plots were sampled prior to the treatment establishment (T0) and at 1, 2, 4, 8, 12, 20, 28, 36 and 48 weeks subsequently (Figure 5.2). The end of summer initiation started in October 2013; the end of winter initiation started in the following March (2014). In the experiment initiated at the end of the summer sampling was not possible during the 1st week due to harsh sea conditions.

The abundance of species was estimated in each plot using a 10 x 10 cm quadrat with 64 subquadrats by calculating the total number of subdivisions in which each species was present and later converting these into percentage cover. This was done firstly for the cover of *F. spiralis* and secondly, by gently pushing the canopy aside, for the understorey species (algae and sessile invertebrates). The number of *F. spiralis* plants and motile animals were counted in the entire quadrat area.

To investigate temporal patterns in fucoid fitness, on each of the two shores, 50 individual plants of *F. spiralis* were randomly selected (25 towards the higher and 25 towards the lower limits of the *F. spiralis* zone). The length of each plant was measured. Each plant was also inspected for signs of heat stress (bleaching) and grazing damage and assigned a score of 1 (bitten) or 0 (not bitten).

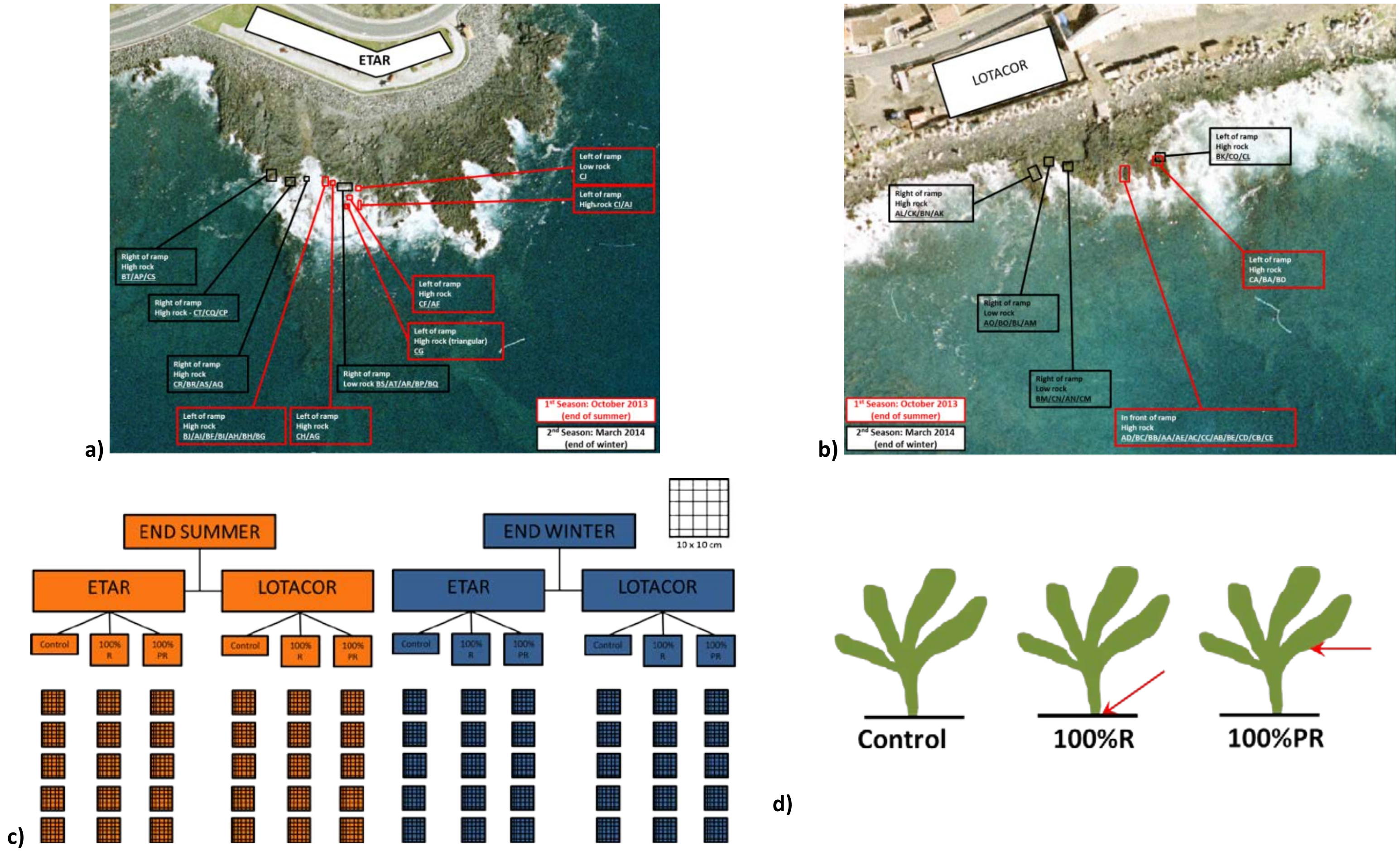


Figure 5.2. *Fucus spiralis* removal experiment: **a)** study location - ETAR da Pranchinha; **b)** study location - Lotacor; **c)** experimental sampling design; **d)** three treatments - Control, 100%R (100% complete Removal of *F. spiralis*), and 100%PR (100% Partial Removal of *F. spiralis*) (red arrow shows the cutting level).

5.2.3. Data analysis

Preliminary data analyses showed that the cover of *F. spiralis* in disturbed quadrats could be divided into three distinct periods: I - post-disturbance (1st, 2nd and 4th weeks (T1-T3)), II - recovery (8th, 12th and 20th weeks (T4-T6)), and III - stabilization (28th, 36th and 48th weeks (T7-T9)). Data from different times were thus pooled together within these periods in order to make data analyses and interpretation of results clearer (Table 5.1).

Table 5.1. Sampling dates and respectively response periods for both experiments (end of summer and end of winter initiation experiments).

SAMPLING	END OF SUMMER INITIATION	END OF WINTER INITIATION	RESPONSE PERIOD
T0	October 2013	March 2014	**T0**
1st week	-	March 2014	**I**
2nd weeks	October 2013	March 2014	
4th weeks	November 2013	April 2014	
8th weeks	December 2013	May 2014	**II**
12th weeks	January 2014	June 2014	
20th weeks	March 2014	August 2014	
28th weeks	May 2014	October 2014	**III**
36th weeks	June 2014	December 2014	
48th weeks	October 2014	March 2015	

From this point forward the treatments will be referred as **Control - C** (no removal of *F. spiralis*), **Removal - R** (100% complete Removal of *F. spiralis*), and **Partial Removal - PR** (100% Partial Removal of *F. spiralis* plants). For the analyses, taxa were grouped into 8 morpho-functional categories (adapted from Steneck and Dethier, 1994) that included: *Fucus spiralis*, corticated foliose algae, crustose algae, articulated coralline algae, C*hthamalus stellatus*, foliose algae, filamentous algae and *Patella candei gomesii*, plus bare rock.

The response of each taxa was analysed using a 2-way mixed model permutational analysis of variance with the following factors: Treatment (3 levels, fixed) and Location (2 levels, random). In addition, the response of the assemblage as a whole was also investigated by running a multivariate analysis. Analyses were run separately for the end of summer and end of winter initiation experiments. Variation in the mean length of *F. spiralis* and the percentage of plants with grazing marks were compared monthly using a

2-way mixed model permutational analysis of variance with the following factors: Shore level (2 levels, fixed), and Location (2 levels, random).

All analyses were run on PRIMER 6 and PERMANOVA$^+$ packages (Clarke and Gorley, 2006) based on Euclidean (in the case of univariate analysis) or Bray-Curtis (in the case of multivariate analysis) distances and using 999 permutations. Where appropriate, data were transformed prior to analysis to remove heterogeneity of variances. In the multivariate analyses, species contributions to differences among treatments were examined using SIMPER.

5.3. RESULTS

5.3.1. *Fucus spiralis*

The response of *F. spiralis* to the canopy removal differed with the time of the initiation of the experiment (Figure 5.3). Over the period investigated, the Control plots show the natural pattern of *F. spiralis* cover at each site. In the end of the summer initiation experiment, cover rapidly declined at both locations in the autumn and winter of 2013, probably in response to storms, with the cover of the controls converging towards the manipulated treatments (Figure 5.3.a). A similar decline occurred in the Controls of the end of winter initiation experiment in the following autumn (2014) (Figure 5.3.b). Following disturbance simulated at the end of the summer initiation, recovery was apparent after eight weeks at Lotacor and 4 weeks at ETAR. At ETAR recovery was 80% complete within a year, whilst at Lotacor a much slower recovery was observed (Figure 5.3.a). At ETAR, growth of newly recruited fucoids exceeded that of Controls, where canopy loss occurred due to winter storms. Recovery was apparent slightly more rapid following the end of winter disturbance (after 4 weeks in both locations) (Figure 5.3.b). Recovery was more rapid at Lotacor, reaching 80% of cover in just under a year, with growth of new recruits exceeding the Controls. At ETAR only 50% of the initial cover had recovered, matching the Control levels that had been reduced by winter storms (Figure 5.3.b). After the disturbance treatments (period I), there were, as expected, significant differences in the cover of *F. spiralis* among treatments both in the end of summer and end of winter initiation experiments (Table 5.2). Inspection of pairwise comparisons showed that the cover of *F. spiralis* was significantly lower in the Removal treatment compared to Control treatment and intermediate in Partial Removal treatment (Figure

5.3.c,d). As time since disturbance elapsed (period II), there were still significant differences among treatments detected in both the end of summer and end of winter initiation removal experiments (Table 5.2). Inspection of pair-wise tests revealed that the cover of *F. spiralis* in Partial Removal treatment recovered converging to that of Control treatment although in Removal treatment the cover of *F. spiralis* was still significantly lower (Figure 5.3.c,d). As time further elapsed (period III), the cover of *F. spiralis* in the three treatments had converged fully both in the end of summer and end of winter initiation removal experiments (Figure 5.3.c,d and Table 5.2). The response of *F. spiralis* to treatments was spatially consistent in the two locations despite differences in temporal patterns of cover between locations (Table 5.2).

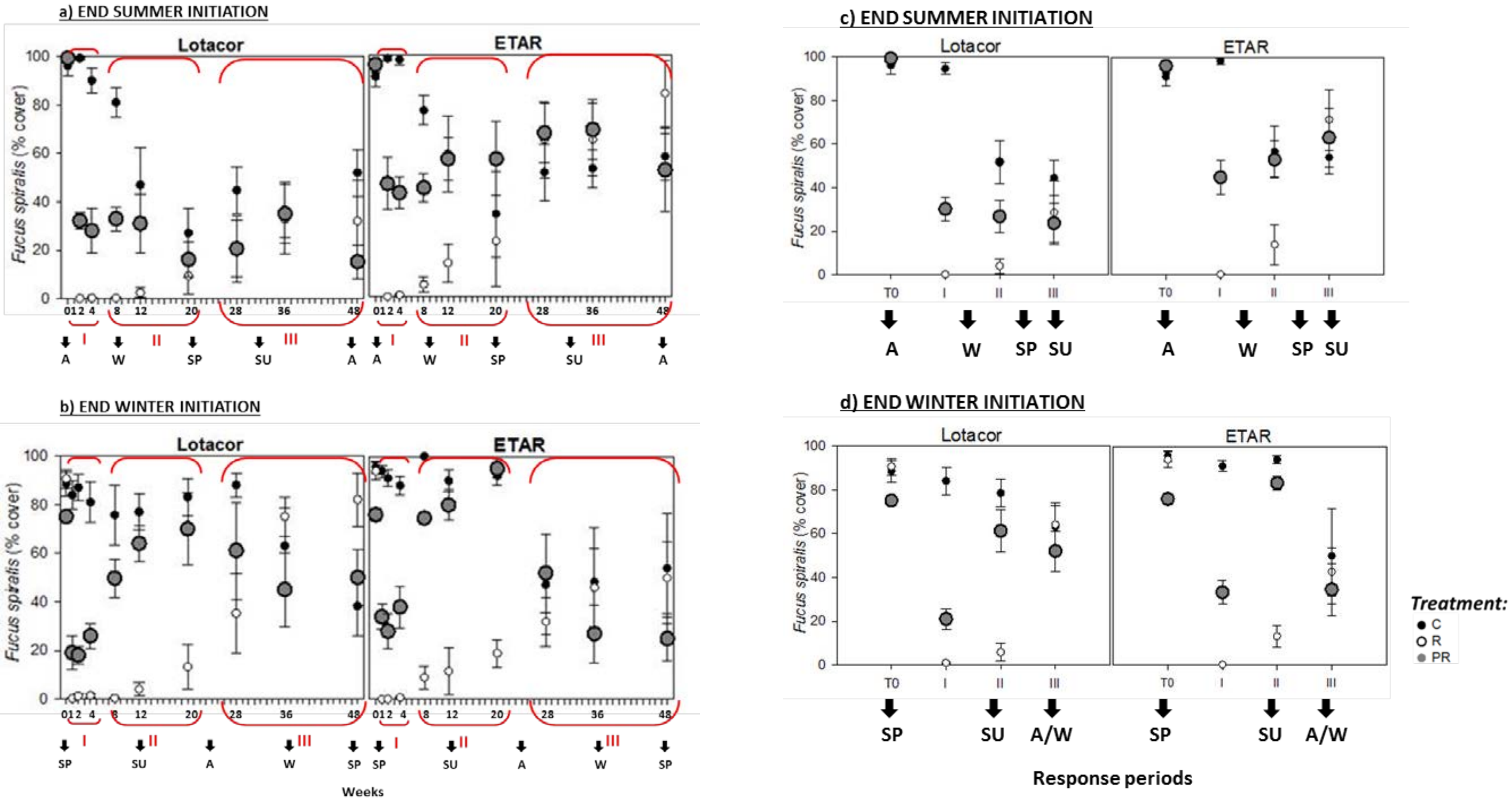
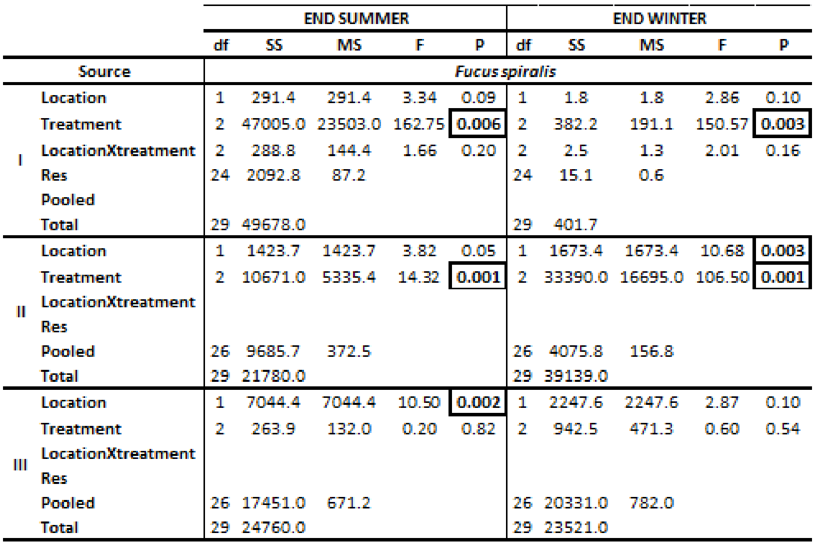


Figure 5.3. Abundance of *Fucus spiralis* in end of summer and end of winter initiated removal experiments for the 3 treatments: **a)** abundances for the end of summer initiation, **b)** abundances for the end of winter initiation, in **c)** end of summer initiation (N.B. non-linear scale) and **d)** end of winter initiation (N.B. non-linear scale) the data has been grouped into three periods of response (I - immediate response period (weeks: 1, 2 and 4), II - recovery period (weeks: 8, 12 and 20), and III - stabilization period (weeks: 28, 36 and 48)) (Location: Lotacor and ETAR; Treatment: Control (C) - black circles, Removal (100%R) - white circles, and Partial Removal (100%PR) - grey circles; Seasons: A - Autumn, W - Winter, SP - Spring, and SU - Summer).

Table 5.2. PERMANOVA results on *Fucus spiralis* for both experiments at the 3 response periods (Response periods: I - immediate response (weeks: 1, 2 and 4), II - recovery (weeks: 8, 12 and 20) and III - stabilization (weeks: 28, 36 and 48)) (bold - statistically significant).



		END SUMMER					END WINTER				
		df	SS	MS	F	P	df	SS	MS	F	P
	Source	*Fucus spiralis*									
I	Location	1	291.4	291.4	3.34	0.09	1	1.8	1.8	2.86	0.10
	Treatment	2	47005.0	23503.0	162.75	**0.006**	2	382.2	191.1	150.57	**0.003**
	LocationXtreatment	2	288.8	144.4	1.66	0.20	2	2.5	1.3	2.01	0.16
	Res	24	2092.8	87.2			24	15.1	0.6		
	Pooled										
	Total	29	49678.0				29	401.7			
II	Location	1	1423.7	1423.7	3.82	0.05	1	1673.4	1673.4	10.68	**0.003**
	Treatment	2	10671.0	5335.4	14.32	**0.001**	2	33390.0	16695.0	106.50	**0.001**
	LocationXtreatment										
	Res										
	Pooled	26	9685.7	372.5			26	4075.8	156.8		
	Total	29	21780.0				29	39139.0			
III	Location	1	7044.4	7044.4	10.50	**0.002**	1	2247.6	2247.6	2.87	0.10
	Treatment	2	263.9	132.0	0.20	0.82	2	942.5	471.3	0.60	0.54
	LocationXtreatment										
	Res										
	Pooled	26	17451.0	671.2			26	20331.0	782.0		
	Total	29	24760.0				29	23521.0			

5.3.2. *Fucus spiralis*: size and grazing damage

At the lower end of the vertical distribution of *F. spiralis*, in both locations, the canopy was biggest in May (ETAR - 8 cm and Lotacor - 5.9 cm) and smallest in August (ETAR - 1.4 cm and Lotacor - 1.7 cm). At the higher level of vertical distribution, smallest sizes of *F. spiralis* occurred in April (ETAR - 6.5 cm and Lotacor - 4.9 cm) in both locations. There was not a consistent pattern of largest sizes at the two locations (Lotacor - October and November (8.9 cm), ETAR - December (11.5 cm)) (Figure 5.4). Analysis of *F. spiralis* length showed a significant location x shore level interaction in ten of the twelve months (from January to May and from July to December). In the remaining two months (April and June), *F. spiralis* was significantly smaller at the lowest shore level (Table 5.3). Inspection of pair-wise tests for the ten months showed, that in nine of the ten months (all except May), *F. spiralis* was significantly smaller at the low shore levels and that these were consistent in the two locations. In May, the pair-wise test revealed that *F. spiralis* was smaller in the low shore level at ETAR (p=0.002), but not at Lotacor (Table 5.3).

At the lower shore levels, grazing marks were more frequent in summer than in winter (June to September - 100% of the canopy plants showed grazing marks) in both locations. At higher shore levels, grazing marks were generally low and the highest percentage was recorded in October in both locations (percentage of canopy plants that presented grazing marks: ETAR - 22% and Lotacor - 24%) (Figure 5.4). There were significant differences between the shore levels for five months (March, June, August, September and October), with the percentage of grazing marks being higher at the low shore level. In December there was a significant location x shore level interaction (Table 5.3). Inspection of pair-wise tests, revealed a significant greater percentage of grazing marks on the lower shore at both the locations (Lotacor: *p*=0.001, and ETAR: *p*=0.001). Occasional bleaching was detected along the study, especially in the summer months, when high levels of solar radiation (unclouded) occurred simultaneously with low tide (emersion period). However, these bleaching events appeared to be overweight by the wave action.

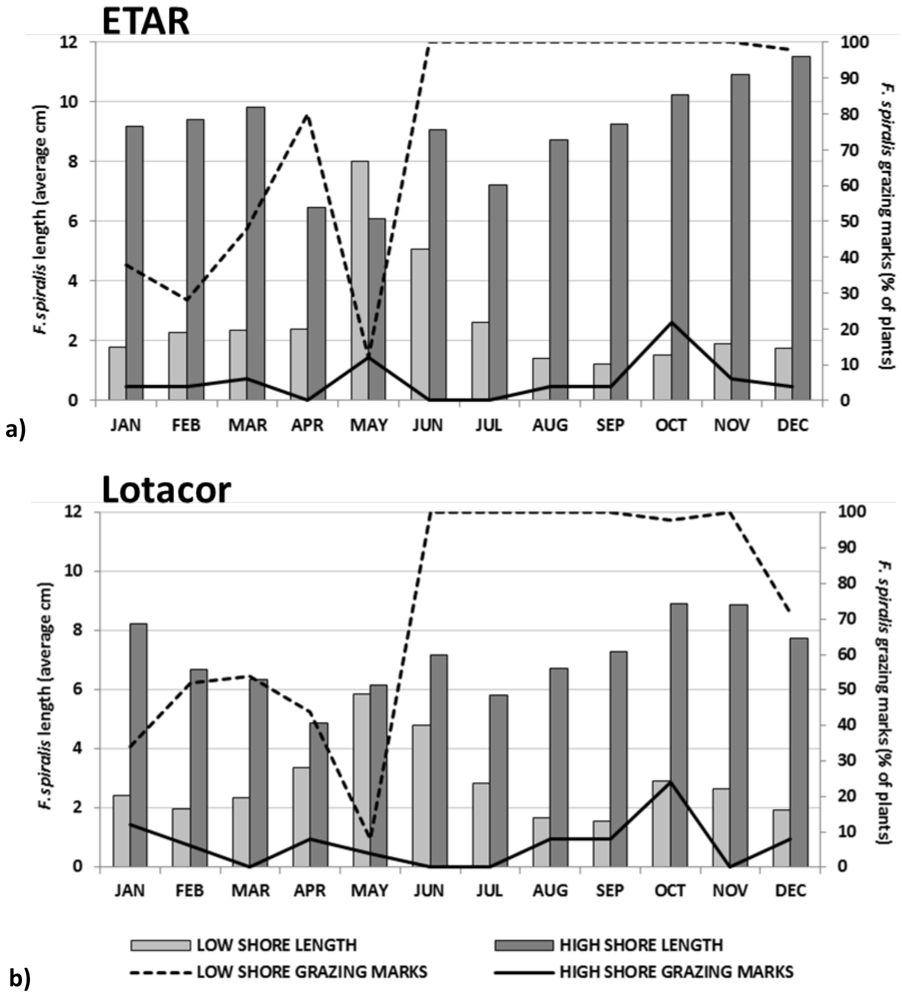


Figure 5.4. *Fucus spiralis* monthly averaged lengths and monthly percentage of plants with grazing marks for low and high shore levels: **a)** ETAR and **b)** Lotacor.

Table 5.3. PERMANOVA monthly results on *Fucus spiralis* length and grazing marks percentage for both low and high shore levels (bold - statistically significant).

		FUCUS HEIGHTS					FUCUS GRAZING				
	Source	**df**	**SS**	**MS**	**F**	**P**	**df**	**SS**	**MS**	**F**	**P**
JANUARY	**Location**	1	8.35E-03	8.35E-03	9.30E-02	0.773	1	100	100	0.23415	0.635
	Level	1	57.568	57.568	70.536	0.081	1	19600	19600	21.778	0.151
	Location X Level	1	0.81615	0.81615	9.088	**0.006**	1	900	900	2.1073	0.147
	Res	96	8.6213	8.98E-02			96	41000	427.08		
	Total	99	67.014				99	61600			
FEBRUARY	**Location**	1	0.23242	0.23242	22.701	**0.001**	1	4225	4225	6.3375	**0.01**
	Level	1	5.7346	5.7346	107.25	0.061	1	30625	30625	10.124	0.185
	Location X Level	1	5.35E-02	5.35E-02	5.2227	**0.023**	1	3025	3025	4.5375	0.04
	Res	96	0.98287	1.02E-02			96	64000	666.67		
	Total	99	7.0034				99	1.02E+05			
MARCH	**Location**	1	0.18955	0.18955	20.387	**0.001**	1	-5.78E-11	-5.78E-11	Negative	
	Level	1	4.9957	4.9957	22.519	0.127	1	57600	57600	86.623	**0.001**
	Location X Level	1	0.22185	0.22185	23.861	**0.001**					
	Res	96	0.89255	9.30E-03							
	Pooled						97	64500	664.95		
	Total	99	6.2996				99	1.22E+05			
APRIL	**Location**	1	3.8027	3.8027	60.806	**0.001**	1	4225	4225	9.0133	**0.004**
	Level	1	17.756	17.756	26293	**0.003**	1	87025	87025	42.975	0.106
	Location X Level	1	6.75E-04	6.75E-04	1.08E-02	0.917	1	2025	2025	4.32	0.042
	Res	96	6.0037	6.25E-02			96	45000	468.75		
	Total	99	27.563				99	1.38E+05			
MAY	**Location**	1	26.01	26.01	6.2138	**0.018**	1	900	900	1.0791	0.384
	Level	1	16.81	16.81	0.5557	0.588	1	100	100	0.1199	0.785
	Location X Level	1	30.25	30.25	7.2268	**0.009**					
	Res	96	401.84	4.1858							
	Pooled						97	80900	834.02		
	Total	99	474.91				99	81900			
JUNE	**Location**	1	1.0921	1.0921	13.633	**0.002**	1	25	25	1	0.563
	Level	1	22.283	22.283	278.18	**0.001**	1	2.45E+05	2.45E+05	9801	**0.001**
	Pooled	97	7.77	8.01E-02			97	2425	25		
	Total	99	31.145				99	2.47E+05			
JULY	**Location**	1	8.41	8.41	2.8214	0.104	1	2.72E-10	2.72E-10	Denominator is 0	
	Level	1	349.69	349.69	18.912	0.149	1	2.50E+05	2.50E+05	Denominator is 0	
	Location X Level	1	18.49	18.49	6.203	**0.018**	1	6.55E-10	6.55E-10	Denominator is 0	
	Res	96	286.16	2.9808			96	-3.54E-10	-3.69E-12		
	Total	99	662.75				99	2.50E+05			
AUGUST	**Location**	1	0.44501	0.44501	5.4368	**0.017**	1	100	100	0.3452	0.675
	Level	1	59.389	59.389	41.997	0.088	1	2.21E+05	2.21E+05	762.54	**0.001**
	Location X Level	1	1.4141	1.4141	17.277	**0.001**					
	Res	96	7.8577	8.19E-02							
	Pooled						97	28100	289.69		
	Total	99	69.105				99	2.49E+05			
SEPTEMBER	**Location**	1	1.02E-02	1.02E-02	1.9036	0.178	1	100	100	0.3452	0.657
	Level	1	9.2914	9.2914	51.655	0.089	1	2.21E+05	2.21E+05	762.54	**0.001**
	Location X Level	1	0.17987	0.17987	33.609	**0.001**					
	Res	96	0.51379	5.35E-03							
	Pooled						97	28100	289.69		
	Total	99	9.9953				99	2.49E+05			
OCTOBER	**Location**	1	4.00E-02	4.00E-02	2.94E-02	0.853	1	-1.56E-10	-1.56E-10	Negative	
	Level	1	1354.2	1354.2	30.623	0.114	1	1.44E+05	1.44E+05	363.81	**0.001**
	Location X Level	1	44.223	44.223	32.539	**0.001**					
	Res	96	130.47	1.3591							
	Pooled						97	38500	396.91		
	Total	99	1529				99	1.83E+05			
NOVEMBER	**Location**	1	4.34E-02	4.34E-02	0.69739	0.401	1	225	225	3.2727	0.073
	Level	1	67.852	67.852	34.329	0.106	1	2.35E+05	2.35E+05	1045.4	0.022
	Location X Level	1	1.9765	1.9765	31.734	**0.001**	1	225	225	3.2727	0.101
	Res	96	5.9792	6.23E-02			96	6600	68.75		
	Total	99	75.851				99	2.42E+05			
DECEMBER	**Location**	1	0.13662	0.13662	17.185	**0.001**	1	3025	3025	9.4286	**0.006**
	Level	1	9.0193	9.0193	35.542	0.095	1	1.56E+05	1.56E+05	27.738	0.118
	Location X Level	1	0.25377	0.25377	31.921	**0.001**	1	5625	5625	17.532	**0.001**
	Res	96	0.76319	7.95E-03			96	30800	320.83		
	Total	99	10.173				99	1.95E+05			

5.3.3. Assemblage responses

In the first period of the experiment (I), there were no significant differences in the assemblage structure among treatments and this was consistent both in the end of summer and end of winter initiation experiments (Table 5.4 and Figure 5.5).

In the second period (II), in the end of winter initiation experiment there were significant differences in the assemblage structure among treatments (Table 5.4). Inspection of pair-wise comparisons showed that assemblages in the Removal treatment were similar to Control treatment but differed significantly from the assemblages in the Partial Removal treatment ((C=R)≠PR) (Figure 5.5). SIMPER analysis revealed that in the end of winter initiation experiment, the assemblages in Partial Removal treatment were characterised by a greater abundance of corticated foliose algae than the assemblages in the Control and Removal treatments (Table 5.5).

In the third period (III), in the end of winter initiation experiment, there was a significant interaction between treatments and locations (Table 5.4). Inspection of pair-wise tests revealed spatially consistency results in both locations - ETAR and Lotacor, with the assemblages in the Removal treatment being similar to the Partial Removal treatment but significantly different from assemblages in the Control treatment ((C≠R)=PR) (Figure 5.5). SIMPER analysis revealed that at the end of the winter initiation experiment, the assemblages in the Removal treatment were characterised by a greater abundance of corticated foliose algae and bare rock then the assemblages in the Control treatment. While the assemblages in Partial Removal treatment revealed similar abundances of corticated foliose algae, foliose algae and bare rock with the assemblages in the Removal treatment (Table 5.5). The n-MDS ordination for the third period (III) showed that two samples from Controls and one sample from Partial Removal at ETAR diverged substantially from the remaining data set (Figure 5.5). These could be related to the fact that the study area is located below an industrial water treatment station and regular sewage releases here reported from August 2014 to June 2015, due to leakage in the sewage pipe (Figure 5.5).

Table 5.4. Multivariate PERMANOVA comparing the structure of assemblages among treatments for both the end of summer and end of winter initiation experiments (Response periods: I - immediate response (weeks: 1, 2 and 4), II - recovery (weeks: 8, 12 and 20) and III - stabilization (weeks: 28, 36 and 48)) (bold - statistically significant).

		END SUMMER					END WINTER				
	Source	df	SS	MS	F	P	df	SS	MS	F	P
I	Location	1	288.38	288.38	0.49	0.69	1	623.03	623.03	0.63	0.51
	Treatment	2	1577.9	788.93	1.35	0.25	2	3054.8	1527.4	1.54	0.20
	LocationXtreatment										
	Res										
	Pooled	26	15199	584.59			26	25850	994.21		
	Total	29	17066				29	29527			
II	Location	1	1353.2	1353.2	1.55	0.21	1	1188.6	1188.6	2.64	0.09
	Treatment	2	4796.8	2398.4	1.99	0.26	2	3251.7	1625.8	3.61	0.011
	LocationXtreatment	2	2411.9	1205.9	1.38	0.23					
	Res	24	20952	873.02							
	Pooled						26	11715	450.59		
	Total	29	29514				29	16156			
III	Location	1	1510	1510	2.66	0.048	1	903.82	903.82	1.06	0.39
	Treatment	2	1283.9	641.96	0.81	0.55	2	860.23	430.11	0.12	0.98
	LocationXtreatment	2	1588.3	794.13	1.40	0.22	2	6948.4	3474.2	4.06	0.002
	Res	24	13601	566.69			24	20531	855.47		
	Pooled										
	Total	29	17983				29	29244			

Table 5.5. SIMPER analysis to the structure of assemblages among treatments for end of winter initiation experiment in the response periods - II and III (Response periods: II - recovery (weeks: 8, 12 and 20) and III - stabilization (weeks: 28, 36 and 48)).

END WINTER - II						
Groups C & R (Average dissimilarity = 33.44)						
Species	C-Av.Abund	R-Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Foliose	1.5	3.52	7.42	1.27	22.19	22.19
Bare rock	5.97	5.27	6.83	1.33	20.43	42.62
Corticated	5.84	5.41	6.45	1.36	19.28	61.9
Barnacles	1.69	1.97	3.34	1.69	9.98	71.88
Groups C & PR (Average dissimilarity = 29.72)						
Species	C-Av.Abund	PR-Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Bare rock	5.97	4.16	7.64	1.40	25.72	25.72
Corticated	5.84	7.87	6.45	1.15	21.71	47.43
Foliose	1.5	2.27	5.16	1.11	17.38	64.81
Encrusting	2.95	1.74	3.63	1.79	12.21	77.02
Groups R & PR (Average dissimilarity = 32.95)						
Species	R-Av.Abund	PR-Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Foliose	3.52	2.27	7.58	1.34	23	23
Corticated	5	7.87	7.53	1.50	22.860	45.86
Bare rock	5	4.16	6.98	1.42	21.170	67.04
Barnacles	2	1.26	3.59	1.67	10.89	77.93
END WINTER - III						
Groups C & R (Average dissimilarity = 41.14)						
Species	C-Av.Abund	R-Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Corticated	39.53	45.52	14.14	1.5	34.37	34.37
Bare rock	24.64	30.31	12.17	1.28	29.59	63.96
Foliose	24.74	16.32	10.01	1.11	24.33	88.29
Groups C & PR (Average dissimilarity = 40.44)						
Species	C-Av.Abund	PR-Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Corticated	39.53	42.86	12.14	1.44	30.01	30.01
Foliose	24.74	17.14	10.80	1.13	26.7	56.71
Bare rock	24.64	24.64	10.74	1.38	26.55	83.26
Groups R & PR (Average dissimilarity = 39.38)						
Species	R-Av.Abund	PR-Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Corticated	46	42.86	14.45	1.39	36.70	36.7
Bare rock	30	24.64	10.7	1.34	27.170	63.87
Foliose	16	17.14	7.27	1.28	18.47	82.34

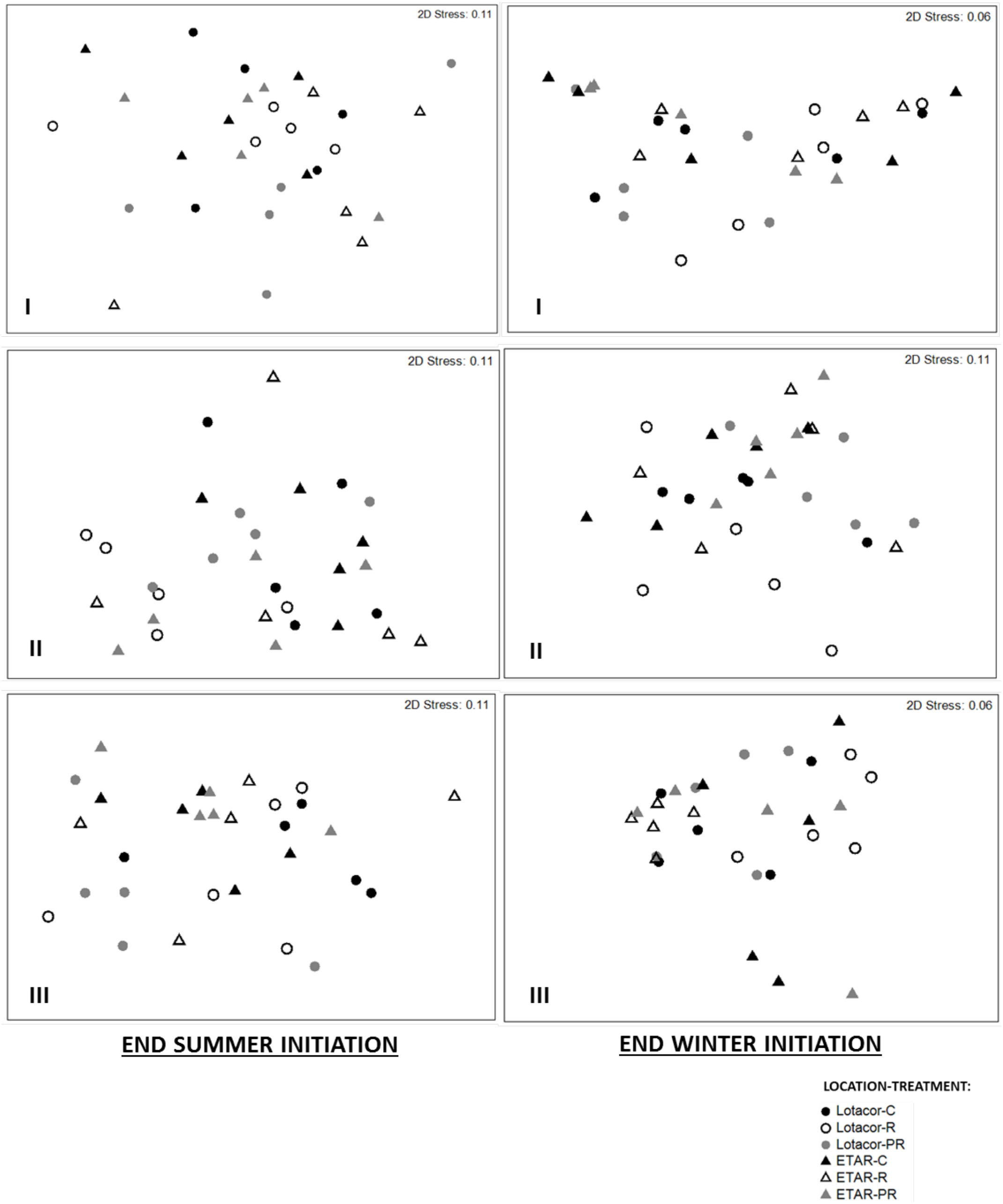


Figure 5.5. n-MDS ordination analysis of assemblages for end of summer and end of winter initiation experiment for the 3 response periods (Treatment: C - Control (black symbols), R - Removal (white symbols) and PR - Partial Removal (grey symbols); Location: ETAR (triangular symbols) and Lotacor (circular symbols); Response periods: I - immediate response (weeks: 1, 2 and 4), II - recovery (weeks: 8, 12 and 20) and III - stabilization (weeks: 28, 36 and 48); Note: *F. spiralis* removed from the analysis).

5.3.4. Responses of individual taxa

Patella candei gomesii appears to have benefitted from the removal of the *F. spiralis* in the beginning of the end of summer initiation experiment (only at ETAR - Removal); also in the end of winter initiation experiment a peak of abundance was observed in the Removal treatment at week 8 (only at Lotacor) (Figures 5.6 and 5.7). *Chthamalus stellatus* appears to have responded positively to the removal of the *F. spiralis* at the beginning of the end of summer initiation experiment in Lotacor (Partial Removal) (Figures 5.6 and 5.7). These differences, however, were not spatially consistent not statistically significant (*P. candei gomesii:* end of summer initiation - p=0.29 (response period I - treatment), end of winter initiation - p=0.46 (response period II - treatment); *C. stellatus:* end of summer initiation - p=0.64 (response period I - treatment)) (Figures 5.8 and 5.9 and Table 5.6). There were no obvious patterns in the bare rock space (Figures 5.8 and 5.9 and Table 5.6).

Corticated foliose algae appear to have benefitted from the removal of the *F. spiralis* in both experiments and locations through the whole experiment time (Figures 5.6 and 5.7). The cover of corticated foliose algae did not respond to treatments during the period I. In the period II, there was a significant interaction between treatments and locations in the end of summer initiation experiment and among treatments in the end of winter initiation experiment (Table 5.6). Inspection of pair-wise tests revealed inconsistent results between the two starting dates: whereas in the end of summer initiation experiment the abundance of corticated foliose algae was significantly larger in the complete Removal (R), in the end of winter initiation experiment that its abundance was significantly larger in Partial Removal areas (PR) (Figure 5.8). In the period III, there was also a significant interaction between location and treatments detected in the end of winter initiation experiment. Pair-wise comparisons revealed an inconsistent response of corticated foliose algae to treatments in the two locations (Figure 5.9).

Crustose algae responded negatively to the removal of the *F. spiralis*, since a decline in their abundance was observed in both experiments (end of summer and end of winter initiation experiments) and treatments (Removal and Partial Removal), only recovering towards the end of the experiments (Figures 5.6 and 5.7). Crustose algae only responded significantly to treatments during the period II (Table 5.6). Inspection of pair-wise tests revealed that in the end of summer initiation experiment the cover of crustose algae decreased significantly as a response to the removal of *F. spiralis* (both Partial and complete Removal (PR and R)) (Figure 5.8). In the end of winter initiation experiment, this trend was also present (Figure 5.7) although statistically the difference between the Controls (C) and the complete Removals (R) was only marginal (*p*=0.09).

Articulated coralline algae appear to have benefitted from the removal of the *F. spiralis* in the end of summer initiation experiment in Lotacor (Partial Removal) (Figures 5.6 and 5.7). There were significant differences in the cover of articulated coralline algae among treatments during period III in end of summer initiation experiment and during period II in the end of winter initiation experiments as indicated, in both cases, by the significant location x treatment interaction (Table 5.6). Inspection of pair-wise tests, however, revealed spatially inconsistent results in both circumstances (Figures 5.8 and 5.9).

Foliose algae appear to have benefitted from the removal of the *F. spiralis* at the beginning of the experiments (Removal and Partial Removal) (Figures 5.6 and 5.7). The cover of foliose algae varied among treatments only during the period II of the end of summer initiation experiment (Table 5.7). Inspection of pair-wise tests showed the cover of foliose algae increased significantly in response to the removal of *F. spiralis*; this was similar in both partial (PR) and complete Removal (R) disturbed treatments (Figure 5.8).

Filamentous algae appear to have benefitted from the removal of the *F. spiralis* in both experiments and locations (Removal and Partial Removal) (Figures 5.6 and 5.7). The cover of filamentous algae only differed significantly among treatments in last period (period III) and only at the end of summer initiation experiment (significant interaction between treatments and locations, Table 5.7). Inspection of pair-wise tests revealed that its abundance tended to increase in the Partial Removals (PR) although this was not consistent in the two locations (Figure 5.8).

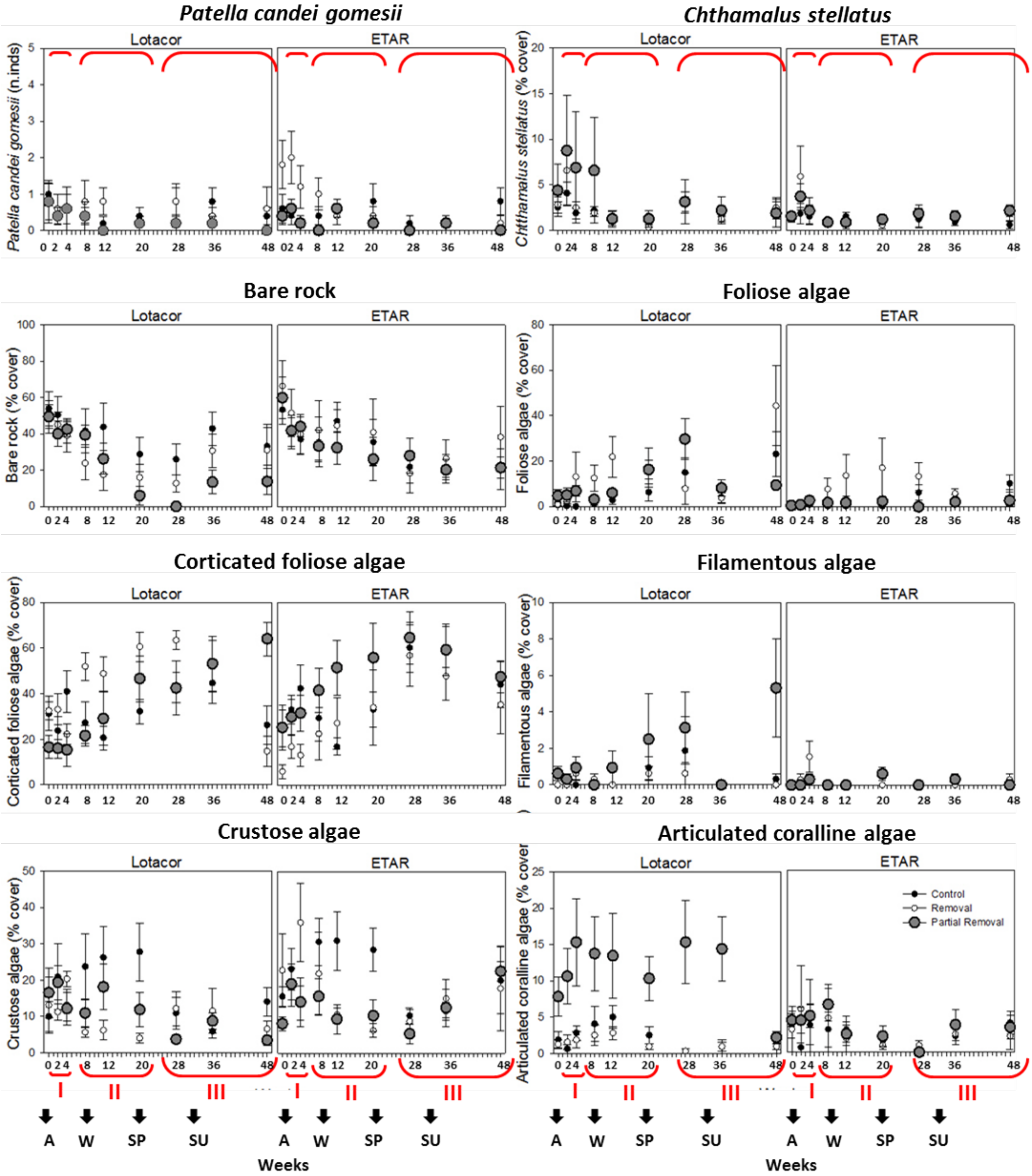


Figure 5.6. Abundance of limpets, barnacles, bare rock and algal functional groups for the 3 treatments along the time of the experiment for the end of summer initiation experiment (Location: Lotacor and ETAR; Treatment: C - Control (black symbols), R - Removal (white symbols) and PR - Partial Removal (grey symbols); Response periods: I - immediate response (weeks: 1, 2 and 4), II - recovery (weeks: 8, 12 and 20) and III - stabilization (weeks: 28, 36 and 48); Seasons: A - Autumn, W - Winter, SP - Spring, and SU - Summer).

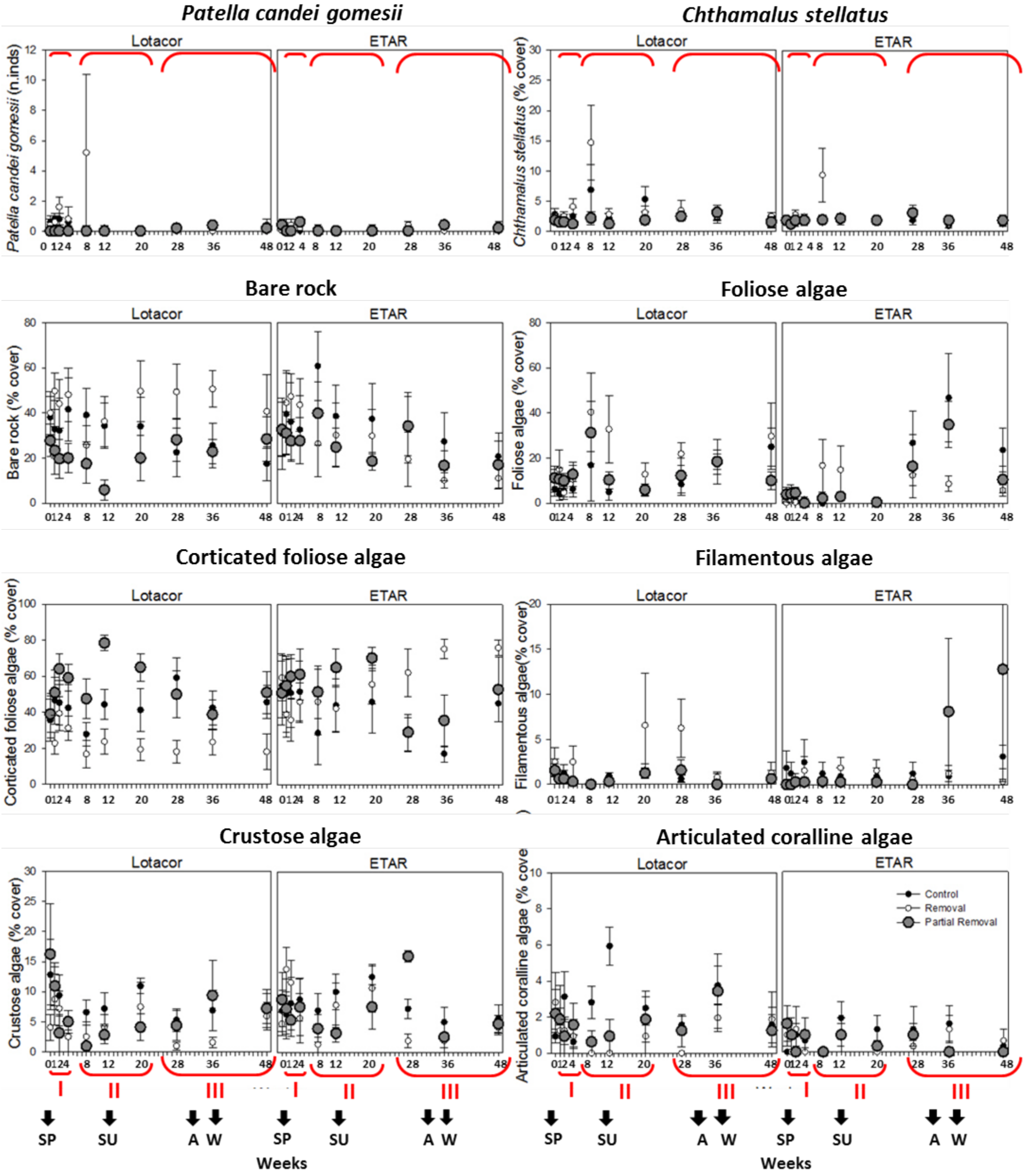
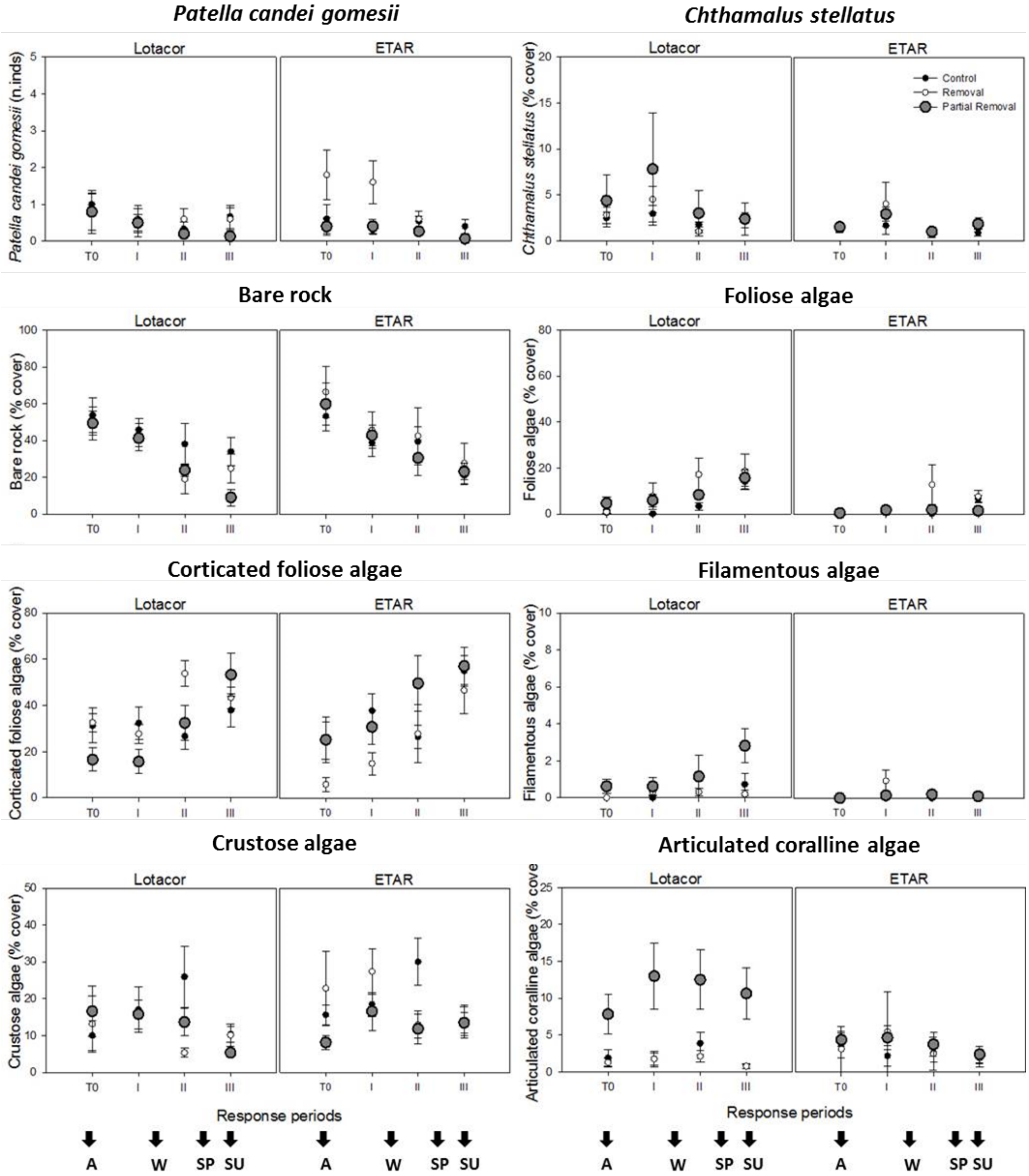


Figure 5.7. Abundance of limpets, barnacles, bare rock and algal functional groups for the 3 treatments along the time of the experiment for the end of winter initiation experiment (Location: Lotacor and ETAR; Treatment: C - Control (black symbols), R - Removal (white symbols) and PR - Partial Removal (grey symbols); Response periods: I - immediate response (weeks: 1, 2 and 4), II - recovery (weeks: 8, 12 and 20) and III - stabilization (weeks: 28, 36 and 48); Seasons: A - Autumn, W - Winter, SP - Spring, and SU - Summer).



Patella candei gomesii

Chthamalus stellatus

Bare rock

Foliose algae

Corticated foliose algae

Filamentous algae

Crustose algae

Articulated coralline algae

Figure 5.8. Abundance of limpets, barnacles, bare rock and algal functional groups for the 3 treatments in the 3 response periods for the end of summer initiation experiment (N.B. non-linear scale) (Location: Lotacor and ETAR; Treatment: C - Control (black symbols), R - Removal (white symbols) and PR - Partial Removal (grey symbols); Response periods: I - immediate response (weeks: 1, 2 and 4), II - recovery (weeks: 8, 12 and 20) and III - stabilization (weeks: 28, 36 and 48); Seasons: A - Autumn, W - Winter, SP - Spring, and SU - Summer).

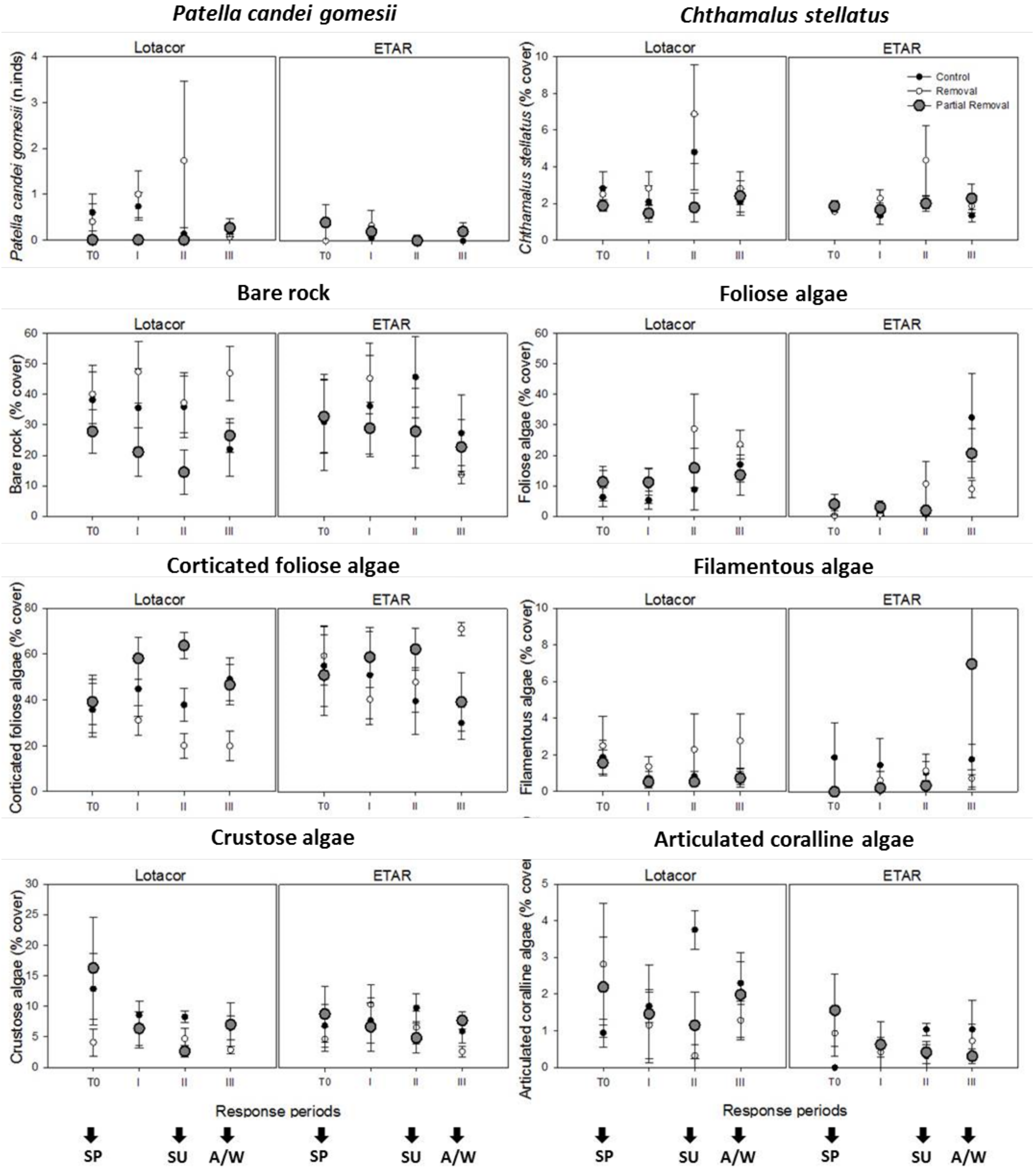


Figure 5.9. Abundance of limpets, barnacles, bare rock and algal functional groups for the 3 treatments in the 3 response periods for the end of winter initiation experiment (N.B. non-linear scale) (Location: Lotacor and ETAR; Treatment: C - Control (black symbols), R - Removal (white symbols) and PR - Partial Removal (grey symbols); Response periods: I - immediate response (weeks: 1, 2 and 4), II - recovery (weeks: 8, 12 and 20) and III - stabilization (weeks: 28, 36 and 48); Seasons: A - Autumn, W - Winter, SP - Spring, and SU - Summer).

Table 5.6. PERMANOVA results on *Patella candei gomesii*, bare rock, corticated foliose algae, crustose algae, articulated coralline algae and *Chthamalus stellatus* for both experiments at the 3 response periods (Response periods: I - immediate response (weeks: 1, 2 and 4), II - recovery (weeks: 8, 12 and 20) and III - stabilization (weeks: 28, 36 and 48)) (bold - statistically significant).

		END SUMMER					END WINTER					END SUMMER					END WINTER					END SUMMER					END WINTER				
		df	SS	MS	F	P	df	SS	MS	F	P	df	SS	MS	F	P	df	SS	MS	F	P	df	SS	MS	F	P	df	SS	MS	F	P
	Source	*Patella candei gomesii*										Bare rock										Corticated foliose algae									
I	Location	1	0.2	0.2	0.57	0.44	1	0.2	0.2	0.83	0.36	1	1.6	1.6	0.01	0.93	1	37.0	37.0	0.06	0.80	1	52.9	52.9	0.28	0.61	1	214.5	214.5	0.30	0.57
	Treatment	2	0.9	0.4	1.38	0.29	2	0.3	0.1	0.18	0.84	2	19.1	9.5	0.04	0.96	2	2269.3	1134.6	1.79	0.19	2	1112.0	556.0	1.12	0.48	2	2570.9	1285.4	1.81	0.16
	LocationXtreatment						2	1.4	0.7	3.30	0.07											2	996.6	498.3	2.61	0.09					
	Res						24	5.1	0.2													24	4581.1	190.9							
	Pooled	26	8.1	0.3								26	6211.8	238.9			26	16458.0	633.0								26	18468.0	710.3		
	Total	29	9.1				29	6.9				29	6232.5				29	18764.0				29	6742.5				29	21254.0			
II	Location	1	0.1	0.1	0.34	0.58	1	0.2	0.2	0.71	0.52	1	846.7	846.7	1.75	0.21	1	190.1	190.1	0.35	0.55	1	63.8	63.8	0.17	0.69	1	667.8	667.8	1.33	0.27
	Treatment	2	0.7	0.3	1.91	0.18	2	0.6	0.3	0.98	0.46	2	688.4	344.2	0.71	0.49	2	1946.5	973.2	1.80	0.21	2	1377.8	688.9	0.59	0.63	2	4839.2	2419.6	4.83	**0.02**
	LocationXtreatment																					2	2352.2	1176.1	3.16	**0.047**					
	Res																					24	8922.4	371.8							
	Pooled	26	4.6	0.2			26	8.3	0.3			26	12605.0	484.8			26	14047.0	540.3								26	13031.0	501.2		
	Total	29	5.3				29	9.2				29	14140.0				29	16183.0				29	12716.0				29	18538.0			
III	Location	1	0.5	0.5	2.68	0.11	1	0.0	0.0	0.02	0.88	1	17.5	17.5	0.07	0.79	1	813.8	813.8	2.27	0.15	1	495.1	495.1	1.69	0.23	1	512.2	512.2	1.45	0.25
	Treatment	2	1.0	0.5	2.40	0.10	2	0.1	0.1	0.84	0.45	2	779.6	389.8	0.85	0.54	2	214.9	107.4	0.11	0.91	2	609.7	304.8	1.04	0.37	2	180.1	90.1	0.03	0.97
	LocationXtreatment											2	918.2	459.1	1.80	0.19	2	2038.8	1019.4	2.84	0.09						2	7099.4	3549.7	10.03	**0.001**
	Res											24	6121.4	255.1			24	8617.6	359.1								24	8497.2	354.1		
	Pooled	26	5.2	0.2			27	1.8	0.1													26	7622.3	293.2							
	Total	29	6.7				30	2.0				29	7836.8				29	11685.0				29	8727.1				29	16289.0			
	Source	Crustose algae										Articulated coralline algae										*Chthamalus stellatus*									
I	Location	1	157.6	157.6	1.49	0.23	1	11.1	11.1	0.23	0.61	1	13.8	13.8	0.29	0.58	1	6.1	6.1	2.32	0.17	1	35.9	35.9	0.96	0.41	1	0.9	0.9	0.47	0.53
	Treatment	2	153.9	76.9	0.73	0.49	2	18.6	9.3	0.19	0.81	2	257.9	128.9	1.33	0.42	2	0.6	0.3	0.11	0.917	2	47.6	23.8	0.64	0.64	2	5.7	2.8	1.48	0.26
	LocationXtreatment											2	193.4	96.7	2.06	0.16															
	Res											24	1125.2	46.9																	
	Pooled	26	2749.3	105.7			26	1252.1	48.2								26	68.6	2.6			26	968.4	37.2			26	49.8	1.9		
	Total	29	3060.7				29	1281.7				29	1590.3				29	75.3				29	1051.9				29	56.4			
II	Location	1	1.6	1.6	0.87	0.37	1	26.9	26.9	1.54	0.23	1	5.1	5.1	3.26	0.09	1	9.8	9.8	8.31	**0.009**	1	0.9	0.9	1.94	0.20	1	0.0	0.0	0.04	0.85
	Treatment	2	27.3	13.7	7.65	**0.002**	2	143.4	71.7	4.10	**0.027**	2	8.2	4.1	2.63	0.12	2	23.9	11.9	2.43	0.28	2	0.5	0.2	0.51	0.63	2	0.2	0.1	0.47	0.66
	LocationXtreatment																2	9.8	4.9	4.15	**0.028**										
	Res																24	28.4	1.2												
	Pooled	26	46.5	1.8			26	454.8	17.5			26	40.6	1.6								26	12.0	0.5			26	6.9	0.3		
	Total	29	75.4				29	625.1				29	53.9				29	72.0				29	13.4				29	7.1			
III	Location	1	200.8	200.8	4.37	**0.047**	1	0.1	0.1	0.07	0.79	1	0.5	0.5	0.63	0.46	1	10.0	10.0	4.42	**0.041**	1	4.4	4.4	1.09	0.32	1	2.6	2.6	1.09	0.31
	Treatment	2	48.1	24.0	0.52	0.60	2	5.3	2.6	2.71	0.08	2	11.2	5.6	1.47	0.44	2	2.4	1.2	0.54	0.60	2	1.4	0.7	0.18	0.85	2	2.6	1.3	0.54	0.57
	LocationXtreatment											2	7.6	3.8	5.19	**0.015**															
	Res											24	17.6	0.7																	
	Pooled	26	1194.7	45.9			26	25.4	1.0								26	58.8	2.3			26	104.5	4.0			26	62.2	2.4		
	Total	29	1443.5				29	30.8				29	37.0				29	71.3				29	110.3				29	67.5			

Table 5.7. PERMANOVA results on foliose and filamentous algae for both experiments at the 3 response periods (Response periods: I - immediate response (weeks: 1, 2 and 4), II - recovery (weeks: 8, 12 and 20) and III - stabilization (weeks: 28, 36 and 48)) (bold - statistically significant).

		END SUMMER					END WINTER					END SUMMER					END WINTER				
		df	SS	MS	F	P	df	SS	MS	F	P	df	SS	MS	F	P	df	SS	MS	F	P
	Source	**Foliose algae**										**Filamentous algae**									
I	**Location**	1	80.8	80.8	2.37	0.14	1	372.6	372.6	7.08	**0.008**	1	0.1	0.1	0.15	0.72	1	0.1	0.1	0.03	0.88
	Treatment	2	98.2	49.1	1.44	0.26	2	68.5	34.2	0.65	0.51	2	1.5	0.8	1.40	0.26	2	3.1	1.6	0.64	0.60
	LocationXtreatment																				
	Res																				
	Pooled	26	884.4	34.0			26	1368.6	52.6			26	14.0	0.5			26	62.8	2.4		
	Total	29	1063.3				29	1809.7				29	15.5				29	66.0			
II	**Location**	1	2.5	2.5	7.85	**0.009**	1	1316.0	1316.0	6.21	**0.014**	1	2.0	2.0	1.83	0.15	1	1.0	1.0	0.26	0.68
	Treatment	2	5.8	2.9	8.96	**0.002**	2	1189.0	594.5	2.81	0.08	2	1.8	0.9	0.81	0.64	2	8.4	4.2	1.04	0.38
	LocationXtreatment																				
	Res																				
	Pooled	26	8.4	0.3			26	5507.0	211.8			26	29.0	1.1			26	105.7	4.1		
	Total	29	16.7				29	8012.0				29	32.8				29	115.2			
III	**Location**	1	863.4	863.4	11.93	**0.002**	1	56.1	56.1	0.18	0.66	1	3.0	3.0	9.62	**0.009**	1	23.1	23.1	0.55	0.70
	Treatment	2	104.7	52.3	0.72	0.49	2	431.6	215.8	0.36	0.73	2	2.4	1.2	1.16	0.48	2	38.3	19.1	0.45	0.91
	LocationXtreatment						2	1201.3	600.7	1.92	0.16	2	2.1	1.0	3.36	**0.046**					
	Res						24	7510.9	313.0			24	7.4	0.3							
	Pooled	26	1882.0	72.4													26	1094.2	42.1		
	Total	29	2850.0				29	9199.8				29	14.8				29	1155.6			

5.4. DISCUSSION

My study planned to assess the community-level consequences to the loss of the northern species *Fucus spiralis* on the Azorean rocky shores, through a manipulative experiment to simulate the loss of macroalgae as a result of increased storminess, that damage or rips off the entire plant (extreme wave action), as well as the result of increased heat stress or grazing, leading to the thinning of macroalgae. In particular I wanted to explore whether expected climate change would constrict the distribution of intertidal algal species at their upper limits with extreme temperature (desiccation), directly affecting the upper limits of these species, and indirectly through driving more grazing pressure at the lower limits. Disturbance would be expected to affect *F. spiralis* throughout its vertical range on the shore.

5.4.1. Community level effects of loss of fucoid canopy

Overall, my results showed no general response of the assemblage to the experimental loss of *F. spiralis* during the initial period after the disturbance and this was consistent in both experiments (end of summer and end of winter initiation). As time elapsed, however, assemblages as a whole responded to the loss of the canopy in the end of winter initiation experiment (but not in the end of summer initiation experiment), suggesting that the assemblage responses between the end of winter initiation experiment (increase temperature stress) and the end of summer initiation experiment (extreme wave action) were not similar and were mediated by season. According to Moore *et al.* (2007a), in the summer, underneath patches of *Fucus* sp. the temperature can be up to 5°C lower than in open rock and the relative humidity can be up to 20% higher than in open rock. In winter, differences in environmental conditions in areas underneath patches of *Fucus* sp. and open rock may not be as relevant.

Even so, the disturbed assemblages revealed signs of recovery from the initial impact after 12 months (48 weeks), this result being similar to that obtained by Crowe *et al.* (2013) in which after 18 months the communities had recovered from the loss of a key canopy alga. This is a rapid period of recovery that contrasts with the work of Jenkins *et al.* (2004), who found that disturbed patches of the long-lived *Ascophyllum nodosum* ((Linnaeus) Le Jolis 1863) on sheltered shores had not fully recovered, even 12 years after the initial removal of *A. nodosum*. This indicates that identity and environmental context of the species lost matters for the recovery of disturbed assemblages. *Fucus spiralis* in Azores seems well adapted to disturbance, as became evident in the Control plots. In both experiments (end of summer and end of winter initiation) *Fucus spiralis* recovered towards the end (one year). In end of summer initiation experiment, both locations showed an accentuated decline in the abundance of *F. spiralis* in Control treatment between initial response (period I) and subsequent recovery (period II). This might have been related to harsher sea conditions, during the winter period which might have ripped-off plants from the experimental patches. This contrasts with Jenkins *et al.* (1999a, 2004) and Benedetti-Cecchi *et al.* (2001b), where lost canopies led to more grazers and algal turfs.

Responses of understorey species to the removal of the canopy were generally similar in both end of summer and end of winter initiations; towards the end of the experiments the effect of the Removal and Partial Removal of the *F. spiralis* tends to dissipate. Moreover, the majority of the functional groups showed spatially inconsistent responses to the removal of the canopy. One exception was the abundance of ephemerals. Their colonization occurred in the earlier stages of the experiment, mostly in disturbed patches, but this was only evident in the end of summer initiation experiment. According to Watt and Scrosati (2013), removal of canopies can lead to a higher abundance of green filamentous algae, which could be related with the release of competition. Hawkins and Harkin (1985) also obtained a bloom of ephemeral algae followed by a smothering of limpets in the Isle of Man after they removed *F. serratus* low at the shore, since the limpets grazing capability was not enough to control the rapid increase of algae. However, that was not the case in the present study, perhaps because the abundance of limpets did not change. Another exception was the crustose algae. Canopy removal had a direct negative effect on the abundance of crustose algae and this effect was clearer in end of winter initiation experiment, which could be related to the increase of thermal stress (summer season). Such decline in crustose algae in response to the loss of canopy species has also been seen in the work developed by Kennelly (1987), and is probably related to increasing levels of thermal stress (desiccation), since in the absence of the amelioration effect of the canopy algae the crustose algae tend to bleach and subsequently die.

According to Jenkins *et al.* (2005) an indirect negative effect of the canopy algae is the sweeping of their fronds, which affects negatively the number of settling larvae of barnacles (see also Hawkins, 1981; Hawkins and Hartnoll, 1983b, 1985), promoting the establishment of algal turfs. It was expected, in this study that the abundance of *Chthamalus stellatus* would increase as a response to the removal of *F. spiralis,* benefiting from reduced sweeping. Although, *Fucus spiralis* has been shown to enhance survival of the northern species, *Semibalanus balanoides* (Linnaeus 1767) high on the shore (e.g. Hawkins, 1983; Hawkins and Hartnoll, 1983b; Jenkins et al., 1999b), Dayton (1971) has shown that the decline of fucoid abundance, due to exposure, led to an increase of abundance of filter feeders. In the present study the expected increase of *C. stellatus* abundance in patches where *F. spiralis* was experimentally removed was not observed.

5.4.2. Distribution and abundance of *Fucus spiralis*

It has already been shown that emersion stress (Schonbeck and Norton, 1978; Hawkins and Hartnoll, 1985) and wave induced forces (Blanchette, 1997), combined with biotic factors, such as grazing (Hawkins, 1981) and competition (Jonsson *et al.*, 2006), have a major influence over the abundance, distribution and fitness of canopy algae such as *F. spiralis.* Analysis of *F. spiralis* lengths and grazing marks emphasize the role of herbivory at the lower levels on the shore. *Fucus spiralis* plants were always taller at the upper level whilst grazing marks were more evident in the lower level, especially during the summer months. The patterns of grazing marks and plant size suggest that *F. spiralis* is especially susceptible to fish grazing (e.g. by *Sarpa salpa*) and that this was more intense during the summer, when calmer sea conditions allow plenty of access of herbivorous fish to higher shores where *F. spiralis* is present. The outcomes of plant-herbivore interactions may change due to global warming, with consequences for community structure and ecosystem functioning (Schiel *et al.*, 2004). According to Petit and Prudent (2008) the range of tropical fishes species has shifted northwards, with evidence of their occurrence in the Azores (e.g. Santos *et al.*, 1995b; Silva *et al.*, 1998; Machado and Barreiros, 2006). Several studies have already provided evidence of the effects of herbivorous fish over the loss of habitat-forming species (Sala *et al.*, 2011; Bianchi *et al.*, 2014; Vergés *et al.*, 2014a, b).

5.4.3. Concluding remarks

Overall, simulation of the predicted disappearance of the *Fucus spiralis* from the Azorean rocky shores, due to the climate changes (increase storminess and desiccation), does not appear to have a major impact on the understorey assemblage, suggesting that these canopies in the Azores do not have a strong ecosystem engineering effect. This could be related with the fact that *F. spiralis* in the Azores is rather small and forms scattered patches in contrast with what is found elsewhere (e.g. British coastlines), so their canopy effect is minimal. In the Azores, *F. spiralis* appears to be mainly vulnerable to predicted increases of wave action (higher disturbance throughout its vertical distribution) and grazing (at the lower limits of distribution). *Fucus spiralis* appears to recover rapidly, being very resilient and well adapted to the high energetic Azorean system. Occasionally bleaching events were observed at the upper limits of distribution of *F. spiralis*, due to the extreme heat during the emersion periods in the summer, but subsequently recovery happened. Thus heat stress seems to be counteracted by wave action (wetting). Increasing grazing pressure*,* due to the predicted shifts in the distribution of tropical fish species northwards including more herbivores, may have an impact on the population of this canopy in the Azores, especially over the summer on plants lower on the shore. The population reproductive output of this canopy alga could be reduced, since the observed herbivores (*Sarpa salpa*, M. Vale *personal observation*) fed mostly on the reproductive conceptacles of plants. The extended period of fertility of *F. spiralis,* however, will moderate the effects of grazing on the reproduction of these plants.

6. GENERAL DISCUSSION

In this general discussion, I first highlight the limitations of this study, followed by a synthesis of the main results achieved. I then discuss the main findings in the light of current knowledge of recent climate changes (temperature and storminess) in the Azores. I also consider and discuss the role of the interaction of global changes with local impacts, particularly the overexploitation of limpets in the Azores. I conclude with some suggestions for future research in the Azores, including advocating long-term studies.

6.1. LIMITATIONS OF THE STUDY

There are several limitations in the work for this thesis. While this study progressed, several unanticipated issues have emerged. In the analysis of the environmental changes (Chapter 2), only the monthly means of the surface air temperature and sea surface temperature were available. This limited understanding of how these environmental variables have influenced the biological responses shown in subsequent chapters. Changes in the return time of extremes events such as hot weather or major storms are essential for interpreting climate change (IPCC, 2001, 2007, 2013; Lima and Wethey, 2012). The time window of data available for the wave action variables (1985-2014) was too short to be able to detect long-term trends, limiting what conclusions could be drawn. The use of the appropriate metrics of an environmental variable and the identification of the appropriate environmental pressure or stressor is essential to provide knowledge to detect, interpret and predict the impacts that these variables will have on ecosystems (Seabra *et al.*, 2015). Also, it became clear that in this study we were comparing the end of a cold period (1980s) with a down turn of a warmer period (2010s); this complicates inference. There are also fundamental problems in snap shot studies of a “then” and “now” nature. Unfortunately these are often all that is available to make comparisons over time (e.g. Sagarin *et al.*, 1999; Zacherl *et al.*, 2003). This is especially the case where there is either cyclicity or considerable fluctuations in the data. This was partially overcome by having data for three years in the 2010s (Chapters 3 and 4), giving some insights into inter-annual variability.

The descriptive studies of patterns (Chapters 3 and 4), focussed on finding evidence of long-term and broad-scale changes at several levels of organization. There were difficulties in the comparability of data for work in chapters 3 and 4. This also affected the analyses that could be performed. In chapter 3, the historical limpet data was scattered in time and space due to past funding and logistical constraints, which limited temporal and spatial coverage. During the resurvey we were not able to obtain enough data to allow a complete temporal and spatial analysis of both species of limpets for Faial Island, due to logistical constraints. Harsh sea conditions, especially in the winter months, also prevented the collection of some samples occasionally. The main constraint in chapter 4 was the comparison between the two sets of data (historic versus recent); since only a single historic survey was available from both studied locations, limiting the selection of statistical analyses to use. Also details of the historic sampling methodologies used in Monte da Guia were not available, although S. J. Hawkins could largely remember what had been done. The raw data had also been lost from the Caloura survey and was extracted from graphs. In the experimental study of processes (Chapter 5), the only constraint was the harsh sea conditions that prevented sampling during the first week of the experiment initiated at the end of the summer. A burst sewage pipe also had a localised impact.

Despite these problems some differences were still detectable between the 1980s and 2010s and spatially across the archipelago.

6.2. SUMMARY OF MAIN FINDINGS

The main focus of my thesis was to explore the responses of intertidal ecosystems to climate change and other impacts, using the Azorean rocky shores as a test system to describe patterns and explore processes. When investigating temporal and spatial environmental patterns in the Azorean archipelago (Chapter 2), I showed a general trend in increased temperature (surface air temperature and sea surface temperature). There was also some evidence of greater storminess including extreme events, mainly in the Western group of the Archipelago. These temporal changes were not monotonic with considerable fluctuations with both cold (1970s and 1980s) and warmer (1950s and 2000s) periods. In recent years, temperatures peaked in the 2000s and have dropped a little since. Across the Azorean archipelago temperatures increased from the West to the East; conversely wave action increased from the East to the West.

At the individual level (Chapter 3), I demonstrated some evidence of temporal and spatial changes in the phenology of limpets (*P. aspera* and *P. candei gomesii*) in Azores.

These changes were probably associated with differences in climate both with time and spatially across the archipelago.

Temporal analyses of the reproductive cycle of *P. aspera* in S. Miguel have shown a summer resting period that apparently has become less sharp and longer, with earlier onset of the autumn-winter spawning. A less clear peak of spawning was also apparent in recent years. These long-term changes in the phenology of this species are probably related to recent climate change. Specifically, with the increase of surface air temperature, which could possibly increase stress in the resting period during summer months leading to a longer and delayed season (Moore *et al.*, 2011). The occurrence of more frequent extreme events (wave action) could lead to earlier spawning as this is known to be prompted by storm events (Orton *et al.*, 1956; Bowman and Lewis, 1977, 1986; Moore *et al.*, 2011). Synchronous peaks in release of male and female gametes was shown in *P. aspera* in the past but were less apparent more recently. In recent years incomplete development in this species was observed with the proportion of individuals reaching mature gonad stages being less than 25%. This result could be related to increased stress. It could also be related with smaller recently mature individuals not capable of reaching full ripeness. Low population densities in the Azores due to the overexploitation of limpets could minimize spawning cues. Analysis of shell length for *P. aspera* showed a significant decrease in size in subtidal populations collected between 1980s-2010s (S. Miguel). There is also the possibility of some kind of signalling occurring between externally fertilizing animals prompting both maturity and ripening in addition to the well-known phenomena of gametes release. This is clearly speculative but would re-inforce Allee effect at low density. These decreases were probably related with the overexploitation of the limpets in the Azores.

For *Patella candei gomesii* from Faial, a low number of recent samples were acquired due to logistical constraints. So care is needed when analysing the long-term changes found in the reproductive cycle of this species. Even so, temporal analysis showed significant differences in the breeding cycle of this species; with the summer resting period appearing to have extended recently as also found in *P. aspera*. This could be related to greater summer stress in the higher shore *P. candei gomesii.*

Analysis of breeding cycles of *P. aspera* and *P. candei gomesii* across the Azorean archipelago revealed the same general pattern, with both the resting period and spawning occurring earlier in the Eastern than in the Western group in both species. These patterns could result from a greater stress due to higher summer temperatures in the East. This stress is less likely to be alleviated by greater wave action in the East, leading to an earlier and longer resting phase. In the East, warmer sea temperatures, might allow more rapid ripening and earlier development to spawning after the resting phase ceases. Both species showed a low proportion of individuals reaching the later spawning stages across the Azorean archipelago in recent years. These patterns confirm that the temporal differences between *P. aspera* in S. Miguel and between *P. candei gomesii* in Faial may be more general across the archipelago.

At the community level (Chapter 4), repeat surveys in the 1980s and 2010s in two Azorean Marine Protected Areas (MPAs) showed long-term differences in the abundance and distribution of the intertidal species. These changes could be attributable to recent climate change in conjunction with the overexploitation of limpets in the Azores. At both sites enforcement of protection is limited, with the exception of the inner Caldeira at Monte da Guia. Results in both islands, suggest a functional change in the community structure over time. At low shore levels a considerable increase in the abundance of algal turf occurred; while on the mid and upper shore levels the abundance of barnacles and grazing gastropods decreased as they were smothered by algal turfs, these results being in accordance with the work of Martins *et al.* (2008a, 2010). At mid-shore level these changes are especially evident, with consumers being replaced by primary producers.

Also, at mid and high shore levels, I showed a pattern of some taxa increasing in abundance on transects with greater wave exposure. In terms of the vertical distribution of the taxa, my results suggest that the species behaved as a block and moved upwards on the whole shore, their upper limits of vertical distribution extending whilst retreating upwards from lower shore levels. All these changes are probably an outcome of recent climate change plus overexploitation of limpets in the Azores. Greater storminess leads to more wave spray on the upper shore allowing organisms to spread upwards; whilst the collection of limpets results in the settlement of algae species upwards (Boaventura *et al.*, 2002a; Martins *et al.*, 2010). Both MPAs still suffer from exploitation of limpets; except the strictly regulated inner Caldeira of Monte da Guia, where zonation patterns typical of near-pristine conditions were shown.

Also at the community level (Chapter 5), I assessed the potential consequences of the loss of a northern cold-water canopy forming species (ecosystem engineer *sensu* Jones *et al.*, 1994) - *Fucus spiralis* from the Azorean ecosystem. This is the only mid shore canopy forming species present in the Azores. Through manipulative experimental work that simulated conditions of canopy removal and thinning due to increased temperature (heat stress) and greater disturbance due to increased storminess, I showed that *F. spiralis* recovered rapidly (12 months). The loss of this ecosystem engineer did not appear to have a major impact on the understorey assemblages.

6.3. CLIMATE CHANGE - TEMPERATURE VERSUS STORMINESS

Anthropogenic driven global warming has already affected the distribution and abundance of many species in recent years (Parmesan and Yohe, 2003; Root *et al.*, 2003; Helmuth *et al.*, 2006b; Fischlin *et al.*, 2007; Greene *et al.*, 2008; Hawkins *et al.*, 2008, 2009). Predictions have been made of even larger effects in the future (Thomas *et al.*, 2004; Pearce-Higgins *et al.*, 2010), suggesting that temperatures will rise and there will be more frequent severe storms at sea (Trenberth *et al.*, 2007). These changes will have a major impact on marine biodiversity and ecosystems (Gilman *et al.*, 2006; Wernberg *et al.*, 2012). According to Hulme *et al.* (2002) for the North-East Atlantic, it is predicted that summer season will became hotter and wetter and winters stormier, which will have a major impact specifically on intertidal species. Temporal patterns in storm frequency will also be altered with extreme events returning more frequently (Benedetti-Cecchi *et al.*, 2006, 2015).

For several years, the main focus of investigations has been on the effects of temperature on the performance and thermal tolerance limits of an organism and hence the geographic distributions patterns of species (Orton, 1929; Hutchins, 1947; Somero, 2002, 2005; Helmuth *et al.*, 2006a). As temperature increases species abundance will change and distributions will shift in accordance to species' thermal tolerance and adaptability (Harley *et al.*, 2006). These changes include shifts in the range and spatial distribution of species (Beaugrand *et al.*, 2002b; Helmuth *et al.*, 2006b; Hawkins *et al.*, 2008, 2009; Burrows *et al.*, 2011, 2014; Poloczanska *et al.*, 2013; Firth *et al.*, 2015; Hiddink *et al.*, 2015) leading to changes in diversity which are expected to accelerate in the future (Helmuth *et al.*, 2006b).

Wave action (exposure) influences the abundance and distribution of intertidal organisms and can have a positive (e.g. alleviate thermal stress through splash) or negative (e.g. disturbance by dislodgment or damage of organisms) effect in the rocky shore species.

My work found evidence of direct and indirect effects of climate change on the abundance and distribution of rocky intertidal species in the Azores (Chapters 4 and 5). On rocky shores, it is well established that the upper limits of zonation of several intertidal organisms are set by thermal and desiccation stress, with these organisms living at or near their thermal tolerance limits (Southward, 1958; Dayton, 1971; Connell, 1972; Schonbeck and Norton, 1978; Hawkins and Hartnoll, 1985; Williams, 1994; Raffaelli and Hawkins, 1996; Somero, 2002; Davenport and Davenport, 2005), especially high shore species (Hawkins and Hartnoll, 1985). With the predicted increase in temperature it would be expected that a downward shift in the upper limit of distribution of the intertidal species would occur (Harley and Helmuth, 2003; Helmuth *et al.*, 2006b). In this thesis, however, my results showed an upward shift of the vertical distribution range of the species over the last decades. Species appear to have moved upwards on the shore as a block, these upward shifts being most evident on the exposed shores. An increase in abundance was mainly observed at more exposed locations (Chapter 4). These changes in abundance and distribution could be explained by the increase in wave action, and subsequently an increase of wave spray higher on the shore. Wave wetting and spray can significantly decrease desiccation allowing species on wave-beaten shores to extend higher on the shore (Lewis, 1964; Hawkins and Jones, 1992; Helmuth *et al.*, 2006a). *Fucus spiralis*, at their higher limits of distribution, showed occasional bleaching events as a response to heat stress (see also Schonbeck and Norton, 1978; Hawkins and Hartnoll, 1985); although the algae appeared to recover (Chapter 5).

An indirect response to the increase of temperature (SST) in the Azores was detected at low levels on the shore, through increasing grazing pressure of the fish *Sarpa salpa* on *Fucus spiralis* (Chapter 5). This result supports the predictions and observations that warm temperate, sub-tropical and tropical organisms including more herbivorous fish species are already and will continue shifting northwards (e.g. Santos *et al.*, 1995b; Parker and Dixon, 1998; Silva *et al.*, 1998; Perry *et al.*, 2005; Machado and Barreiros, 2006; Fodrie *et al.*, 2010; Sala *et al.*, 2011; Nakamura *et al.*, 2013) in response to recent climate change. There was some evidence of spatial constriction of *F. spiralis* by physical factors such as heat stress at the upper limit (see also Schonbeck and Norton, 1978; Hawkins and Hartnoll, 1985), as well as possible increased herbivory from fish, primarily towards the lower limit. Disturbance due to wave action is likely to occur throughout its zone (see also Blanchette, 1997)(Figure 6.1).

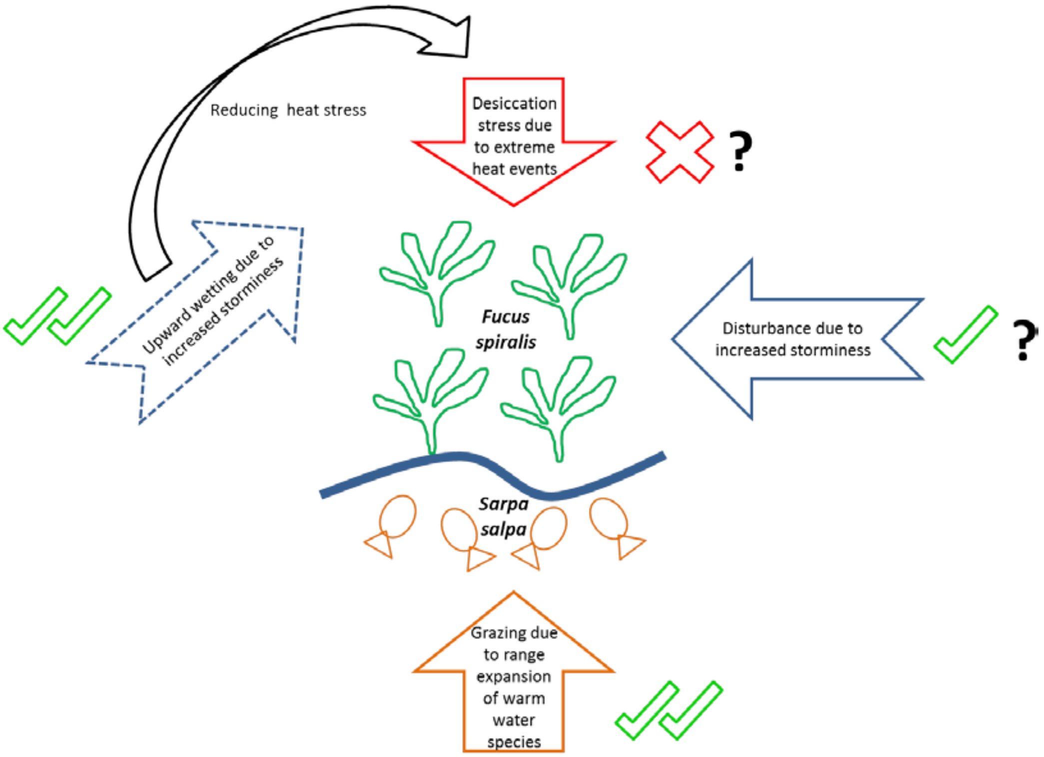


Figure 6.1. A schematic diagram of the influence of various climate change related factors on *Fucus spiralis* in the Azores.

Differences in temperature and wave action explained the majority of the spatial and temporal patterns that were seen throughout this thesis, suggesting that climate change has had some influence on Azorean rocky ecosystem. Even so, my results suggest that, generally in the Azorean ecosystem, the increasing temperature (desiccation, heat stress) was overridden by increasing wave action (storminess). This is ultimately determined by the small tidal range of the Azores and its presence in the middle of the Atlantic Ocean with a regime of large wave swell and storms (Martins, 2009).

6.4. INTERACTION OF GLOBAL CHANGE WITH LOCAL EXPLOITATION OF KEY SPECIES

Coastal ecosystems are anthropogenically impacted at the global (e.g. recent climate change), regional (e.g. eutrophication), and local (e.g. overexploitation of living resources and habitat loss) scales (Firth and Hawkins, 2011; Hawkins *et al.*, 2013a,b; Mieszkowska *et al.*, 2014b; Smale and Vance, 2015). According to several studies (e.g. Walther *et al.*, 2002; Hawkins *et al.*, 2009; Garcia *et al.*, 2014), the greatest threat to biodiversity and ecosystems arises from the interactions of these impacts. The overexploitation of limpets (*Patella aspera* and *Patella candei gomesii*) in the Azores has led to a decline in the populations of these species in much of the archipelago (Martins *et al.*, 1987a,b; Santos *et al.*, 1990, 1995a; Hawkins *et al.*, 2000; Martins *et al.*, 2010). In the Azorean archipelago, evidence that the overexploitation of intertidal living resources, specifically of limpets that are a keystone intertidal grazer (Jenkins *et al.*, 2005; Coleman *et al.*, 2006), has a major effect at the community structure have been provided by several studies (Martins *et al.*, 1987a,b; Hawkins *et al.*, 2000; Martins *et al.*, 2008a, 2010).

At the organism-level, the direct effects of climate change will have impacts on the performance of individuals at several stages of life history such as reproductive phenology (Moore *et al.*, 2011), through changes in physiology (Dahlhoff *et al.*, 2002), and behaviour (Sanford, 2002). Also, evidence of continued exploitation of these species has been found in this thesis (Chapter 3). Long-term studies on Azorean limpet species, suggest that the reproductive cycle of these species has changed as a direct response to the increased global warming and earlier seasonal onset of storminess (Chapter 3). Both temporal and spatial analysis of the reproductive cycles of two limpet species have shown also that a lower proportion of the individuals reach ripe gonad stages reducing likely spawning success. According to Moore *et al.* (2011) this could be a direct result of the increased warming. More speculatively it could also be a result of a lack of synchrony at lower populations' densities (Allee effect) (see above pp. 187). A significant decrease in the size of both limpet species was observed (Chapter 3). This could be a direct result of the overexploitation of this living resource, since overexploited populations tend to show an overall decrease in their average size (Siegfried *et al.*, 1994; Hawkins *et al.*, 2000; Moreno, 2001; Fenberg and Roy, 2008, 2012; Fenberg *et al.*, 2010; Jimenez *et al.*, 2011). These phenological changes can have a major impact in the population of these species in the Azores, since they may affect the reproductive output and subsequently the recruitment success of these endemic species in the Azorean ecosystem (Chapter 3). Specially in the case of *Patella aspera*, a protandrous hermaphrodite species (Martins *et al.*, 1987b), size-selective harvesting has a major impact on the sex-ratio of this species, leading to a smaller reproductive output and subsequently greater risk of recruitment failure (Ribeiro *et al.*, 2009; Borges *et al.*, 2015).

According to Hawkins *et al.* (2000) these endemic species (Côrte-Real *et al.*, 1996; Weber and Hawkins, 2002, 2005; Sá-Pinto *et al.*, 2005, 2008) are extremely vulnerable and at risk of complete extinction. There is not a recruitment reservoir from outside the Azores as indicated by genetic work (Côrte-Real *et al.*, 1996; Sá-Pinto *et al.*, 2005). In the Azores, the overexploitation of limpets is undoubtedly the major pressure on these endemic populations. I have shown, however, that recent climate change has also an influence on the reproductive success of these species making them even more vulnerable.

Heip *et al.* (2009) stated that changes in abundance of key species will affect ecosystem functioning more than changes in species diversity. The role of limpet grazing in the intertidal shores is of extreme importance, since they maintain the eulittoral zone free of algae preventing their upward spread until the algae reach their desiccation upper limit (Hawkins and Hartnoll, 1983b; Hawkins *et al.*, 1990a; Boaventura *et al.*, 2002a). Removal of top-down control by herbivores can lead to an increase of algal abundance, resulting in disequilibrium of the ecosystem due to enhancement of primary production (Lubchenco, 1978). Throughout this study, evidence of changes in Azorean rocky shore community structure, due to the exploitation of limpets (key intertidal grazing species), were found confirming work by Martins *et al.* (2010). Especially on the mid shore, a functional change in the community structure has occurred as a direct consequence of limpet exploitation, which subsequently has had effects in the remaining levels on the shore (Chapter 4) (Figure 6.2).

At the higher level on the shore, despite the increased heat stress, an upward shift of the vertical distribution range of the high shore intertidal species (e.g. *T. striatus*) has occurred. This upward shift was more evident in the exposed locations, probably being related with the increase of wetness at higher shore levels overriding the extreme temperatures.

At mid-shore levels, the consumers (limpets and barnacles) have been replaced by primary producers. In the absence of limpet grazers (exploited) and increased wetting by waves have allowed the upward spread of the algal turf towards their thermal tolerance limit (Chapter 4) (Figure 6.2). An interaction between algae, limpets and barnacles (key taxa), all competing for space, occurs in the transition between low and mid shore levels (Hawkins and Hartnoll, 1983b; 1985; Boaventura *et al.*, 2002a, c). Yet, in the Azores that dynamic equilibrium has been disrupted, due to the human consumption of limpets leading to a major increase in the abundance of algal turf. As consequence, there has been a reduction in free space available for recruitment of limpets and settlement of barnacle larvae (Martins *et al.*, 2008a, 2010). In the Azores, the only known place that shows an intertidal ecosystem approaching near pristine conditions is inside Monte da Guia (Faial Island). This no-take and no-entry marine protected area is the only place in the Azores where the management measures are effectively enforced. This location is the only example of a healthy system indicative of how shores were before human exploitation initiated (see also work in Chile - Moreno *et al.*, 1984; Oliva and Castilla, 1986; Godoy and Moreno, 1989; Castilla, 1999; Moreno, 2001, and South Africa - Hockey and Bosman, 1986; Siegfried *et al.*, 1994; Griffiths and Branch, 1997).

Further down the shore at low tide mark level, abundance of turf forming primary producers have increased significantly, reflecting once again the lack of grazing limpets. Some species have shifted deeper into the subtidal zone (e.g. the sea-urchin *A. lixula* absent in recent surveys), probably due to the increase in disturbance (wave action) (Chapter 4) (Figure 6.2).

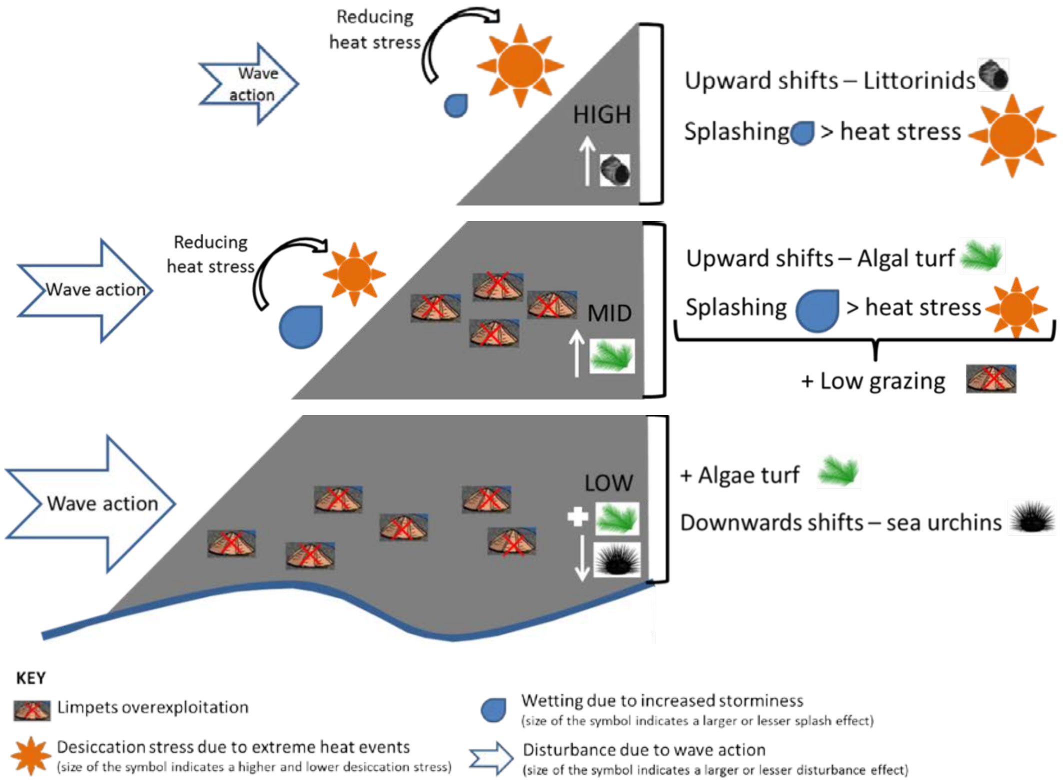


Figure 6.2. Possible interactions of recent climate change with limpet exploitation on vertical distribution patterns of rocky shore assemblages.

It is likely, that human exploitation of limpets has had a much greater effect, than the increases in temperature and storminess, in the Azorean ecosystem. Even so, recent climate change has had some influence over this ecosystem. This, on top of the overexploitation, will disrupt even more the rocky intertidal ecosystems of the Azores.

6.5. FUTURE RESEARCH

Long-term research is crucial to distinguish global climate signals from the background noise of natural variability (Hawkins *et al.*, 2013a,b; Mieszkowska *et al.*, 2014b; Firth *et al.*, 2015). These data sets provide a baseline against which changes can be compared, providing information to help diagnose the relative importance of global change compared to regional and local scale impacts. Several long-term studies have revealed the effects of recent climate change on the marine ecosystems contributing to an increase of knowledge and understanding of the current and future potential impacts of climate change on the marine environment (e.g. Barry *et al.*, 1995; Southward *et al.*, 1995, 2005; Sagarin *et al.*, 1999; Sims *et al.*, 2001; Beaugrand and Reid, 2003; Genner *et* *al.*, 2004, 2010; Mieszkowska *et al.*, 2007; Heip *et al.*, 2011; Menge *et al.*, 2011; Moore *et al.*, 2011; Poloczanska *et al.*, 2011; Beaugrand *et al.*, 2013, 2015). Long-term observations are vital for better understanding of the state of our seas and coastlines (Hawkins *et al.*, 2008, 2009). It is crucial to incorporate past changes, current patterns and future forecasts into marine conservation and management plans (Mieszkowska *et al.*, 2006a; Firth and Hawkins, 2011; Hawkins *et al.*, 2013b).

During the course of this thesis I have started an on-going monitoring programme on the rocky intertidal shores of São Miguel Island that intends to establish a baseline against which future changes in the intertidal can be compared (not included in the thesis). This monitoring programme comprises two complementary sampling approaches: a semi-quantitative broad-scale survey (similar to MarClim project) and more focussed quantitative sampling. The design includes both protected and unprotected shores in order to disentangle the impacts of changes in climate from those driven by other local impacts (e.g. harvesting). It also provides evidence of lack of enforcement of protected areas. Considering the location of the Azorean archipelago and the existing knowledge of how the rocky intertidal ecosystem is being affected by the overexploitation of key intertidal species and by the recent climate change, it is extremely important to continue with these long-term observations. Such information is essential for responsive and more effective management measures. Had such a programme existed the influence of climate change on the rocky shores of the Azores would have been detected much earlier and could have been quantified more easily. Implementation and enforcement of MPAs in the Azores is also a pressing priority. Such implementation would also ensure that any monitoring would be effective. They would also provide resilience to climatic driven change by reducing the pressure of exploitation as species at risk.

7. REFERENCES

Adger NW, Arnell NW and Tompkins EL. 2005. Successful Adaptation to Climate Change across Scales. *Global Environmental Change,* 15: 77-86.

Airoldi L, Abbiati M, Beck MW, Hawkins SJ, Jonsson PR, Martin D, Moschella PS, Sundelöf A, Thompson RC and Åberg P. 2005. An Ecological Perspective on the Deployment and Design of Low-Crested and Other Hard Coastal Defence Structures. *Coastal Engineering,* 52: 1073-1087.

Airoldi L, Balata D and Beck MW. 2008. The Gray Zone: Relationships between Habitat Loss and Marine Diversity and Their Applications in Conservation. *Journal of Experimental Marine Biology and Ecology,* 366: 8-15.

Airoldi L and Beck MW. 2007. Loss, Status and Trends for Coastal Marine Habitats of Europe. *Oceanography and Marine Biology: An Annual Review,* 45: 345-405.

Airoldi L and Hawkins SJ. 2007. Negative Effects of Sediment Deposition on Grazing Activity and Survival of the Limpet *Patella vulgata*. *Marine Ecology Progress Series,* 332: 235-240.

Alexander LV and Tett SFB. 2005. Recent Observed Changes in Severe Storms over the United Kingdom and Iceland. *Geophysical Research Letters,* 32: 1-4.

Alheit J and Niquen M. 2004. Regime Shifts in the Humboldt Current Ecosystem. *Progress In Oceanography,* 60: 201-222.

Allen JR, Slinn DJ, Shammon TM, Hartnoll RG and Hawkins SJ. 1998. Evidence for Euthrophication of the Irish Sea over Four Decades. *Limnology and Oceanography,* 43: 1970-1974.

Altieri AH, Van Wesenbeeck BK, Bertness MD and Silliman BR. 2010. Facilitation Cascade Drives Positive Relationship between Native Biodiversity and Invasion Success. *Ecology,* 91: 1269-1275.

Anderson DM, Burkholder JM, Cochlan WP, Glibert PM, Gobler CJ, Heil CA, Kudela RM, Parsons ML, Rensel JEJ, Townsend DW, Trainer VL and Vargo GA. 2008. Harmful Algal Blooms and Eutrophication: Examining Linkages from Selected Coastal Regions of the United States. *Harmful Algae,* 8: 39-53.

Araújo JN, MacKinson S, Stanford RJ, Sims DW, Southward AJ, Hawkins SJ, Ellis JR and Hart PJB. 2006. Modelling Food Web Interactions, Variation in Plankton Production, and Fisheries in the Western English Channel Ecosystem. *Marine Ecology Progress Series,* 309: 175-187.

Arenas F, Sánchez I, Hawkins SJ and Jenkins SR. 2006. The Invasibility of Marine Algal Assemblages: Role of Functional Diversity and Identity. *Ecology,* 87: 2851-2861.

Arrontes J, Arenas F, Fernández C, Rico JM, Oliveros J, Martínez B, Viejo RM and Alvarez D. 2004. Effect of Grazing by Limpets on Mid-Shore Species Assemblages in Northern Spain. *Marine Ecology Progress Series,* 277: 177-133.

Attrill MJ and Power M. 2002. Climatic Influence on a Marine Fish Assemblage. *Nature,* 417: 275-278.

Ávila SP, Madeira P, Rebelo AC, Melo C, Hipólito A, Pombo J, Botelho AZ and Cordeiro R. 2015. *Phorcus sauciatus* (Koch, 1845) (Gastropoda: Trochidae) in Santa Maria, Azores Archipelago: The Onset of a Biological Invasion. *Journal of Molluscan Studies,* 10.1093/mollus/eyv012: 1-6.

Azevedo JMN, Portugal Ferreira MR and Martins JA. 1991. The Emergent Volcanism of Flores Island, Azores (Portugal). *Arquipélago. Life and Earth Science,* 9: 37-46.

Azevedo LB, Schryver AM, Hendriks AJ and Huijbregts MAJ. 2015. Calcifying Species Sensitivity Distributions for Ocean Acidification. *Environmental Science and Technology,* 49: 1495-1500.

Bacon S and Carter DJT. 1991. Wave Climate Changes in the North Atlantic and North Sea. *International Journal of Climatology,* 11: 545-558.

Ballantine WJ. 1961. A Biologically-Defined Exposure Scale for the Comparative Description of Rocky Shores. *Field Studies,* 1: 73-84.

Barry JP, Baxter CH, Sagarin RD and Gilman SE. 1995. Climate-Related, Long-Term Faunal Changes in a California Rocky Intertidal Community. *Science,* 267: 672-675.

Beare D, Burns F, Jones E, Peach K, Portilla E, Greig T, McKenzie E and Reid D. 2004. An Increase in the Abundance of Anchovies and Sardines in the North-Western North Sea since 1995. *Global Change Biology,* 10: 1209-1213.

Beaugrand G. 2005. Monitoring Pelagic Ecosystems Using Plankton Indicators. *ICES Journal of Marine Science,* 62: 333-338.

Beaugrand G, Edwards M, Raybaud V, Goberville E and Kirby RR. 2015. Future Vulnerability of Marine Biodiversity Compared with Contemporary and Past Changes. *Nature Climate Change,* 10.1038/nclimate2650.

Beaugrand G and Ibañez F. 2004. Monitoring Marine Plankton Ecosystems. II: Long-Term Changes in North Sea Calanoid Copepods in Relation to Hydro-Climatic Variability. *Marine Ecology Progress Series,* 284: 35-47.

Beaugrand G, Ibañez F, Lindley JA and Reid PC. 2002a. Diversity of Calanoid Copepods in the North Atlantic and Adjacent Seas: Species Associations and Biogeography. *Marine Ecology Progress Series,* 232: 179-195.

Beaugrand G, Mcquatters-Gollop A, Edwards M and Goberville E. 2013. Long-Term Responses of North Atlantic Calcifying Plankton to Climate Change. *Nature Climate Change,* 3: 263-267.

Beaugrand G and Reid PC. 2003. Long-Term Changes in Phytoplankton, Zooplankton and Salmon Related to Climate. *Global Change Biology,* 9: 801-817.

Beaugrand G, Reid PC, Ibañez F, Lindley JA and Edwards E. 2002b. Reorganization of North Atlantic Marine Copepod Biodiversity and Climate. *Science,* 296: 1692-1694.

Bell RG, Goring DG and De Lange WP. 2000. Sea-Level Change and Storm Surges in the Context of Climate Change. *IPENZ Transactions,* 27: 1- 10.

Ben Rais Lasram F, Guilhaumon F, Albouy C, Somot S and Thuiller W. 2010. The Mediterranean Sea as a 'Cul-De-Sac' for Endemic Fishes Facing Climate Change. *Global Change Biology,* 16: 3233-3245.

Benedetti-Cecchi L, Bertocci I, Vaselli S and Maggi E. 2006. Temporal Variance Reverses the Impact of High Mean Intensity of Stress in Climate Change Experiments. *Ecology,* 87: 2489-2499.

Benedetti-Cecchi L, Bulleri F, Acunto S and Cinelli F. 2001a. Scales of Variation in the Effects of Limpets on Rocky Shores in the Northwest Mediterranean. *Marine Ecology Progress Series,* 209: 131-141.

Benedetti-Cecchi L, Menconi M and Cinelli F. 1999. Pre-Emption of the Substratum and the Maintenance of Spatial Pattern on a Rocky Shore in the Northwest Medditerranean. *Marine Ecology Progress Series,* 181: 13-23.

Benedetti-Cecchi L, Pannacciulli F, Bulleri F, Moschella PS, Airoldi L, Relini G and Cinelli F. 2001b. Predicting the Consequences of Anthropogenic Disturbance: Large-Scale Effects of Loss of Canopy Algae on Rocky Shores. *Marine Ecology Progress Series,* 214: 137-150.

Benedetti-Cecchi L, Tamburello L, Maggi E and Bulleri F. 2015. Experimental Perturbations Modify the Performance of Early Warning Indicators of Regime Shift. *Current Biology,* 25: 1867-1872.

Benson AJ and Trites AW. 2002. Ecological Effects of Regime Shifts in the Bering Sea and Eastern North Pacific Ocean. *Fish and Fisheries,* 3: 95-113.

Berke SK, Mahon AR, Lima FP, Halanych KM, Wethey DS and Woodin SA. 2010. Range Shifts and Species Diversity in Marine Ecosystem Engineers: Patterns and Predictions for European Sedimentary Habitats. *Global Ecology and Biogeography,* 19: 223-232.

Bertness MD and Leonard GH. 1997. The Role of Positive Interactions in Communities: Lessons from Intertidal Habitats. *Ecology,* 78: 1976-1989.

Bertness MD, Leonard GH, Levine JM, Schmidt PR and Ingraham AO. 1999. Testing the Relative Contribution of Positive and Negative Interactions in Rocky Intertidal Communities. *Ecology,* 80: 2711-2726.

Bianchi CN, Corsini-Foka M, Morri C and Zenetos A. 2014. Thirty Years After: Dramatic Changes in the Coastal Marine Ecosystems of Kos Island (Greece), 1981-2013. *Mediterranean Marine Science,* 15: 482-497.

Bindoff NL, Willebrand J, Artale V, Cazenave A, Gregory J, Gulev S, Hanawa K, Le Quéré C, Levitus S, Nojiri Y, Shum CK, Talley LD and Unnikrishnan A. 2007. Observations: Oceanic Climate Change and Sea Level. *In:* Solomon S, Qin D, Manning M, Chen Z, Marquis M, Averyt KB, Tignor M and Miller HL (eds). *Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change.* Cambridge University Press, Cambridge, UK.

Blanchette CA. 1997. Size and Survival of Intertidal Plants in Response to Wave Action: A Case Study with *Fucus gardneri*. *Ecology,* 78: 1563-1578.

Boaventura D, Alexander M, Della Santina P, Smith ND, Ré P, Cancela Da Fonseca L and Hawkins SJ. 2002a. The Effects of Grazing on the Distribution and Composition of Low-Shore Algal Communities on the Central Coast of Portugal and on the Southern Coast of Britain. *Journal of Experimental Marine Biology and Ecology,* 267: 185-206.

Boaventura D, Cancela Da Fonseca L and Hawkins SJ. 2002b. Analysis of Competitive Interactions between the Limpets *Patella depressa* Pennant and *Patella vulgata* L. On the Northern Coast of Portugal. *Journal of Experimental Marine Biology and Ecology,* 271: 171-188.

Boaventura D, Cancela Da Fonseca L and Hawkins SJ. 2003. Size Matters: Competition within Populations of the Limpet *Patella depressa*. *Journal of Animal Ecology,* 72: 435-446.

Boaventura D, Ré P, Cancela Da Fonseca L and Hawkins SJ. 2002c. Intertidal Rocky Shore Communities of the Continental Portuguese Coast: Analysis of Distribution Patterns. *Marine Ecology,* 23: 169-190

Borges CDG, Doncaster CP, Maclean MA and Hawkins SJ. 2015. Broad-Scale Patterns of Sex Ratios in *Patella* spp.: A Comparison of Range Edge and Central Range Populations in the British Isles and Portugal. *Journal of the Marine Biological Association of the United Kingdom,* 95: 1141-1153.

Borthagaray AI and Carranza A. 2007. Mussels as Ecosystem Engineers: Their Contribution to Species Richness in a Rocky Littoral Community. *Acta Oecologica,* 31: 243-250.

Bouma TJ, Ortells V and Ysebaert T. 2009. Comparing Biodiversity Effects among Ecosystem Engineers of Contrasting Strength: Macrofauna Diversity in *Zostera noltii* and *Spartina anglica* Vegetations. *Helgoland Marine Research,* 63: 3-18.

Bowman RS and Lewis JR. 1977. Annual Fluctuations in the Recruitment of *Patella vulgata* L. *Journal of the Marine Biological Association of the United Kingdom,* 57: 793-815.

Bowman RS and Lewis JR. 1986. Geographical Variation in the Breeding Cycles and Recruitment of *Patella* spp. *Hydrobiologia,* 142: 41-56.

Bradshaw C, Veale LO and Brand AR. 2002. The Role of Scallop-Dredge Disturbance in Long-Term Changes in Irish Sea Benthic Communities: A Re-Analysis of an Historical Dataset. *Journal of Sea Research,* 47: 161-184.

Bradshaw WE and Holzapfel CM. 2006. Evolutionary Response to Rapid Climate Change. *Science,* 312: 1477-1478

Branch GM. 1975. Mechanisms Reducing Intraspecific Competition in *Patella* spp.: Migration, Differentiation and Territorial Behaviour. *Journal of Animal Ecology,* 44: 575-600.

Branch GM. 1981. The Biology of Limpets: Physical Factors, Energy Flow, and Ecological Interactions. *Oceanography and Marine Biology: An Annual Review,* 19: 235-380.

Branch G and Branch M. 1981. *The Living Shores of Southern Africa*. C. Struik Publishers, Cape Town, South Africa.

Branch GM and Cherry MI. 1985. Activity Rhytms of the Pulmonate Limpet *Siphonaria capensis* Q. and G. As an Adaptation to Osmotic Stress, Predation and Wave Action. *Journal of Experimental Marine Biology and Ecology,* 87: 153-168.

Brander K, Blom G, Borges MF, Erzini K, Henderson G, MacKenzie BR, Mendes H, Ribeiro J, Santos AMP and Toresen R. 2003. Changes in Fish Distribution in the Eastern North Atlantic: Are We Seeing a Coherent Response to Changing Temperature? *ICES Marine Science Symposia,* 219: 261-270.

Briggs JC. 1974. *Marine Biogeography.* McMillan, New York, USA.

Brook BW, Sodhi NS and Bradshaw CJA. 2008. Synergies among Extinction Drivers under Global Change. *Trends in Ecology and Evolution,* 23: 453-460.

Bruno JF and Bertness MD. 2001. Habitat Modification and Facilitation in Benthic Marine Communities. *In:* Bertness MD, Gaines SD and Hay ME (eds*). Marine Community Ecology*. Sinauer Associates Inc, New York, USA.

Buckley BA, Owen M-EA and Hofmann GE. 2001. Adjusting the Thermostat: The Threshold Induction Temperature for the Heat-Shock Response in Intertidal Mussels (Genus *Mytilus*) Changes as a Function of Thermal History. *Journal of Experimental Biology,* 204: 3571-3579.

Bulleri F. 2005. Role of Recruitment in Causing Differences between Intertidal Assemblages on Seawalls and Rocky Shores. *Marine Ecology Progress Series,* 287: 53-65.

Bulleri F, Benedetti-Cecchi L, Cusson M, Maggi E, Arenas F, Aspden R, Bertocci I, Crowe TP, Davoult D, Eriksson BK, Fraschetti S, Golléty C, Griffin JN, Jenkins SR, Kotta J, Kraufvelin P, Molis M, Sousa Pinto I, Terlizzi A, Valdivia N and Paterson DM. 2012. Temporal Stability of European Rocky Shore Assemblages: Variation across a Latitudinal Gradient and the Role of Habitat-Formers. *Oikos,* 121: 1801-1809.

Bulleri F, Chapman MG and Underwood AJ. 2005. Intertidal Assemblages on Seawalls and Vertical Rocky Shores in Sydney Harbour, Australia. *Austral Ecology,* 30: 655-667.

Bulleri F, Menconi M, Cinelli F and Benedetti-Cecchi L. 2000. Grazing by Two Species of Limpets on Artificial Reefs in the Northwest Mediterranean. *Journal of Experimental Marine Biology and Ecology,* 255: 1-19.

Burrows MT, Harvey R and Robb L. 2008. Wave Exposure Indices from Digital Coastlines and the Prediction of Rocky Shore Community Structure. *Marine Ecology Progress Series,* 353: 1-12.

Burrows MT and Hawkins SJ. 1998. Modelling Patch Dynamics on Rocky Shores Using Deterministic Cellular Automata. *Marine Ecology Progress Series,* 167: 1-13.

Burrows MT and Hughes RN. 1989. Natural Foraging of the Dogwhelk, *Nucella lapillus* (Linnaeus); the Weather and Whether to Feed. *Journal of Molluscan Studies,* 55: 285-295.

Burrows MT, Schoeman DS, Buckley LB, Moore P, Poloczanska ES, Brander KM, Brown C, Bruno JF, Duarte CM, Halpern BS, Holding J, Kappel CV, Kiessling W, O'Connor MI, Pandolfi JM, Parmesan C, Schwing FB, Sydeman WJ and Richardson AJ. 2011. The Pace of Shifting Climate in Marine and Terrestrial Ecosystems. *Science,* 334: 652-655.

Burrows MT, Schoeman DS, Richardson AJ, Molinos JG, Hoffmann A, Buckley LB, Moore PJ, Brown CJ, Bruno JF, Duarte CM, Halpern BS, Hoegh-Guldberg O, Kappel CV, Kiessling W, O'Connor MI, Pandolfi JM, Parmesan C, Sydeman WJ, Ferrier S, Williams KJ and Poloczanska ES. 2014. Geographical Limits to Species-Range Shifts Are Suggested by Climate Velocity. *Nature,* 507: 492-495.

Caldeira K and Wickett ME. 2003. Anthropogenic Carbon and Ocean Ph. *Nature,* 425: 365.

Caley M, Carr M, Hixon M, Hughes T, Jones G and Menge B. 1996. Recruitment and the Local Dynamics of Open Marine Populations. *Annual Review of Ecology and Systematics,* 27: 477-500.

Capasso E, Jenkins SR, Frost M and Hinz H. 2010. Investigation of Benthic Community Change over a Century-Wide Scale in the Western English Channel. *Journal of the Marine Biological Association of the United Kingdom,* 90: 1161-1172.

Cardigos F, Tempera F, Ávila S, Gonçalves J, Colaço A and Santos RS. 2006. Non-Indigenous Marine Species of the Azores. *Helgoland Marine Research,* 60: 160-169.

Cardinale BJ, Duffy JE, Gonzalez A, Hooper DU, Perrings C, Venail P, Narwani A, Mace GM, Tilman D, Wardle DA, Kinzig AP, Daily GC, Loreau M, Grace JB, Larigauderie A, Srivastava DS and Naeem S. 2012. Biodiversity Loss and Its Impact on Humanity. *Nature,* 486: 59-67.

Castilla JC. 1999. Coastal Marine Communities: Trends and Perspectives from Human-Exclusion Experiments. *Trends in Ecology and Evolution,* 14: 280-283.

Castilla JC, Lagos NA and Cerda M. 2004. Marine Ecosystem Engineering by the Alien Ascidian *Pyura praeputialis* on a Mid-Intertidal Rocky Shore. *Marine Ecology Progress Series,* 268: 119-130.

Castilla JC and Paine RT. 1987. Predation and Community Organization on Eastern Pacific, Temperate Zone, Rocky Intertidal Shores. *Revista Chilena de Historia Natural,* 60: 131-151.

Cavieres LA and Badano EI. 2009 Do Facilitative Interactions Increase Species Richness at the Entire Community Level? *Journal of Ecology,* 97: 1181-1191.

Chainho P, Fernandes A, Amorim A, Ávila SP, Canning-Clode J, Castro JJ, Costa AC, Costa JL, Cruz T, Gollasch S, Grazziotin-Soares C, Melo R, Micael J, Parente MI, Semedo J, Silva T, Sobral D, Sousa M, Torres P, Veloso V and Costa MJ. 2015. Non-Indigenous Species in Portuguese Coastal Areas, Coastal Lagoons, Estuaries and Islands. *Estuarine, Coastal and Shelf Science,* online publication: 1-13.

Chapman MG. 2000. Poor Design of Behavioural Experiments Gets Poor Results: Examples from Intertidal Habitats. *Journal of Experimental Marine Biology and Ecology,* 250: 77-95.

Chapman ARO and Johnson CR. 1990. Disturbance and Organization of Macroalgal Assemblages in the Northwest Atlantic. *Hydrobiologia,* 192: 77-121.

Chapman MG and Underwood AJ. 2011. Evaluation of Ecological Engineering of “Armoured” Shorelines to Improve Their Value as Habitat. *Journal of Experimental Marine Biology and Ecology,* 400: 302-313.

Chen IC, Hill JK, Ohlemüller R, Roy DB and Thomas CD. 2011. Rapid Range Shifts of Species Associated with High Levels of Climate Warming. *Science,* 333: 1024-1026.

Cheung WWL, Dunne J, Sarmiento JL and Pauly D. 2011. Integrating Ecophysiology and Plankton Dynamics into Projected Maximum Fisheries Catch Potential under Climate Change in the North-East Atlantic. *ICES Journal of Marine Science,* 68: 1008-1018.

Cheung WWL, Lam VWY, Sarmiento JL, Kearney K, Watson R and Pauly D. 2009. Projecting Global Marine Biodiversity Impacts under Climate Change Scenarios. *Fish and Fisheries,* 10: 235-251.

Cheung WWL, Lam VWY, Sarmiento JL, Kearney K, Watson REG, Zeller D and Pauly D. 2010. Large-Scale Redistribution of Maximum Fisheries Catch Potential in the Global Ocean under Climate Change. *Global Change Biology,* 16: 24-35.

Cheung WWL, Pinnegar J, Merino G, Jones MC and Barange M. 2012. Review of Climate Change Impacts on Marine Fisheries in the Uk and Ireland. *Aquatic Conservation: Marine and Freshwater Ecosystems,* 22: 368-388.

Cheung WWL, Watson R and Pauly D. 2013. Signature of Ocean Warming in Global Fisheries Catch. *Nature,* 497: 365-369.

Church JA, Gregory JM, Huybrechts P, Kuhn M, Lambeck K, Nhuan NT, Qin D and Woodworth PL. 2001. Changes in Sea Level. *In:* Houghton JT, Ding Y, Griggs DJ, Noguer M, Van der Linden PJ, Dai X, Maskell K and Johnston CA (eds). *Climate Change 200: The Scientific Basis. Contribution of Working Group I to the Third Assessment Report of the Intergovernmental Panel on Climate Change.* Cambridge University Press, Cambridge, UK.

Clare DS, Robinson LA and Frid CLJ. 2015. Community Variability and Ecological Functioning: 40 Years of Change in the North Sea Benthos. *Marine Environmental Research,* 107: 24-34.

Clarke A. 1996. The Influence of Climate Change on the Distribution and Evolution of Organisms. *In:* Johnston IA and Bennett AF (eds). *Animals and Temperature: Phenotypic and Evolutionary Adaptation.* Cambridge University Press, Cambridge, UK.

Clarke A, Murphy EJ, Meredith MP, King JC, Peck LS, Barnes DKA and Smith RC. 2007. Climate Change and the Marine Ecosystem of the Western Antarctic Peninsula. *Philosophical Transactions of the Royal Society B: Biological Sciences,* 362: 149-166.

Clarke KR and Gorley RN. 2006. *Primer V6: User Manual/Tutorial.* Primer-E Ltd., Plymouth, UK.

Coleman RA, Underwood AJ, Benedetti-Cecchi L, Åberg P, Arenas F, Arrontes J, Castro J, Hartnoll RG, Jenkins SR, Paula J, Della Santina P and Hawkins SJ. 2006. A Continental Scale Evaluation of the Role of Limpet Grazing on Rocky Shores. *Oecologia,* 147: 556-564.

Colman J. 1933. The Nature of the Intertidal Zonation of Plants and Animals. *Journal of the Marine Biological Association of the United Kingdom,* 18: 435-476.

Comiso JC, Parkinson CL, Gersten R and Stock L. 2008. Accelerated Decline in the Arctic Sea Ice Cover. *Geophysical Research Letters,* 35: 1-6.

Connell JH. 1961a. Effects of Competition, Predation by *Thais lapillus*, and Other Factors on Natural Populations of the Barnacle *Balanus balanoides*. *Ecological Monographs,* 31: 61-104.

Connell JH. 1961b. The Influence of Interspecific Competition and Other Factors on the Distribution of the Barnacle *Chthamalus stellatus*. *Ecology,* 42: 710-723.

Connell JH. 1972. Community Interactions on Marine Rocky Intertidal Shores. *Annual Review of Ecology and Systematics,* 3: 169-192.

Coppini G, De Dominicis M, Zodiatis G, Lardner R, Pinardi N, Santoleri R, Colella S, Bignami F, Hayes DR, Soloviev D, Georgiou G and Kallos G. 2011. Hindcast of Oilspill Pollution During the Lebanon Crisis in the Eastern Mediterranean, July-August 2006. *Marine Pollution Bulletin,* 62: 140-153.

Côrte-Real HBSM, Hawkins SJ and Thorpe JP. 1992. Genetic Confirmation That Intertidal and Subtidal Morphs of *Patella ulyssiponensis aspera* Röding (Mollusca: Gastropoda: Patellidae) Are Conspecific. *Arquipélago. Life and Earth Science,* 10: 55-66.

Côrte-Real HBSM, Hawkins SJ and Thorpe JP. 1996. Population Differentiation and Taxonomic Status of the Exploited Limpet *Patella candei* in the Macaronesian Islands (Azores, Madeira, Canaries). *Marine Biology,* 125: 141-152.

Creese RG. 1980. An Analysis of Distribution and Abundance of Populations of the High-Shore Limpet, *Notoacmea petterdi* (Tenison-Woods) *Oecologia,* 45: 252-260.

Crisp DJ. 1961. Territorial Behaviour in Barnacle Settlement. *Journal of Experimental Biology,* 38: 429-446.

Crisp DJ and Southward AJ. 1958. The Distribution of Intertidal Organisms Along the Coasts of the English Channel. *Journal of the Marine Biological Association of the United Kingdom,* 37: 157-208.

Cropper T. 2013. The Weather and Climate of Macaronesia: Past, Present and Future. *Weather,* 6: 300-307.

Crowe TP, Cusson M, Bulleri F, Davoult D, Arenas F, Aspden R, Benedetti-Cecchi L, Bevilacqua S, Davidson I, Defew E, Fraschetti S, Golléty C, Griffin JN, Herkül K, Kotta J, Migné A, Molis M, Nicol SK, Noël LM-LJ, Pinto IS, Valdivia N, Vaselli S and Jenkins SR. 2013. Large-Scale Variation in Combined Impacts of Canopy Loss and Disturbance on Community Structure and Ecosystem Functioning. *PLoS One,* 8: e66238.

Crowe TP, Frost NJ and Hawkins SJ. 2011. Interactive Effects of Losing Key Grazers and Ecosystem Engineers Vary with Environmental Context. *Marine Ecology Progress Series,* 430: 223-234.

Crowe TP, Thompson RC, Bray S and Hawkins SJ. 2000. Impacts of Anthropogenic Stress on Rocky Intertidal Communities. *Journal of Aquatic Ecosystem Stress and Recovery,* 7: 273-297.

Cúrdia J, Rodrigues AS, Martins AMF and Costa MJ. 2005. The Reproductive Cycle of *Patella candei gomesii* Drouët, 1858 (Mollusca: Patellogastropoda), an Azorean Endemic Subspecies. *Invertebrate Reproduction and Development,* 48: 137-145.

Dahlhoff EP, Buckley BA and Menge BA. 2001. Physiology of the Rocky Intertidal Predator *Nucella ostrina* Along an Environmental Stress Gradient. *Ecology,* 82: 2816-2829.

Dahlhoff EP, Stillman JH and Menge BA. 2002. Physiological Community Ecology: Variation in Metabolic Activity of Ecologically Important Rocky Intertidal Invertebrates Along Environmental Gradients. *Integrative and Comparative Biology,* 42: 862-871.

Davenport J and Davenport JL. 2005. Effects of Shore Height, Wave Exposure and Geographical Distance on Thermal Niche Width of Intertidal Fauna. *Marine Ecology Progress Series,* 292: 41-50.

Davies S. 1969. Physiological Ecology of *Patella* III: Desiccation Effects. *Journal of the Marine Biological Association of the United Kingdom,* 49: 291-304.

Davies AJ, Johnson MP and Maggs CA. 2007. Limpet Grazing and Loss of *Ascophyllum nodosum* Canopies on Decadal Time Scales. *Marine Ecology Progress Series,* 339: 131-141.

Davis AJ, Jenkinson LS, Lawton JL, Shorrocks B and Wood S. 1998. Making Mistakes When Predicting Shifts in Species Range in Response to Global Warming. *Nature,* 391: 783-786.

Dayton PK. 1971. Competition, Disturbance, and Community Organization: The Provision and Subsequent Utilization of Space in a Rocky Intertidal Community. *Ecological Monographs,* 41: 351-389.

deBoer WF and Prins HHT. 2002. Human Exploitation and Benthic Community Structure on a Tropical Intertidal Flat. *Journal of Sea Research,* 48: 225-240.

Delworth TL, Zhang R and Mann ME. 2007. Decadal to Centennial Variability of the Atlantic from Observations and Models. *Geophysical Monographs Series,* 173: 131-148.

Denny MW, Dowd WW, Bilir L and Mach KJ. 2011. Spreading the Risk: Small-Scale Body Temperature Variation among Intertidal Organisms and Its Implications for Species Persistence. *Journal of Experimental Marine Biology and Ecology,* 400: 175-190.

Devictor V, Van Swaay C, Brereton T, Brotons L, Chamberlain D, Heliölä J, Herrando S, Julliard R, Kuussaari M, Lindström Å, Reif J, Roy DB, Schweiger O, Settele J, Stefanescu C, Van Strien A, Van Turnhout C, Vermouzek Z, Devries MW, Wynhoff I and Jiguet F. 2012. Differences in the Climate Debts of Birds and Butterflies at a Continental Scale. *Nature Climate Change,* 2: 121 - 124.

deYoung B, Barange M, Beaugrand G, Harris R, Perry RI, Scheffer M and Werner F. 2008. Regime Shifts in Marine Ecosystems: Detection, Prediction and Management. *Trends in Ecology and Evolution,* 23: 402-409.

Donald KM, Preston J, Williams ST, Reid DG, Winter D, Alvarez R, Buge B, Hawkins SJ, Templado J and Spencer HG. 2012. Phylogenetic Relationships Elucidate Colonization Patterns in the Intertidal Grazers *Osilinus* Philippi, 1847 and *Phorcus* Risso, 1826 (Gastropoda: Trochidae) in the Northeastern Atlantic Ocean and Mediterranean Sea. *Molecular Phylogenetics and Evolution,* 62: 35-45.

Drápela K and Drápelová I. 2011. Application of Mann-Kendall Test and the Sen’s Slope Estimates for Trend Detection in Deposition Data from Bílý Kříž (Beskydy Mts., the Czech Republic) 1997-2010. *Beskdy,* 4: 133-146.

Drinkwater KF, Beaugrand G, Kaeriyama M, Kim S, Ottersen G, Perry RI, Pörtner H-O, Polovina JJ and Takasuka A. 2010. On the Processes Linking Climate to Ecosystem Changes. *Journal of Marine Systems,* 79: 374-388.

Dulvy NK, Jennings S, Rogers SI and Maxwell DL. 2006. Threat and Decline in Fishes: An Indicator of Marine Biodiversity *Canadian Journal of Fisheries and Aquatic Sciences,* 63: 1267-1275.

Durant JM, Stenseth NC, Anker-Nilssen T, Harris MP, Thompson PM and Wanless S. 2005. Marine Birds and Climate Fluctuation in the North Atlantic. *In:* Stenseth NC, Ottersen G, Hurrell JW and Belgrano A. (eds). *Marine Ecosystems and Climate Variation: The North Atlantic - A Comparative Perspective.* Oxford University Press, Oxford, UK.

Edenhofer O, Knopf B, Barker T, Baumstark L, Bellevrat E, Chateau B, Criqui P, Isaac M, Kitous A, Kypreos S, Leimbach M, Lessmann K, Magné B, Scrieciu Ş, Turton H and Van Vuuren DP. 2010. The Economics of Low Stabilization: Model Comparison of Mitigation Strategies and Costs. *The Energy Journal,* 31: 11-48.

Edwards M, Reid P and Planque B. 2001. Long-Term and Regional Variability of Phytoplankton Biomass in the North-East Atlantic (1960-1995). *ICES Journal of Marine Science,* 58: 39-49.

Edwards M and Richardson AJ. 2004. Impact of Climate Change on Marine Pelagic Phenology and Trophic Mismatch. *Nature,* 430: 881-884.

Elsner JB, Kossin JP and Jagger TH. 2008. The Increasing Intensity of the Strongest Tropical Cyclones. *Nature,* 455: 92-95.

Eriksson BK, Rubach A and Hillebrand H. 2007. Dominance by a Canopy Forming Seaweed Modifies Resource and Consumer Control of Bloom-Forming Macroalgae. *Oikos,* 116: 1211-1219.

Feely RA, Sabine CL, Lee K, Berelson W, Kleypas JV, Fabry J and Millero FJ. 2004. Impact of Anthropogenic Co2 on the Caco3 System in the Oceans. *Science,* 305: 362-366.

Fenberg PB, Hellberg ME, Mullen L and Roy K. 2010. Genetic Diversity and Population Structure of the Size-Selectively Harvested Owl Limpet, *Lottia gigantea*. *Marine Ecology,* 31: 574-583.

Fenberg PB and Roy K. 2008. Ecological and Evolutionary Consequences of Size-Selective Harvesting: How Much Do We Know? *Molecular Ecology,* 17: 209-220.

Fenberg PB and Roy K. 2012. Anthropogenic Harvesting Pressure and Changes in Life History: Insights from a Rocky Intertidal Limpet. *The American Naturalist,* 180: 200-210.

Ferraz R. 1998. *Avaliação Do Recurso De Lapas - Patella ulyssiponensis aspera* (Christiaens, 1973) e *Patella candei candei* (Röding, 1978) - *No Arquipélago Dos Açores.* BSc Final report, University of Algarve, Portugal.

Ferraz R, Menezes GM and Santos RS. 2001. Limpet (*Patella* spp.) (Mollusca: Gastropoda) Exploitation in the Azores, During the Period 1993-1998. *Arquipelago: Life and Marine Sciences, Supplement 2 (Part B)*: 59-65.

Ferreira JG. 2012. *Latitudinal and Climatic Driven Changes in Local Patterns of Intertidal Macroalgae: Implications for Biodiversity and Ecosystem Functioning.* PhD thesis, University of Bangor, Bangor, UK.

Ferreira JG, Arenas F, Martínez B, Hawkins SJ and Jenkins SR. 2014. Physiological Response of Fucoid Algae to Environmental Stress: Comparing Range Centre and Southern Populations. *New Phytologist,* 10.1111/nph.12749: 1-16.

Figueiredo MAO, Kain JM and Norton TA. 2000. Responses of Crustose Corallines to Epiphyte and Canopy Cover. *Journal of Phycology,* 36: 17-24.

Firth LB and Hawkins SJ. 2011. Introductory Comments - Global Change in Marine Ecosystems: Patterns, Processes and Interactions with Regional and Local Scale Impacts. *Journal of Experimental Marine Biology and Ecology,* 400: 1-6.

Firth LB, Knights AM and Bell SS. 2011. Air Temperature and Winter Mortality: Implications for the Persistence of the Invasive Mussel, *Perna viridis* in the Intertidal Zone of the South-Eastern United States. *Journal of Experimental Marine Biology and Ecology,* 400: 250-256.

Firth LB, Mieszkowska N, Grant LM, Bush LE, Davies AJ, Frost MT, Moschella PS, Burrows MT, Cunningham PN, Dye SR and Hawkins SJ. 2015. Historical Comparisons Reveal Multiple Drivers of Decadal Change of an Ecosystem Engineer at the Range Edge. *Ecology and Evolution,* 5: 3210-3222.

Firth LB, Schofield M, White FJ, Skov MW and Hawkins SJ. 2014. Biodiversity in Intertidal Rock Pools: Informing Engineering Criteria for Artificial Habitat Enhancement in the Built Environment. *Marine Environmental Research,* 102: 122-130.

Firth LB, Thompson RC, White FJ, Schofield M, Skov MW, Hoggart SPG, Jackson J, Knights AM and Hawkins SJ. 2013. The Importance of Water-Retaining Features for Biodiversity on Artificial Intertidal Coastal Defence Structures. *Diversity and Distributions,* 19: 1275-1283.

Firth LB and Williams GA. 2009. The Influence of Multiple Environmental Stressors on the Limpet *Cellana toreuma* During the Summer Monsoon Season in Hong Kong. *Journal of Experimental Marine Biology and Ecology,* 375: 70-75.

Fischer-Piette E. 1963. La Distribution Des Principaux Organismes Intercotidaux Nord-Ibériques En 1954-1955. *Annales de l’Institut Océanographique Paris,* 40: 165-311.

Fischer-Piette E and Crisp, D.J. 1959. Répartition Des Principales Espèces Intercotidales De La Côte Atlantique Française: En 1954-1955. *Annales de l’Institut Océanographique Paris.*

Fischlin A, Midgley GF, Price JT, Leemans R, Gopal B, Turley C, Rounsevell MDA, Dube OP, Tarazona J and Velichko AA. 2007. Ecosystems, Their Properties, Goods, and Services. *In:* Palutikof JP, Canziani OF, Parry ML, Van Der Linden PJ and Hanson CE (eds). *Climate Change 2007: Impacts, Adaptation and Vulnerability. Contribution of Working Group II to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change.* Cambridge University Press, Cambridge, UK.

Fodrie FJ, Heck JKL, Powers SP, Graham WM and Robinson KL. 2010. Climate-Related, Decadal-Scale Assemblage Changes of Seagrass-Associated Fishes in the Northern Gulf of Mexico. *Global Change Biology,* 16: 48-59.

Foster BA. 1971. On the Determinants of the Upper Limit of Intertidal Distribution of Barnacles (Crustacea:Cirripedia). *Journal of Animal Ecology,* 40: 33-48.

Frank PW. 1965. The Biodemography of an Intertidal Snail Population. *Ecology,* 46: 831-844.

Fretter V and Graham A. 1981. The Prosobranch Molluscs of Britain and Denmark. *Journal of Molluscan Studies,* 9: 1-37.

Frid CLJ. 2011. Temporal Variability in the Benthos: Does the Sea Floor Function Differently over Time? *Journal of Experimental Marine Biology and Ecology,* 400: 99-107.

Friedlingstein P, Solomon S, Plattner G-K, Knutti R, Ciais P and Raupach MR. 2011. Long-Term Climate Implications of Twenty-First Century Options for Carbon Dioxide Emission Mitigation. *Nature Climate Change,* 1: 457-461.

Fuller A, Dawson T, Helmuth B, Hetem RS, Mitchell D and Maloney SK. 2010. Physiological Mechanisms in Coping with Climate Change. *Physiological and Biochemical Zoology,* 83: 713-720.

Füssel H-M. 2008. *The Risks of Climate Change: A Synthesis of New Scientific Knowledge since the Finalization of the Ipcc Fourth Assessment Report (Ar4)*. Potsdam Institute for Climate Impact Research (PIK).

Garcia RA, Cabeza M, Rahbek C and Araújo MB. 2014. Multiple Dimensions of Climate Change and Their Implications for Biodiversity. *Science,* 344: 1247579-1247571-1247510.

Gaston AT, Gilchrist HG, Mallory ML and Smith PA. 2009. Changes in Seasonal Events, Peak Food Availability, and Consequent Breeding Adjustment in a Marine Bird: A Case of Pregressive Mismatching. *Condor,* 111: 111-119.

Gates DM. 1980. *Biophysical Ecology.* Springer, New York, USA.

Geffen AJ, Nash RDM, Dau K and Harwood AJP. 2011. Sub-Cohort Dynamics of 0-Group Plaice, *Pleuronectes platessa* L., in the Northern Irish Sea: Settlement, Growth and Mortality. *Journal of Experimental Marine Biology and Ecology,* 400: 108-119.

Genner MJ, Sims DW, Southward AJ, Budd GC, Masterson P, McHugh M, Rendle P, Southall EJ, Wearmouth VJ and Hawkins SJ. 2010. Body Size-Dependent Responses of a Marine Fish Assemblage to Climate Change and Fishing over a Century-Long Scale. *Global Change Biology,* 16: 517-527.

Genner MJ, Sims DW, Wearmouth VJ, Southall EJ, Southward AJ, Henderson PA and Hawkins SJ. 2004. Regional Climate Warming Drives Long-Term Community Changes of British Marine Fish. *Proceedings of the Royal Society B: Biological Sciences,* 271: 655-661.

Gilman SE, Wethey DS and Helmuth B. 2006. Variation in the Sensitivity of Organismal Body Temperature to Climate Change over Local and Geographic Scales. *Proceedings of the National Academy of Sciences,* 103: 9560-9565.

Giménez L. 2011. Exploring Mechanisms Linking Temperature Increase and Larval Phenology: The Importance of Variance Effects. *Journal of Experimental Marine Biology and Ecology,* 400: 227-235.

Godoy C and Moreno CA. 1989. Indirect Effects of Human Exclusion from the Rocky Intertidal in Southern Chile: A Case of Cross-Linkage between Herbivores. *Oikos,* 54: 101-106.

Greene CH, Pershing AJ, Cronin TM and Ceci N. 2008. Arctic Climate Change and Its Impacts on the Ecology of the North Atlantic. *Ecology,* 89: 24-38.

Greve W, Reiners F, Nast J and Hoffmann S. 2004. Helgoland Roads Meso- and Macrozooplankton Time-Series 1974 to 2004: Lessons from 30 Years of Single Spot, High Frequency Sampling at the Only Off-Shore Island of the North Sea. *Helgoland Marine Research,* 58: 274-288.

Griffiths CL and Branch GM. 1997. The Exploitation of Coastal Invertebrates and Seaweeds in South Africa: Historical Trends, Ecological Impacts and Implications for Management. *Transactions of the Royal Society of South Africa,* 52: 121-148.

Griffiths CL, Robinson TB, Lange L and Mead A. 2010. Marine Biodiversity in South Africa: An Evaluation of Current States of Knowledge. *PLoS One,* 5: e12008.

Guerra MT and Gaudêncio MJ. 1986. Aspects of the Ecology of *Patella* spp. On the Portuguese Coast. *Hydrobiologia,* 142: 57-69.

Guidetti P and Sala E. 2007. Community-Wide Effects of Marine Reserves in the Mediterranean Sea. *Marine Ecology Progress Series,* 335: 43-56.

Guiry MD and Guiry GM. 2015. Algaebase. *World-wide electronic publication* [Online]. Available: Algaebase taxon LSID: urn:lsid:algaebase.org:taxname:99530 [Accessed September 2015].

Hallegraeff GM. 2010. Ocean Climate Change, Phytoplankton Community Responses, and Harmful Algal Blooms: A Formidable Predictive Challenge. *Journal of Phycology,* 46: 220-235.

Halpin PM, Menge BA and Hofmann GE. 2004. Experimental Demonstration of Plasticity in the Heat Shock Response of the Intertidal Mussel *Mytilus californianus*. *Marine Ecology Progress Series,* 276: 137-145.

Harley CDG and Helmuth B. 2003. Local- and Regional-Scale Effects of Wave Exposure, Thermal Stress, and Absolute Versus Effective Shore Level on Patterns of Intertidal Zonation. *Limnology and Oceanography,* 48: 1498-1508.

Harley CDG, Randall Hughes A, Hultgren KM, Miner BG, Sorte CJ, Thornber CS, Rodriguez LF, Tomanek L and Williams SL. 2006. The Impacts of Climate Change in Coastal Marine Systems. *Ecology Letters,* 9: 228-241.

Hartnoll RG and Hawkins SJ. 1985. Patchiness and Fluctuations on Moderately Exposed Rocky Shores. *Ophelia,* 24: 53-63.

Harvell CD, Mitchell CE, Ward JR, Altizer S, Dobson AP, Ostfeld RS and Samuel MD. 2002. Climate Warming and Disease Risks for Terrestrial and Marine Biota. *Science,* 296: 2158-2162.

Hatton H. 1938. Essais De Bionomie Explicative Sur Quelques Especes Intercotidales D'algues Et D'animaux. *Annales de l'Institut Oceanographique Monaco,* 17: 241-348.

Hawkins SJ. 1981. The Influence of Season and Barnacles on the Algal Colonization of *Patella vulgata* Exclusion Areas. *Journal of the Marine Biological Association of the United Kingdom,* 61: 1-15.

Hawkins SJ. 1983. Interaction of *Patella* and Macroalgae with Settling *Semibalanus balanoides* (L.). *Journal of Experimental Marine Biology and Ecology,* 71: 55-72.

Hawkins SJ, Allen JR and Bray S. 1999. Restoration of Temperate Marine and Coastal Ecosystems: Nudging Nature. *Aquatic Conservation: Marine and Freshwater Ecosystems,* 9: 23-46.

Hawkins SJ, Burnay LP, Neto AI, Tristão Da Cunha R and Frias Martins AM. 1990a. A Description of the Zonation Patterns of Molluscs and Other Important Biota on the South Coast of São Miguel, Azores. *Acoreana,* Supplement: 21-38.

Hawkins SJ, Côrte-Real HBSM, Martins HR, Santos RS and Frias Martins AM. 1990b. A Note on the Identity of *Patella* in the Azores. *Acoreana,* Supplement: 167-173.

Hawkins SJ, Côrte-Real HBSM, Pannacciulli FG, Weber LC and Bishop JDD. 2000. Thoughts on the Ecology and Evolution of the Intertidal Biota of the Azores and Other Atlantic Islands. *Hydrobiologia,* 440: 3-17.

Hawkins SJ, Firth LB, Mchugh M, Poloczanska ES, Herbert RJH, Burrows MT, Kendall MA, Moore PJ, Thompson RC, Jenkins SR, Sims DW, Genner MJ and Mieszkowska N. 2013a. Data Rescue and Re-Use: Recycling Old Information to Address New Policy Concerns. *Marine Policy,* 42: 91-98.

Hawkins SJ and Harkin E. 1985. Preliminary Canopy Removal Experiments in Algal Dominated Communities Low on the Shore and in the Shallow Subtidal on the Isle of Man. *Botanica Marina,* 28: 223-230.

Hawkins SJ and Hartnoll RG. 1980. A Study of the Small-Scale Relationship between Species Number and Area on a Rocky Shore. *Estuarine and Coastal Marine Science,* 10: 201-214.

Hawkins SJ and Hartnoll RG. 1982. Settlement Patterns of *Semibalanus balanoides* (L.) in the Isle of Man (1977-1981). *Journal of Experimental Marine Biology and Ecology,* 62: 271-283.

Hawkins SJ and Hartnoll RG. 1983a. Changes in a Rocky Shore Community: An Evaluation of Monitoring. *Marine Environmental Research,* 9: 131-181.

Hawkins SJ and Hartnoll RG. 1983b. Grazing of Intertidal Algae by Marine Invertebrates. *Oceanography and Marine Biology: An Annual Review,* 21: 195-282.

Hawkins SJ and Hartnoll RG. 1985. Factors Determining the Upper Limits of Intertidal Canopy-Forming Algae. *Marine Ecology Progress Series,* 20: 265-271.

Hawkins SJ and Jones HD. 1992. *Marine Field Course Guide: (1) Rocky Shores.* Immel Publisher, London, UK.

Hawkins SJ, Mieszkowska N, Firth LB, Bohn K, Burrows MT, MacLean MA, Thompson RC, Chan BKK, Little C and Williams GA. 2015. Looking Backwards to Look Forwards: The Role of Natural History in Temperate Reef Ecology. *Marine and Freshwater Research,* 10.1071/MF14413.

Hawkins SJ, Moore PJ, Burrows MT, Poloczanska E, Mieszkowska N, Herbert RJH, Jenkins SR, Thompson RC, Genner MJ and Southward AJ. 2008. Complex Interactions in a Rapidly Changing World: Responses of Rocky Shore Communities to Recent Climate Change. *Climate Research,* 37: 123-133.

Hawkins SJ, Southward AJ and Genner MJ. 2003. Detection of Environmental Change in a Marine Ecosystem - Evidence from the Western English Channel. *Science of The Total Environment,* 310: 245-256.

Hawkins SJ, Sugden HE, Mieszkowska N, Moore PJ, Poloczanska E, Leaper R, Herbert RJH, Genner MJ, Moschella PS, Thompson RC, Jenkins SR, Southward AJ and Burrows MT. 2009. Consequences of Climate-Driven Biodiversity Changes for Ecosystem Functioning of North European Rocky Shores. *Marine Ecology Progress Series,* 396: 245-259.

Hawkins SJ, Vale M, Firth LB, Burrows MT, Mieszkowska N and Frost M. 2013b. Sustained Observation of Marine Biodiversity and Ecosystems. *Oceanography,* 1: 1.

Hawkins SJ, Watson DC, Hill AS, Harding SP, Kyriakides MA, Hutchinson S and Norton TA. 1989. A Comparison of Feeding Mechanisms in Microphagous, Herbivous, Intertidal, Prosobranchs in Relation to Resource Partitioning. *Journal of Molluscan Studies,* 55: 151-165.

Hays GC, Richardson AJ and Robinson C. 2005. Climate Change and Marine Plankton. *Trends in Ecology and Evolution,* 20: 337-344.

Hegerl GC, Jones PD and Barnett TP. 2001. Effect of Observational Sampling Error on the Detection of Anthropogenic Climate Change. *Journal of Climate,* 14: 198-207.

Heip C, Barange M, Danovaro R, Gehlen M, Grehan A, Meysman F, Oguz T, Papathanassiou V, Philippart C, She J, Tréguer P, Warren R, Wassmann P, Weaver P and Yu R. 2011. *CLAMER/Marine Board Special Report - Synthesis of European Research on the Effects of Climate Change on Marine Environments*.

Heip C, Hummel H, Van Avesaath P, Appeltans W, Arvanitidis C, Aspden R, Austen M, Boero F, Bouma TJ, Boxshall G, Buchholz F, Crowe T, Delaney A, Deprez T, Emblow C, Feral JP, Gasol JM, Gooday A, Harder J, Ianora A, Kraberg A, MacKenzie B, Ojaveer H, Paterson D, Rumohr H, Schiedek D, Sokolowski A, Somerfield P, Sousa Pinto I, Vincx M, Węsławski JM and Nash R. 2009. *MARBEF: Marine Biodiversity and Ecosystem Functioning*. Printbase, Dublin, Ireland.

Hellmann JJ, Byers JE, Bierwagen BG and Dukes JS. 2008. Five Potential Consequences of Climate Change for Invasive Species. *Conservation Biology,* 22: 534-543.

Helmuth B. 1998. Intertidal Mussel Microclimates: Predicting the Body Temperature of a Sessile Invertebrate. *Ecological Monographs,* 68: 29-52.

Helmuth B. 2002. How Do We Measure the Environment? Linking Intertidal Thermal Physiology and Ecology through Biophysics. *Integrative and Comparative Biology,* 42: 837-845.

Helmuth B, Broitman BR, Blanchette CA, Gilman S, Halpin PM, Harley CDG, O'Donnell MJ, Hofmann GE, Menge B and Strickland D. 2006a. Mosaic Patterns of Thermal Stress in the Rocky Intertidal Zone: Implications for Climate Change. *Ecological Monographs,* 76: 461-479.

Helmuth B, Broitman BR, Yamane L, Gilman SE, Mach K, Mislan KAS and Denny MW. 2010. Organismal Climatology: Analyzing Environmental Variability at Scales Relevant to Physiological Stress. *Journal of Experimental Biology,* 213: 995-1003.

Helmuth B, Harley CDG, Halpin PM, O'Donnell M, Hofmann GE and Blanchette CA. 2002. Climate Change and Latitudinal Patterns of Intertidal Thermal Stress. *Science,* 298: 1015-1017.

Helmuth B and Hofmann GE. 2001. Microhabitats, Thermal Heterogeneity and Patterns of Physiological Stress in the Rocky Intertidal Zone. *The Biological Bulletin,* 201: 374-384.

Helmuth B, Mieszkowska N, Moore P and Hawkins SJ. 2006b. Living on the Edge of Two Changing Worlds: Forecasting the Responses of Rocky Intertidal Ecosystems to Climate Change. *Annual Review of Ecology, Evolution, and Systematics,* 37: 373-404.

Helmuth B, Yamane L, Lalwani S, Matzelle A, Tockstein A and Gao N. 2011. Hidden Signals of Climate Change in Intertidal Ecosystems: What (Not) to Expect When You Are Expecting. *Journal of Experimental Marine Biology and Ecology,* 400: 191-199.

Henderson PA. 2007. Discrete and Continuous Change in the Fish Community of the Bristol Channel in Response to Climate Change. *Journal of the Marine Biological Association of the United Kingdom,* 87: 589-598.

Henderson PA and Seaby RM. 2005. The Role of Climate in Determining the Temporal Variation in Abundance, Recruitment and Growth of Sole *Solea solea* in the Bristol Channel. *Journal of the Marine Biological Association of the United Kingdom,* 85: 197-204.

Henderson PA, Seaby RMH and Somes JR. 2011. Community Level Response to Climate Change: The Long-Term Study of the Fish and Crustacean Community of the Bristol Channel. *Journal of Experimental Marine Biology and Ecology,* 400: 78-89.

Henderson SJ and Whittaker RJ. 2003. *Islands*. eLS.

Herbert RJ, Hawkins SJ, Sheader M and Southward AJ. 2003. Range Extension and Reproduction of the Barnacle *Balanus perforatus* in the Eastern English Channel. *Journal of the Marine Biological Association of the United Kingdom,* 83: 73-82.

Herbert RJH, Southward AJ, Sheader M and Hawkins SJ. 2007. Influence of Recruitment and Temperature on Distribution of Intertidal Barnacles in the English Channel. *Journal of the Marine Biological Association of the United Kingdom,* 87: 487-499.

Hiddink JG, Burrows MT and Molinos JG. 2015. Temperature Tracking by North Sea Benthic Invertebrates in Response to Climate Change. *Global Change Biology,* 21: 117-129.

Hiddink JG and Ter Hofstede R. 2008. Climate Induced Increases in Species Richness of Marine Fishes. *Global Change Biology,* 14: 453-460.

Hijmans RJ and Graham CH. 2006. The Ability of Climate Envelope Models to Predict the Effect of Climate Change on Species Distributions. *Global Change Biology,* 12: 2272-2281.

Hill AS, Veale LO, Pennington D, Whyte SG, Brand AR and Hartnoll RG. 1999. Changes in Irish Sea Benthos: Possible Effects of 40 Years of Dredging. *Estuarine, Coastal and Shelf Science,* 48: 739-750.

Hinz H, Prieto V and Kaiser M. 2009. Trawl Disturbance on Benthic Communities: Chronic Effects and Experimental Predictions. *Ecological Applications,* 19: 761-773.

Hiscock K, Southward AJ, Titley I and Hawkins SJ. 2004. Effect of Changing Temperature on Benthic Marine Life in Britain and Ireland. *Aquatic Conservation: Marine and Freshwater Ecosystems,* 14: 333-362.

Hockey PAR and Bosman AL. 1986. Man as an Intertidal Predator in Transkei: Disturbance, Community Convergence and Management of a Natural Food Resource. *Oikos*: 46, 3-14.

Hoegh-Guldberg O and Bruno JF. 2010. The Impact of Climate Change on the World's Marine Ecosystems. *Science,* 328: 1523-1528.

Hoegh-Guldberg O, Mumby PJ, Hooten AJ, Steneck RS, Greenfield P, Gomez E, Harvell CD, Sale PF, Edwards AJ, Caldeira K, Knowlton N, Eakin CM, Iglesias-Prieto R, Muthiga N, Bradbury RH, Dubi A and Hatziolos ME. 2007. Coral Reefs under Rapid Climate Change and Ocean Acidification. *Science,* 318: 1737.

Hofmann GE and Todgham AE. 2010. Living in the Now: Physiological Mechanisms to Tolerate a Rapidly Changing Environment. *Annual Review of Physiology,* 72: 127-145.

Holme NA. 1961. The Bottom Fauna of the English Channel. *Journal of the Marine Biological Association of the United Kingdom,* 41: 397-461.

Holme NA. 1983. Fluctuations in the Benthos of the Western English Channel. *Proceedings of the 17th European Marine Biology Symposium Oceanologia Acta*. pp. 121-124.

Holme NA. 1984. Fluctuations of *Ophiothrix Fragilis* in the Western English Channel. *Journal of the Marine Biological Association of the United Kingdom,* 64: 351-378.

Holmes S, Walker G and Vandermeer J. 2005. Barnacles, Limpets and Periwinkles: The Effects of Direct and Indirect Interactions on Cyprid Settlement and Success. *Journal of Sea Research,* 53: 181-204.

Houghton RA. 2007. Balancing the Global Carbon Budget. *Annual Review of Earth and Planetary Sciences,* 35: 313-347.

Huggett J and Griffiths CL. 1986. Some Relationships between Elevation, Physicochemical Variables and Biota of Intertidal Rock Pools. *Marine Ecology Progress Series,* 29: 189-197.

Hughes MG and Heap AD. 2009. National-Scale Wave Energy Resource Assessment for Australia. *Renewable Energy,* 35: 1783-1791.

Hulme M, Jenkins GJ, Lu X, Turnpenny JR, Mitchell TD, Jones RG, Lowe J, Murphey JM, Hassel D, Boorman P, McDonald R and Hill D. 2002. *Climate Change Scenarios for the United Kingdom: The UKCIP02 Scientific Report*. Tyndall Centre for Climate Change Research.

Hurrell JW. 1995. Decadal Trends in the North Atlantic Oscillation: Regional Temperatures and Precipitation. *Science, New Series,* 269: 676-679.

Hurrell JW and Deser C. 2009. North Atlantic Climate Variability: The Role of the North Atlantic Oscillation. *Journal of Marine Systems,* 78: 28-41.

Hurrell JW, Kushnir Y and Visbeck M. 2001. The North Atlantic Oscillation. *Science,* 291: 603-605.

Hutchins LW. 1947. The Bases for Temperature Zonation in Geographical Distribution. *Ecological Monographs,* 17: 325-335.

IDAG, The International AD HOC Detection and Attribution Group. 2005. Detecting and Attributing External Influences on the Climate System: A Review of Recent Advances. *Jornal of Climate,* 18: 1291-1314.

IH, Instituto Hidrográfico. 2000. *Roteiro Da Costa De Portugal Arquipélago Dos Açores.* Ministério da Defesa Nacional - Marinha, Lisbon, Portugal.

Ingólfsson A and Hawkins SJ. 2008. Slow Recovery from Disturbance: A 20 Year Study of Ascophyllum Canopy Clearances. *Journal of the Marine Biological Association of the United Kingdom,* 88: 689-691.

IGEO, Instituto Geográfico Português. 2012. *I. Atlas De Portugal* [Online]. Available: www.igeo.pt [Accessed October 2012].

IPCC, Intergovernmental Panel on Climate Change. 2003. *Climate Change 2001: The Scientific Basis. Contribution of Working Group I to the Third Assessment Report of the Intergovernmental Panel on Climate Change.* Cambridge University Press, Cambridge, UK.

IPCC, Intergovernmental Panel on Climate Change. 2007. *Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change.* Cambridge University Press, Cambridge, UK.

IPCC, Intergovernmental Panel on Climate Change. 2013. *Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. In:* Stocker TF, Qin D, Plattner G-K, Tignor MMB, Allen SK, Boschung J, Nauels A, Xia Y, Bex V and Midgley PM (eds). Cambridge University Press, Cambridge, UK.

Janke K. 1990. Biological Interactions and Their Role in Community Structure in the Rocky Intertidal of Helgoland (German Bight, North Sea). *Helgolander Meeresunters,* 44: 219-263.

Jeffree CE and Jeffree EP. 1996. Redistribution of the Potential Geographical Ranges of Mistletoe and Colarado Beetle in Europe in Response to the Temperature Component of Climate Change. *Functional Ecology,* 10: 562-577.

Jenkins SR. 2005. Larval Habitat Selection, Not Larval Supply, Determines Settlement Patterns and Adult Distribution in Two Chthamalid Barnacles. *Journal of Animal Ecology,* 74: 893-904.

Jenkins SR, Coleman RA, Della Santina P, Hawkins SJ, Burrows MT and Hartnoll RG. 2005. Regional Scale Differences in the Determinism of Grazing Effects in the Rocky Intertidal. *Marine Ecology Progress Series,* 287: 77-86.

Jenkins SR and Hartnoll RG. 2001. Food Supply, Grazing Activity and Growth Rate in the Limpet *Patella vulgata* L.: A Comparison between Exposed and Sheltered Shores. *Journal of Experimental Marine Biology and Ecology,* 258: 123-139.

Jenkins SR and Hawkins SJ. 2003. Barnacle Larval Supply to Sheltered Rocky Shores: A Limiting Factor? *Hydrobiologia,* 503: 143-151.

Jenkins SR, Hawkins SJ and Norton TA. 1999a. Direct and Indirect Effects of a Macroalgal Canopy and Limpet Grazing in Structuring a Sheltered Inter-Tidal Communitv. *Marine Ecology Progress Series,* 188: 81-92.

Jenkins SR, Hawkins SJ and Norton TA. 1999b. Interaction between a Fucoid Canopy and Limpet Grazing in Structuring a Low Shore Intertidal Community. *Journal of Experimental Marine Biology and Ecology,* 233: 41-63.

Jenkins SR, Moore P, Burrows MT, Garbary DJ, Hawkins SJ, Ingólfsson A, Sebens KP, Snelgrove PVR, Wethey DS and Woodin SA. 2008. Comparative Ecology of North Atlantic Shores: Do Differences in Players Matter for Process? *Ecology,* 89: 3-23.

Jenkins SR, Norton TA and Hawkins SJ. 1999c. Settlement and Post-Settlement Interactions between *Semibalanus balanoides* (L.) (Crustacea: Cirripedia) and Three Species of Fucoid Canopy Algae. *Journal of Experimental Marine Biology and Ecology,* 236: 49-67.

Jenkins SR, Norton TA and Hawkins SJ. 2004. Long Term Efects of *Ascophyllum nodosum* Canopy Removal on Mid Shore Community Structure. *Journal of the Marine Biological Association of the United Kingdom,* 84: 4491-4496.

Jernakoff P. 1985. The Effect of Overgrowth by Algae on the Survival of the Intertidal Barnacle *Tesseropora rosea* Krauss. *Journal of Experimental Marine Biology and Ecology,* 94: 89-87.

Jeschke JM and Strayer DL. 2008. Usefulness of Bioclimatic Models for Studying Climate Change and Invasive Species. *Annals of the New York Academy of Sciences,* 1134: 1-24.

Jimenez H, Dumas P, Léopold M and Ferraris J. 2011. Invertebrate Harvesting on Tropical Urban Areas: Trends and Impact on Natural Populations (New Caledonia, South Pacific). *Fisheries Research,* 108: 195-204.

Johnson CR, Banks SC, Barrett NS, Cazassus F, Dunstan PK, Edgar GJ, Frusher SD, Gardner C, Haddon M, Helidoniotis F, Hill KL, Holbrook NJ, Hosie GW, Last PR, Ling SD, Melbourne-Thomas J, Miller K, Pecl GT, Richardson AJ, Ridgway KR, Rintoul SR, Ritz DA, Ross DJ, Sanderson JC, Shepherd SA, Slotwinski A, Swadling KM and Taw N. 2011. Climate Change Cascades: Shifts in Oceanography, Species' Ranges and Subtidal Marine Community Dynamics in Eastern Tasmania. *Journal of Experimental Marine Biology and Ecology,* 400: 17-32.

Johnson MP, Frost NJ, Mosley WJ, Roberts MF and Hawkins SJ. 2003. The Area-Independent Effects of Habitat Complexity on Biodiversity Vary between Regions. *Ecology Letters,* 6: 126-132.

Johnson MP, Hanley ME, Frost NJ, Mosley WJ and Hawkins SJ. 2008. The Persistent Spatial Patchiness of Limpet Grazing. *Journal of Experimental Marine Biology and Ecology,* 365: 136-141.

Johnson MP, Hawkins SJ, Hartnoll RG and Norton TA. 1998a. The Establishment of Fucoid Zonation on Algal-Dominated Rocky Shores: Hypotheses Derived from a Simulation Model. *Functional Ecology,* 12: 259-269.

Johnson MP, Hughes RN, Burrows MT and Hawkins SJ. 1998b. Beyond the Predation Halo: Small Scale Gradients in Barnacle Populations Affected by the Relative Refuge Value of Crevices. *Journal of Experimental Marine Biology and Ecology,* 231: 163-170.

Jones CG, Lawton JH and Shachak M. 1994. Organisms as Ecosystem Engineers. *Oikos,* 69: 373-386.

Jones NS. 1946. Browsing of *Patella*. *Nature,* 158: 557-558.

Jones NS. 1948. Observations and Experiments on the Biology of *Patella vulgata* at Port St. Mary, Isle of Man. *Proceedings and Transactions of the Liverpool Biological Society,* 56: 60-77.

Jones SJ, Mieszkowska N and Wethey DS. 2009. Linking Thermal Tolerances and Biogeography: *Mytilus edulis* (L.) at Its Southern Limit on the East Coast of the United States. *Biological Bulletin,* 217: 73-85.

Jonsson PR, Granhag L, Moschella PS, Åberg P, Hawkins SJ and Thompson RC. 2006. Interactions between Wave Action and Grazing Control the Distribution of Intertidal Macroalgae. *Ecology,* 87: 1169-1178.

Kalnay E, Kanamitsu M, Kistler R, Collins W, Deaven D, Gandin L, Iredell M, Saha S, White G, Woollen J, Zhu Y, Leetmaa A, Reynolds R, Chelliah M, Ebisuzaki W, Higgins W, Janowiak J, Mo KC, Ropelewski C, Wang J, Jenne R and Joseph D. 1996. The NCEP/NCAR 40-Year Reanalysis Project. *Bulletin of the American Meteorological Society,* 77: 437-471.

Kennelly SJ. 1987. Physical Disturbances in an Australian Kelp Community. II. Effects of Understory Species Due to Differences in Kelp Cover. *Marine Ecology Progress Series,* 40: 155-165.

Kerr RA. 2000. A North Atlantic Climate Pacemaker for the Centuries. *Science,* 288: 1984-1985.

Kirihara S, Nakamura T, Kon N, Fujita D and Notoya M. 2006. Recent Fluctuations in Distribution and Biomass of Cold and Warm Temperature Species of Laminarialean Algae at Cape Ohma, Northern Honshu, Japan. *Journal of Applied Phycology,* 18: 521-527.

Klein B and Siedler G. 1989. On the Origin of the Azores Current. *Journal of Geophysical Research,* 94: 6159-6168.

Kleypas JA and Langdon C. 2006. Coral Reefs and Changing Seawater Chemistry. *In:* Phinney JT, Hoegh-Guldberg O, Kleypas JA, Skirving W and Strong A (eds). *Coral Reefs and Climate Change: Scienece and Management.* AGU Monograph Series Coastal Estuarine Studies 61. American Geophysical Union, Washington, DC, USA.

Knight JR, Folland CK and Scaife AA. 2006. Climate Impacts of the Atlantic Multidecadal Oscillation. *Geophysical Research Letters,* 33: 1-4.

Kordas RL, Harley CDG and O'Connor MI. 2011. Community Ecology in a Warming World: The Influence of Temperature on Interspecific Interactions in Marine Systems. *Journal of Experimental Marine Biology and Ecology,* 400: 218-226.

Koufopanou V, Reid DG, Ridgway SA and Thomas RH. 1999. A Molecular Phylogeny of the Patellid Limpets (Gastropoda: Patellidae) and Its Implications for the Origins of Their Antitropical Distribution. *Molecular Phylogenetics and Evolution,* 11: 138-156.

Kroeker KJ, Kordas RL, Crim RN and Singh GG. 2010. Meta-Analysis Reveals Negative yet Variable Effects of Ocean Acidification on Marine Organisms. *Ecology Letters,* 13: 1419-1434.

Kurihara H. 2008. Effects of Co2-Driven Ocean Acidification on the Early Developmental Stages of Invertebrates. *Marine Ecology Progress Series,* 373: 275-284.

Kushnir Y, Cardone VJ, Greenwood JG and Cane MA. 1997. The Recent Increase in North Atlantic Wave Heights. *Journal of Climate,* 10: 2107-2113.

Lejeusne C, Chevaldonné P, Pergent-Martini C, Boudouresque CF and Pérez T. 2009. Climate Change Effects on a Miniature Ocean: The Highly Diverse, Highly Impacted Mediterranean Sea. *Trends in Ecology and Evolution,* 25: 250-260.

Leonard GH. 2000. Latitudinal Variation in Species Interactions: A Test in the New England Rocky Intertidal Zone. *Ecology,* 81: 1015-1030.

Levitan DR. 1988. Asynchronous Spawning and Aggregative Behaviour in the Sea Urchin *Diadema antillarum* (Philippi). *In:* Burke RD, *et al.* (eds). *Echinoderm Biology*. Balkema, Rotterdam.

Levitan DR. 1991. Influence of Body Size and Population Density on Fertilization Success and Reproductive Output in a Free-Spawning Invertebrate. *Biological Bulletin,* 181: 261-268.

Levitan DR and Petersen C. 1995. Sperm Limitation in the Sea. *Trends in Ecology and Evolution*, 10: 228-231.

Levitan DR and Sewell MA. 1998. Fertilization Success in Freespawning Marine Invertebrates: Review of the Evidence and Fisheries Implications. Canadian Special Publication of Fisheries and Aquatic Sciences. *In:* Jamieson GS and Campbell A (eds). *Proceedings of the North Pacific Symposium on Invertebrate Stock Assessment and Management.* NRC Research Press, Canada.

Lewis JR. 1964. *The Ecology of Rocky Shores.* English Universities Press, London, UK.

Lewis JR. 1968. Water Movements and Their Role in Rocky Shore Ecology. *Sarsia,* 34: 13-36.

Lewis JR. 1972. Problems and Approaches to Baseline Studies in Coastal Communities. *In:* Ruivo M (ed). *Marine Pollution and Sea Life.* Fishing News (Books) Ltd, London, UK.

Lewis JR. 1986. Latitudinal Trends in Reproduction, Recruitment and Population Characteristics of Some Rocky Littoral Molluscs and Cirripedes. *Hydrobiologia,* 142: 1-13.

Lewis JR. 1996. Coastal Benthos and Global Warming: Strategies and Problems. *Marine Pollution Bulletin,* 32: 698-700.

Lewis JR. 1999. Coastal Zone Conservation and Management: A Biological Indicator of Climatic Influences. *Aquatic Conservation: Marine and Freshwater Ecosystems,* 9: 401-405.

Lewis JR, Bowman RS, Kendall MA and Williamson P. 1982. Some Geographical Components in Population Dynamics: Possibilities and Realities in Some Littoral Species. *Netherlands Journal of Sea Research,* 16: 18-28.

Lilley SA and Schiel DR. 2006. Community Effects Following the Deletion of a Habitat-Forming Alga from Rocky Marine Shores. *Oecologia,* 148: 672-681.

Lima FP, Queiroz N, Ribeiro PA, Hawkins SJ and Santos AM. 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 FP, Ribeiro PA, Queiroz N, Hawkins SJ and Santos AM. 2007. Do Distributional Shifts of Northern and Southern Species of Algae Match the Warming Pattern? *Global Change Biology,* 13: 2592-2604.

Lima FP and Wethey DS. 2012. Three Decades of High-Resolution Coastal Sea Surface Temperatures Reveal More Than Warming. *Nature Communications,* 3: 704.

Lindegarth M and Gamfeldt L. 2005. Comparing Categorical and Continuous Ecological Analyses: Effects of "Wave Exposure" on Rocky Shores. *Ecology,* 86: 1346-1357.

Ling SD, Johnson CR, Frusher S and King CK. 2008. Reproductive Potential of a Marine Ecosystem Engineer at the Edge of a Newly Expanded Range. *Global Change Biology,* 14: 907-915.

Ling SD, Johnson CR, Ridgway K, Hobday AJ and Haddon M. 2009. Climate-Driven Range Extension of a Sea Urchin: Inferring Future Trends by Analysis of Recent Population Dynamics. *Global Change Biology,* 15: 719-731.

Little C. 1989. Factors Governing Patterns of Foraging Activity in Littoral Marine Herbivours Molluscs. *Journal of Molluscan Studies,* 55: 273-284.

Little C, Morritt D, Paterson DM, Stirling P and Williams GA. 1990. Preliminary Observations on Factors Affecting Foraging Activity in the Limpet *Patella vulgata*. *Journal of the Marine Biological Association of the United Kingdom,* 70: 181-195.

Little C, Williams GA and Trowbridge CD. 2010. *The Biology of Rocky Shores.* Oxford University Press, Oxford, UK.

Lockwood BL and Somero GN. 2011. Invasive and Native Blue Mussels (Genus *Mytilus*) on the California Coast: The Role of Physiology in a Biological Invasion. *Journal of Experimental Marine Biology and Ecology,* 400: 167-174.

Lowell RB. 1984. Desiccation of Intertidal Limpets: Effects of Shell Size, Fit to Substratum, and Shape. *Journal of Experimental Marine Biology and Ecology,* 77: 197-207.

Lowry R. 1998. *Vassarstats: Website for Statistical Computation* [Online]. Poughkeepsie, NY: Vassar College. Available: http://www.vassarstats.net/ [Accessed October 2012].

Lubchenco J. 1978. Plant Species Diversity in a Marine Intertidal Community: Importance of Herbivore Food Preference and Algal Competitive Abilities. *The American Naturalist,* 112: 23-39.

Lubchenco J and Gaines SD. 1981. A Unified Approach to Marine Plant-Herbivore Interactions. I. Populations and Communities. *Annual Review of Ecology and Systematics,* 12: 405-437.

Lubchenco J and Menge BA. 1978. Community Development and Persistence in a Low Rocky Intertidal Zone. *Ecological Monographs,* 48: 67-94.

Lüning K and Asmus R. 1991. Physical Characteristics of Littoral Ecosystems with Special Reference to Marine Plants. *In:* Mathieson AC and Nienhuis PH (eds). *Intertidal and Littoral Ecosystems (Ecosystems of the World 24).* Elsevier, Amsterdam, Netherlands.

Lüning K, Yarish C and Kirkman H. 1990. *Seaweeds: Their Environment, Biogeography, and Ecophysiology.* Wiley, New York, USA.

MacDonald RW, Harner T and Fyfe J. 2005. Recent Climate Change in the Arctic and Its Impact on Contaminant Pathways and Interpretation of Temporal Trend Data. *The Science of theTotal Environment,* 342: 5-86.

Machado LF and Barreiros JP. 2006. First Record of *Seriola fasciata* (Carangidae) in the Azores. A Northernmost Occurrence in the North-East Atlantic. *Cybium, International Journal of Ichthyology,* 30: 77-78.

Maddock L, Boalch GT and Harbour DS. 1981. Populations of Phytoplankton in the Western English Channel between 1964 and 1974. *Journal of the Marine Biological Association of the United Kingdom,* 61: 565-583.

Maddock L, Harbour DS and Boalch GT. 1989. Seasonal and Year-to-Year Changes in the Phytoplankton from the Plymouth Area, 1963-1986. *Journal of the Marine Biological Association of the United Kingdom,* 69: 229-244.

Mangel M and Clark CW. 1986. Towards a Unified Foraging Theory. *Ecology,* 67: 1127-1138.

Mangialajo L, Chiantore M and Cattaneo-Vietti R. 2008. Loss of Fucoid Algae Along a Gradient of Urbanisation and Structure of Benthic Assemblages. *Marine Ecology Progress Series,* 358: 63-74.

Martin D, Bertasi F, Colangelo MA, De Vries M, Frost M, Hawkins SJ, MacPherson E, Moschella PS, Satta MP, Thompson RC and Ceccherelli VU. 2005. Ecological Impact of Coastal Defence Structures on Sediment and Mobile Fauna: Evaluating and Forecasting Consequences of Unavoidable Modifications of Native Habitats. *Coastal Engineering,* 52: 1027-1051.

Martins GM. 2009. *Community Structure and Dynamics of the Azorean Rocky Intertidal: Exploitation of Keystone Species.* PhD thesis, University of Plymouth, Plymouth, UK.

Martins GM, Amaral AF, Wallenstein FM and Neto AI. 2009. Influence of a Breakwater on Nearby Rocky Intertidal Community Structure. *Marine Environmental Research,* 67: 237-245.

Martins GM, Faria J, Furtado M and Neto AI. 2014. Shells of *Patella aspera* as 'Islands' for Epibionts. *Journal of the Marine Biological Association of the United Kingdom,* 94: 1027-1032.

Martins GM, Jenkins SR, Hawkins SJ, Neto AI, Medeiros AR and Thompson RC. 2011. Illegal Harvesting Affects the Success of Fishing Closure Areas. *Journal of the Marine Biological Association of the United Kingdom,* 91: 929-937.

Martins GM, Jenkins SR, Hawkins SJ, Neto AI and Thompson RC. 2008a. Exploitation of Rocky Intertidal Grazers: Population Status and Potential Impacts on Community Structure and Functioning. *Aquatic Biology,* 3: 1-10.

Martins GM, Thompson RC, Hawkins SJ, Neto AI and Jenkins SR. 2008b. Rocky Intertidal Community Structure in Oceanic Islands: Scales of Spatial Variability. *Marine Ecology Progress Series,* 356: 15-24.

Martins GM, Thompson RC, Neto AI, Hawkins SJ and Jenkins SR. 2010. Exploitation of Intertidal Grazers as a Driver of Community Divergence. *Journal of Applied Ecology,* 47: 1282-1289.

Martins HR, Santos RS and Hawkins SJ. 1987a. *Estudos Sobre as Lapas Dos Açores. Exploração E Avaliação*. Governo Regional dos Açores, Horta, Azores, Portugal.

Martins HR, Santos RS and Hawkins SJ. 1987b. Exploitation of Limpets (*Patella* sp.) in the Azores with a Preliminary Analysis of the Stocks. *ICES International Council for the Exploration of the Sea*, K53: 1-13.

Martins HR, Santos RS, Hawkins SJ and Nash RDM. 1992. Expedition Azores 1989: Ecology and Taxonomy of the Fauna and Flora of the Marine Littoral. An Introduction. *Arquipélago. Life and Marine Science,* 10: 39-43.

Mathieson AC, Dawes CJ and Hehre EJ. 1998. Floristic and Zonation Studies of Seaweeds from Mount Desert Island, Maine: An Historical Comparison. *Rhodora,* 100: 333-379.

Mazaris AD, Kallimanis AS, Sgardelis SP and Pantis JD. 2008. Do Long-Term Changes in Sea Surface Temperature at the Breeding Areas Affect the Breeding Dates and Reproduction Performance of Mediterranean Loggerhead Turtles? Implications for Climate Change. *Journal of Experimental Marine Biology and Ecology,* 367: 219-226.

McCarthy MA. 1997. The Allee Effect, Finding Mates and Theoretical Models. *Ecological Modelling,* 103: 99-102.

McGinty N, Power AM and Johnson MP. 2011. Variation among North-East Atlantic Regions in the Responses of Zooplankton to Climate Change: Not All Areas Follow the Same Path. *Journal of Experimental Marine Biology and Ecology,* 400: 120-131.

McQuatters-Gollop A, Edwards M, Helaouët P, Johns DG, Owens NJP, Raitsos DE, Schroeder D, Skinner J and Stern RF. 2015. The Continuous Plankton Recorder Survey: How Can Long-Term Phytoplankton Datasets Contribute to the Assessment of Good Environmental Status? *Estuarine, Coastal and Shelf Science,* 162: 88-97.

Meehl GA, Stocker TF, Collins WD, Friedlingstein P, Gaye AT, Gregory JM, Kitoh A, Knutti R, Murphy JM, Noda A, Raper SCB, Watterson IG, Weaver AJ and Zhao Z-C. 2007. Global Climate Projections. *In:* Solomon S, Qin D, Manning M, Chen Z, Marquis M, Averyt KB, Tignor M and Miller HL (eds). *Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change.* Cambridge University Press, Cambridge, UK.

Menezes GM. 1991. *Aspectos Da Biologia E Ecologia De Patella ulyssiponensis aspera E P. candei candei (Mollusca, Gastropoda, Patellidae) Dos Açores. Potencial Da Sua Exploração.* BSc Final report, University of Lisbon, Lisbon, Portugal.

Menge BA. 1976. Organization of the New England Rocky Intertidal Community: Role of Predation, Competition, and Environmental Heterogeneity. *Ecological Monographs,* 46: 355-393.

Menge BA. 2000. Top-Down and Bottom-up Community Regulation in Marine Rocky Intertidal Habitats. *Journal of Experimental Marine Biology and Ecology,* 250: 257-289.

Menge BA, Gouhier TC, Freidenburg T and Lubchenco J. 2011. Linking Long-Term, Large-Scale Climatic and Environmental Variability to Patterns of Marine Invertebrate Recruitment: Toward Explaining "Unexplained" Variation. *Journal of Experimental Marine Biology and Ecology,* 400: 236-249.

Merzouk A and Johnson LE. 2011. Kelp Distribution in the Northwest Atlantic Ocean under a Changing Climate. *Journal of Experimental Marine Biology and Ecology,* 400: 90-98.

Mieszkowska N, Burrows MT, Pannacciulli FG and Hawkins SJ. 2014a. Multidecadal Signals within Co-Occurring Intertidal Barnacles *Semibalanus balanoides* and *Chthamalus* spp. Linked to the Atlantic Multidecadal Oscillation. *Journal of Marine Systems,* 133: 70-76.

Mieszkowska N, Hawkins SJ, Burrows MT and Kendall MA. 2007. Long-Term Changes in the Geographic Distribution and Population Structures of *Osilinus lineatus* (Gastropoda: Trochidae) in Britain and Ireland. *Journal of the Marine Biological Association of the United Kingdom,* 87: 537-545.

Mieszkowska N, Kendall MA, Hawkins SJ, Leaper R, Williamson P, Hardman-Mountford NJ and Southward AJ. 2006a. Changes in the Range of Some Common Rocky Shore Species in Britain - a Response to Climate Change? *Hydrobiologia,* 555: 241-251.

Mieszkowska N, Leaper R, Moore P, Kendall MA, Burrows MT, Lear D, Poloczanska E, Hiscock K, Moschella PS, Thompson RC, Herbert RJ, Laffoley D, Baxter J, Southward AJ and Hawkins SJ. 2006b. *Marine Biodiversity and Climate Change: Assessing and Predicting the Influence of Climatic Change Using Intertidal Rocky Shore Biota.* Scottish Natural Heritage Commissioned Report No. 202 (ROAME No. F01AA402), Scotland.

Mieszkowska N, Sugden H, Firth LB and Hawkins SJ. 2014b. The Role of Sustained Observations in Tracking Impacts of Environmental Change on Marine Biodiversity and Ecosystems. *Philosophical Transactions of the Royal Society A,* 372: 20130339.

Miller KM and Carefoot TH. 1989. The Role of Spatial and Size Refuges in the Interaction between Juvenile Barnacles and Grazing Limpets. *Journal of Experimental Marine Biology and Ecology,* 134: 157-174.

Milly PCD, Wetherald RT, Dunne KA and Delworth TL. 2002. Increasing Risk of Great Floods in a Changing Climate. *Nature,* 415: 514-517.

Moore HB. 1934. The Relation of Shell Growth to Environment in *Patella vulgata*. *Proceedings of the Malacological Society,* 21: 217-222.

Moore HB. 1972. Aspects of Stress in the Tropical Marine Environment. *Advances in Marine Biology,* 10: 217-269.

Moore P, Hawkins SJ and Thompson RC. 2007a. Role of Biological Habitat Amelioration in Altering the Relative Responses of Congeneric Species to Climate Change. *Marine Ecology Progress Series,* 334: 11-19.

Moore P, Thompson RC and Hawkins SJ. 2007b. Effects of Grazer Identity on the Probability of Escapes by a Canopy-Forming Macroalga. *Journal of Experimental Marine Biology and Ecology,* 344: 170-180.

Moore PJ, Thompson RC and Hawkins SJ. 2011. Phenological Changes in Intertidal Con-Specific Gastropods in Response to Climate Warming. *Global Change Biology,* 17: 709-719.

Moore SK, Trainer VL, Mantua NJ, Parker MS, Laws EA, Backer LC and Fleming LE. 2008. Impacts of Climate Variability and Future Climate Change on Harmful Algal Blooms and Human Health. *Environmental Health,* 7: S4.

Moreno CA. 2001. Community Patterns Generated by Human Harvesting on Chilean Shores: A Review. *Aquatic Conservation: Marine and Freshwater Ecosystems,* 11: 19-30.

Moreno CA, Sutherland JP and Jara HF. 1984. Man as a Predator in the Intertidal Zone of Southern Chile. *Oikos,* 42: 155-160.

Morris S and Taylor AC. 1983. Diurnal and Seasonal Variation in Physico-Chemical Conditions within Intertidal Rock Pools. *Estuarine, Coastal and Shelf Science,* 17: 339-355.

Morritt D, Leung KMY, Pirro MD, Yau C, Wai T-C and Williams GA. 2007. Responses of the Limpet, *Cellana grata* (Gould 1859), to Hypo-Osmotic Stress During Simulated Tropical, Monsoon Rains. *Journal of Experimental Marine Biology and Ecology,* 352: 78-88.

Morton B and Britton JC. 2000. The Origins of the Coastal and Marine Flora and Fauna of the Azores. *Oceanography and Marine Biology,* 38: 13-84.

Morton B, Britton JC and Frias Martins AM. 1998. *Coastal Ecology of the Açores.* Sociedade Afonso Chaves - Associação de Estudos Açoreanos, Ponta Delgada, Azores, Portugal.

Moschella PS, Abbiati M, Åberg P, Airoldi L, Anderson JM, Bacchiocchi F, Bulleri F, Dinesen GE, Frost M, Gacia E, Granhag L, Jonsson PR, Satta MP, Sundelöf A, Thompson RC and Hawkins SJ. 2005. Low-Crested Coastal Defence Structures as Artificial Habitats for Marine Life: Using Ecological Criteria in Design. *Coastal Engineering,* 52: 1053-1071.

Müller R, Laepple T, Bartsch I and Wiencke C. 2009. Impact of Oceanic Warming on the Distribution of Seaweeds in Polar and Cold-Temperate Waters. *Botanica Marina,* 52: 617-638.

Nakamura Y, Feary DA, Kanda M and Yamaoka K. 2013. Tropical Fishes Dominate Temperate Reef Fish Communities within Western Japan. *PLoS One,* 8: e81107.

Neto AI. 1997. *Studies on Algal Communities of São Miguel, Azores.* PhD thesis, University of Azores, Azores, Portugal.

Nicastro KR, Zardi GI, Teixeira S, Neiva J, Serrao EA and Pearson GA. 2013. Shift Happens: Trailing Edge Contraction Associated with Recent Warming Trends Threatens a Distinct Genetic Lineage in the Marine Macroalga *Fucus vesiculosus*. *BMC Biology,* 11: 6.

NOAA, National Oceanic and Atmospheric Administration. 2015. *NCEP/NCAR Reanalysis Monthly Means* [Online]. Available: http://www.esrl.noaa.gov/psd/data/timeseries/ 2015].

Oliva D and Castilla JC. 1986. The Effect of Human Exclusion on the Population Structure of Key-Hole Limpets *Fissurella crassa* and *F. limbata* on the Coast of Central Chile. *Marine Ecology,* 7: 201-2017.

Orr JC, Fabry VJ, Aumont O, Bopp L, Doney SC, Feely RA, Gnanadesikan A, Gruber N, Ishida A, Joos F, Key RM, Lindsay K, Maier-Reimer E, Matear R, Monfray P, Mouchet A, Najjar RG, Plattner G-K, Rodgers KB, Sabine CL, Sarmiento JL, Schlitzer R, Slater RD, Totterdell IJ, Weirig M-F, Yamanaka Y and Yool A. 2005. Anthropogenic Ocean Acidification over the Twenty-first Century and Its Impact on Calcifying Organisms. *Nature,* 437: 681-686.

Orton JH. 1929. On the Occurrence of *Echinus esculentus* on the Foreshore in the British Isles. *Journal of the Marine Biological Association of the United Kingdom,* 16: 289-296.

Orton JH, Southward AJ and Dodd JM. 1956. Studies in the Biology of Limpets II. The Breeding of *Patella vulgata* in Britain. *Journal of the Marine Biological Association of the United Kingdom,* 35: 149-176.

Ottersen G, Planque B, Belgrano A, Post E, Reid PC and Stenseth NC. 2001. Ecological Effects of the North Atlantic Oscillation. *Oecologia,* 128: 1-14.

Paeth H, Hense A, Glowienka-Hense R, Voss R and Cubasch U. 1999. The North Atlantic Oscillation as an Indicator for Greenhouse-Gas Induced Regional Climate Change. *Climate Dynamics,* 15: 953-960.

Paine RT. 1966. Food Web Complexity and Species Diversity. *The American Naturalist,* 100: 65-75.

Paine RT. 1969. The *Pisaster-Tegula* Interaction: Prey Patches, Predator Food Preference, and Intertidal Community Structure. *Ecology,* 50: 950-961.

Paine RT. 1976. Size-Limited Predation: An Observational and Experimental Approach with the *Mytilus-Pisaster* Interaction. *Ecology,* 57: 858-873.

Paine RT. 1994. *Marine Rocky Shores and Community Ecology: An Experimentalist's Perspective*. Ecology Institute, Oldendorf/Luhe, Germany.

Parker RO, Dixon RL. 1998. Changes in a North Carolina Reef Fish Community after 15 Years of Intense Fishing: Global Warming Implications. *Transactions of the AmericanFisheries Society,* 127: 908-920.

Parmesan C. 1996. Climate and Species' Range. *Nature,* 382: 765-766.

Parmesan C. 2006. Ecological and Evolutionary Responses to Recent Climate Change. *Annual Review of Ecology, Evolution, and Systematics,* 37: 637-669.

Parmesan C. 2007. Influences of Species, Latitudes and Methodologies on Estimates of Phenological Response to Global Warming. *Global Change Biology,* 13: 1860-1872.

Parmesan C, Ryrholm N, Stefanescu C, Hill JK, Thomas CD, Descimon H, Huntley B, Kaila L, Kullberg J, Tammaru T, Tennent WJ, Thomas JA and Warren M. 1999. Poleward Shifts in Geographical Ranges of Butterfly Species Associated with Regional Warming. *Nature,* 399: 579-583.

Parmesan C and Yohe G. 2003. A Globally Coherent Fingerprint of Climate Change Impacts across Natural Systems. *Nature,* 421: 37-42.

Parry ML, Canziani OF, Palutikof JP, Van Der Linden PJ and Hanson CE. 2007. *Climate Change 2007: Impacts, Adaptation and Vulnerability. Contribution of Working Group II to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press, Cambridge, UK.

Pearce-Higgins JW, Dennis P, Whittingham MJ and Yalden DW. 2010. Impacts of Climate on Prey Abundance Account for Fluctuations in a Population of a Northern Wader at the Southern Edge of Its Range. *Global Change Biology,* 16: 12-23.

Pearson RG and Dawson TP. 2003. Predicting the Impacts of Climate Change on the Distribution of Species: Are Bioclimate Envelope Models Useful? *Global Ecology and Biogeography,* 12: 361-371.

Pennington D, Veale LO and Hartnoll RG. 1998. Re-Analysis of an Historical Benthic Data Set from the Irish Sea. *Estuarine, Coastal and Shelf Science,* 46: 769-776.

Pereira HM, Leadley PW, Proenca V, Alkemade R, Scharlemann JP, Fernandez-Manjarres JF, Araujo MB, Balvanera P, Biggs R, Cheung WW, Chini L, Cooper HD, Gilman EL, Guenette S, Hurtt GC, Huntington HP, Mace GM, Oberdorff T, Revenga C, Rodrigues P, Scholes RJ, Sumaila UR and Walpole M. 2010. Scenarios for Global Biodiversity in the 21st Century. *Science,* 330: 1496-1501.

Perez KO, Carlson RL, Shulman MJ and Ellis JC. 2009. Why Are Intertidal Snails Rare in the Subtidal? Predation, Growth and the Vertical Distribution of *Littorina littorea* (L.) in the Gulf of Maine. *Journal of Experimental Marine Biology and Ecology,* 369: 79-86.

Perry AL, Low PJ, Ellis JR and Reynolds JD. 2005. Climate Change and Distribution Shifts in Marine Fishes. *Science,* 308: 1912-1915.

Petchey L, McPhearson PT, Casey TM and Morin PJ. 1999. Environmental Warming Alters Food-Web Structure and Ecosystem Function. *Nature,* 402: 69-72.

Peterson CH. 1982. Clam Predation by Whelks (*Busycon* spp.): Experimental Tests of the Importance of Prey Size, Prey Density, and Seagrass Cover. *Marine Biology,* 66: 159-170.

Petit J and Prudent G. 2008. *Climate Change and Biodiversity in the European Union Overseas Entities.* IUCN, Gland, Switzerland and Brussels, Belgium.

Philippart C. 2011. Marine Eutrophication. *In:* Heip C (ed). *Marine Board Special Report: Climate Change and Marine Ecosystem Research - Synthesis of European Research on the Effects of Climate Change on Marine Environments.*

Philippart CJM, Anadón R, Danovaro R, Dippner JW, Drinkwater KF, Hawkins SJ, Oguz T, O'Sullivan G and Reid PC. 2007. *Climate Change Impacts on the European Marine and Coastal Environment - Ecosystem Approach. Position Paper 9 of the Marine Board of the European Science Foundation.* Strasbourg, France.

Philippart CJM, Anadón R, Danovaro R, Dippner JW, Drinkwater KF, Hawkins SJ, Oguz T, O'Sullivan G and Reid PC. 2011. Impacts of Climate Change on European Marine Ecosystems: Observations, Expectations and Indicators. *Journal of Experimental Marine Biology and Ecology,* 400: 52-69.

Pinsky ML, Worm B, Fogarty MJ, Sarmiento JL and Levin SA. 2013. Marine Taxa Track Local Climate Velocities. *Science,* 341: 1239.

Poloczanska ES, Brown CJ, Sydeman WJ, Kiessling W, Schoeman DS, Moore PJ, Brander K, Bruno JF, Buckley LB, Burrows MT, Duarte CM, Halpern BS, Holding J, Kappel CV, O'Connor MI, Pandolfi JM, Parmesan C, Schwing F, Thompson SA and Richardson AJ. 2013. Global Imprint of Climate Change on Marine Life. *Nature Climate Change,* 3: 919-925.

Poloczanska ES, Hawkins SJ, Southward AJ and Burrows MT. 2008. Modeling the Response of Populations of Competing Species to Climate Change. *Ecology,* 89: 3138-3149.

Poloczanska ES, Hoegh-Guldberg O, Cheung W, Pörtner HO and Burrows M. 2014. Cross-Chapter Box on Observed Global Responses of Marine Biogeography, Abundance, and Phenology to Climate Change. *Climate Change 2014: Impacts, Adaptation, and Vulnerability. Part A: Global and Sectoral Aspects. Contribution of Working Group Iii to the Fifth Assessment Report of the Intergovermental Panel on Climate Change.* Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA.

Poloczanska ES, Smith S, Fauconnet L, Healy J, Tibbetts IR, Burrows MT and Richardson AJ. 2011. Little Change in the Distribution of Rocky Shore Faunal Communities on the Australian East Coast after 50 Years of Rapid Warming. *Journal of Experimental Marine Biology and Ecology,* 400: 145-154.

Porter WP and Gates DM. 1969. Thermodynamic Equilibria of Animals with Environment. *Ecological Monographs,* 39: 227-244.

Pörtner HO and Farrell AP. 2008. Physiology and Climate Change. *Science,* 322: 690-692.

Power M and Attrill MJ. 2002. Factors Affecting Long-Term Trends in the Estuarine Abundance of Pogge (*Agonus cataphractus*). *Estuarine, Coastal and Shelf Science,* 54: 941-949.

MarClim Project, Marine Biodiversity and Climate Change [Online]. Available: http://www.mba.ac.uk/marclim/.

Quinn GP and Keough MJ. 2002. *Experimental Design and Data Analysis for Biologists.* Cambridge University Press, Cambridge, UK.

Radach G, Berg J and Hagmeier E. 1990. Long-Term Changes of the Annual Cycles of Meteorological, Hydrographic, Nutrient and Phytoplankton Time Series at Helgoland and at Lv Elbe 1 in the German Bight. *Continental Shelf Research,* 10: 305-328.

Raffaelli D and Hawkins SJ. 1996. *Intertidal Ecology.* Chapman and Hall, London, UK.

Raimondi PT. 1990. Patterns, Mechanisms, Consequences of Variability in Settlement and Recruitment of an Intertidal Barnacle. *Ecological Monographs,* 60: 283-309.

Raven J, Caldeira K, Elderfield H, Hoegh-Guldberg O, Liss P, Riebesell U, Shepherd J, Turley C and Watson A. 2005. *Ocean Acidification Due to Increasing Atmospheric Carbon Dioxide.* Royal Society, London, UK.

Reed DC and Foster MS. 1984. The Effects of Canopy Shadings on Algal Recruitment and Growth in a Giant Kelp Forest. *Ecology,* 65: 937-948.

Reid PC, Johns DG, Edwards M, Starr M, Poulin M and Snoeijs P. 2007. A Biological Consequence of Reducing Arctic Ice Cover: Arrival of the Pacific Diatom *Neodenticula seminae* in the North Atlantic for the First Time in 800 000 Years. *Global Change Biology,* 13: 1910-1921.

Reid PC, Planque B and Edwards M. 1998. Is Observed Variability in the Long-Term Results of the Continuous Plankton Recorder Survey a Response to Climate Change? *Fisheries Oceanography,* 7: 282-288.

Ribeiro PA, Xavier R, Santos AM and Hawkins SJ. 2009. Reproductive Cycles of Four Species of *Patella* (Mollusca: Gastropoda) on the Northern and Central Portuguese Coast. *Journal of the Marine Biological Association of the United Kingdom,* 89: 1215-1221.

Ribera MA, Garreta AG, Gallardo T, Cormaci M, Furnari G and Giaccone G. 1992. Checklist of Mediterranean Seaweeds. 1. Fucophyceae (Warming, 1884). *Botanica Marina,* 35: 109-130.

Ridgway TM, Stewart BA and Branch GM. 1999. Limited Population Diferentiation in the Bearded Limpet *Patella barbara* (Gastropoda: Patellidae) Along the Coast of South Africa. *Journal of the Marine Biological Association of the United Kingdom,* 79: 639-651.

Riebesell U, Zondervan I, Rost B, Tortell PD, Zeebe RE and Morel FMM. 2000. Reduced Calcification of Marine Plankton in Response to Increased Atmospheric Co2. *Nature,* 407: 364-367.

Rivadeneira MM and Fernández M. 2005. Shifts in Southern Endpoints of Distribution in Rocky Intertidal Species Along the South-Eastern Pacific Coast. *Journal of Biogeography,* 32: 203-209.

Root TL, Price JT, Hall KR, Schneider SH, Rosenzweigk C and Pounds JA. 2003. Fingerprints of Global Warming on Wild Animals and Plants. *Nature,* 421: 57-60.

Roy K, Collins AG, Becker BJ, Begovic E and Engle JM. 2003. Anthropogenic Impacts and Historical Decline in Body Size of Rocky Intertidal Gastropods in Southern California. *Ecology Letters,* 6: 205-211.

Russell BD and Connell SD. 2010. Honing the Geoengineering Strategy. *Science,* 327: 144-145.

Russell FS. 1973. A Summary of Observations on the Occurrence of Planktonic Stages of Fish Off Plymouth 1924-1972. *Journal of the Marine Biological Association of the United Kingdom,* 53: 347 -355.

Russell FS, Southward AJ, Boalch GT and Butler EI. 1971. Changes in Biological Conditions in the English Channel Off Plymouth During the Last Half Century. *Nature,* 234: 468-470.

Sá-Pinto A, Branco M, Harris DJ and Alexandrino P. 2005. Phylogeny and Phylogeography of the Genus *Patella* Based on Mitochondrial DNA Sequence Data. *Journal of Experimental Marine Biology and Ecology,* 325: 95-110.

Sá-Pinto A, Branco M, Sayanda D and Alexandrino P. 2008. Patterns of Colonization, Evolution and Gene Flow in Species of the Genus *Patella* in the Macaronesian Islands. *Molecular Ecology,* 17: 519-532.

Sabine CL, Feely RA, Gruber N, Key RM, Lee K, Bullister JL, Wanninkhof R, Wong CS, Wallace DWR, Tilbrook B, Millero FJ, Peng T-H, Kozyr A, Ono T and Rios AF. 2004. The Oceanic Sink for Anthropogenic Co2. *Science,* 305: 367-371.

Sagarin RD, Barry JP, Gilman SE and Baxter CH. 1999. Climate-Related Change in an Intertidal Community over Short and Long Time Scales. *Ecological Monographs,* 69: 465-490.

Sagarin RD and Gaines SD. 2002. Geographical Abundance Distributions of Coastal Invertebrates: Using One-Dimensional Ranges to Test Biogeographic Hypotheses. *Journal of Biogeography,* 29: 985-997.

Saikkonen K, Taulavuori K, Hyvönen T, Gundel PE, Hamilton CE, Vänninen I, Nissinen A and Helander M. 2012. Climate Change - Driven Species' Range Shifts Filtered by Photoperiodism. *Nature Climate Change,* 2: 239-242.

Sala E, Ballesteros E, Dendrinos P, Di Franco A, Ferretti F, Foley D, Fraschetti S, Friedlander A, Garrabou J, Güçlüsoy H, Guidetti P, Halpern BS, Hereu B, Karamanlidis AA, Kizilkaya Z, MacPherson E, Mangialajo L, Mariani S, Micheli F, Pais A, Riser K, Rosenberg AA, Sales M, Selkoe KA, Starr R, Tomas F and Zabala M. 2012. The Structure of Mediterranean Rocky Reef Ecosystems across Environmental and Human Gradients, and Conservation Implications. *PLoS One,* 7: e32742.

Sala E, Kizilkaya Z, Yildirim D and Ballesteros E. 2011. Alien Marine Fishes Deplete Algal Biomass in the Eastern Mediterranean. *PLoS One,* 6: e17356.

Sala OE, Chapin IIIFS, Armesto JJ, Berlow E, Bloomfield J, Dirzo R, Huber-Sanwald E, Huenneke LF, Jackson RB, Kinzig A, Leemans R, Lodge DM, Mooney HA, Oesterheld M, Poff NL, Sykes MT, Walker BH, Walker M and Wall DH. 2000. Global Biodiversity Scenarios for the Year 2100. *Science,* 287: 1770-1774.

Sanford E. 2002. Water Temperature, Predation, and the Neglected Role of Physiological Rate Effects in Rocky Intertidal Communities. *Integrative and Comparative Biology,* 42: 881-891.

Santos FD, Valente MA, Miranda PMA, Aguiar A, Azevedo EB, Tomé AR and Coelho F. 2004. Climate Change Scenarios in the Azores and Madeira Islands. *World Resource Review,* 16: 473-491.

Santos RS, Delgado R and Ferraz R. 2010. *Background Document for Azorean Limpet Patella aspera.* Biodiversity Series, OSPAR Commision.

Santos RS, Hawkins SJ, Monteiro LR, Alves M and Isidro EJ. 1995a. Case Studies and Reviews: Marine Research, Resources and Conservation in the Azores. *Aquatic Conservation: Marine and Freshwater Ecosystems,* 5: 311-354.

Santos RS, Martins HR and Hawkins SJ. 1990. *Relatório De Estudos Sobre O Estado Das Populações De Lapas Do Archipélago Dos Açores E Da Ilha Da Madeira*. Governo Regional dos Açores, Horta, Azores, Portugal.

Santos RS, Nash RDM and Hawkins SJ. 1995b. Age, Growth and Sex Ratio of the Azorean Rock-Pool Blenny, Parablennius Sanguinolentus Parvicornis. *Journal of the Marine Biological Association of the United Kingdom,* 75: 751-754.

Sarmiento JL, Slater R, Barber R, Bopp L, Doney SC, Hirst AC, Kleypas J, Matear R, Mikolajewicz U, Monfray P, Soldatov V, Spall SA and Stouffer R. 2004. Response of Ocean Ecosystems to Climate Warming. *Global Biogeochemical Cycles,* 18: 1-23.

Schiel DR. 2011. Biogeographic Patterns and Long-Term Changes on New Zealand Coastal Reefs: Non-Trophic Cascades from Diffuse and Local Impacts. *Journal of Experimental Marine Biology and Ecology,* 400: 33-51.

Schiel DR and Lilley SA. 2011. Impacts and Negative Feedbacks in Community Recovery over Eight Years Following Removal of Habitat-Forming Macroalgae. *Journal of Experimental Marine Biology and Ecology,* 407: 108-115.

Schiel DR, Steinbeck JR and Foster MS. 2004. Ten Years of Induced Ocean Warming Causes Comprehensive Changes in Marine Benthic Communities. *Ecology,* 85: 1833-1839.

Schneider SH. 1993. Scenarios of Global Warming. *In:* Kareiva PM, Kingsolver JG and Huey RB (eds). *Biotic Interactions and Global Change.* Sinauer Associates, New York, USA.

Schneider SH. 2001. What Is 'Dangerous' Climate Change? *Nature,* 411: 17-19.

Schonbeck MW and Norton TA. 1978. Factors Controlling the Upper Limits of Fucoid Algae on the Shore. *Journal of Experimental Marine Biology and Ecology,* 31: 303-313.

Schonbeck MW and Norton TA. 1980. Factors Controlling the Lower Limits of Fucoid Algae on the Shore. *Journal of Experimental Marine Biology and Ecology,* 43: 131-150.

Schwartz MD. 2013. Introduction. *In:* Schwartz MD (ed). *Phenology: An Integrative Environmental Science.* Springer, Dordrecht, Netherlands.

Seabra R, Wethey DS, Santos AM and Lima FP. 2011. Side Matters: Microhabitat Influence on Intertidal Heat Stress over a Large Geographical Scale. *Journal of Experimental Marine Biology and Ecology,* 400: 200-208.

Seabra R, Wethey DS, Santos AM and Lima FP. 2015. Understanding Complex Biogeographic Responses to Climate Change. *Scientific Reports,* 5: 12930.

Segal E. 1956a. Adaptive Differences in Water-Holding Capacity in an Intertidal Gastropod. *Ecology,* 37: 174-178.

Segal E. 1956b. Microgeographic Variation as Thermal Acclimation in an Intertidal Mollusc. *The Biological Bulletin,* 111: 129-152.

Segal E and Dehnel PA. 1962. Osmotic Behavior in an Intertidal Limpet, *Acmaea limatula*. *The Biological Bulletin,* 122: 417-430.

Serralheiro A and Madeira J. 1993. Stratigraphy and Geochronology of Santa Maria Island (Azores). *Acoreana,* 7: 575-592.

Sexton JP, Mcintyre PJ, Angert AL and Rice KJ. 2009. Evolution and Ecology of Species Range Limits. *Annual Review of Ecology, Evolution, and Systematics,* 40: 415-436.

Siegfried WR, Hockey PAR and Branch GM. 1994. The Exploitation of Intertidal and Subtidal Biotic Resources of Rocky Shores in Chile and South Africa — an Overview. *In:* Siegfried WR (ed). *Rocky Shores: Exploitation in Chile and South Africa.* Springer Berlin Heidelberg.

Silva AA, Duarte PC, Giga A and Menezes G. 1998. First Record of the Spined Pygmy Shark, *Squaliolus laticaudus* (Smith and Radcliffe, 1912) in the Azores, Extending Its Distribution in the North-Eastern Atlantic. *Arquipelago. Life and Marine Sciences,* 16A: 57-62.

Silva ACF, Hawkins SJ, Boaventura DM, Brewster E and Thompson RC. 2010. The Use of the Intertidal Zone by Mobile Predators: The Influence of Wave Exposure, Tidal Phase and Elevation on Abundance and Diet. *Marine Ecology Progress Series,* 406: 197-210.

Simkanin C, Powers A, Myers A, McGrath D, Southward AJ, Mieszkowska N, Leaper R and O'Riordan R. 2005. Using Historical Data to Detect Temporal Changes in the Abundances of Intertidal Species on Irish Shores. *Journal of the Marine Biological Association of the United Kingdom,* 85: 1329-1340.

Simpson SD, Jennings S, Johnson MP, Blanchard JL, Schön PJ, Sims DW and Genner MJ. 2011. Continental Shelf-Wide Response of a Fish Assemblage to Rapid Warming of the Sea. *Current Biology,* 21: 1565-1570.

Sims DW, Genner MJ, Southward AJ and Hawkins SJ. 2001. Timing of Squid Migration Reflects North Atlantic Climate Variability. *Proceedings of the Royal Society B: Biological Sciences,* 268: 2607-2611.

Sims DW, Wearmouth VJ, Genner MJ, Southward AJ and Hawkins SJ. 2004. Low-Temperature-Driven Early Spawning Migration of a Temperate Marine Fish. *Journal of Animal Ecology,* 73: 333-341.

Smale D. 2008. Spatial Variability in the Distribution of Dominant Shallow-Water Benthos at Adelaide Island, Antarctica. *Journal of Experimental Marine Biology and Ecology,* 357: 140-148.

Smale DA and Barnes DKA. 2008. Likely Responses of the Antarctic Benthos to Climate-Related Changes in Physical Disturbance During the 21st Century, Based Primarily on Evidence from the West Antarctic Peninsula Region. *Ecography,* 31: 289-305.

Smale DA, Barnes DKA and Fraser KPP. 2007a. The Influence of Depth, Site Exposure and Season on the Intensity of Iceberg Scouring in Nearshore Antarctic Waters. *Polar Biology,* 30: 769-779.

Smale DA, Barnes DKA and Fraser KPP. 2007b. The Influence of Ice Scour on Benthic Communities at Three Contrasting Sites at Adelaide Island, Antarctica. *Austral Ecology,* 32: 878-888.

Smale DA, Burrows MT, Moore P, O'Connor N and Hawkins SJ. 2013. Threats and Knowledge Gaps for Ecosystem Services Provided by Kelps Forests: A North-East Atlantic Perspective. *Ecology and Evolution,* 3: 4016-4038.

Smale DA and Vance T. 2015. Climate-Driven Shifts in Species' Distributions May Exacerbate the Impacts of Storm Disturbances on North-East Atlantic Kelp Forests. *Marine and Freshwater Research,* published online.

Somero GN. 2002. Thermal Physiology and Vertical Zonation of Intertidal Animals: Optima, Limits, and Costs of Living. *Integrative and Comparative Biology,* 42: 780-789.

Somero GN. 2005. Linking Biogeography to Physiology: Evolutionary and Acclimatory Adjustments of Thermal Limits. *Frontiers in Zoology,* 2: 1.

Sorte CJB, Jones SJ and Miller LP. 2011. Geographic Variation in Temperature Tolerance as an Indicator of Potential Population Responses to Climate Change. *Journal of Experimental Marine Biology and Ecology,* 400: 209-217.

Sorte CJB, Williams SL and Carlton JT. 2010. Marine Range Shifts and Species Introductions: Comparative Spread Rates and Community Impacts. *Global Ecology and Biogeography,* 19: 303-316.

Southward AJ. 1958. The Zonation of Plants and Animals on Rocky Sea Shores. *Biological Reviews,* 33: 137-177.

Southward AJ. 1963. The Distribution of Some Plankton Animals in the English Channel and Approaches. Iii. Theories About Long-Term Biological Changes, Including Fish. *Journal of the Marine Biological Association of the United Kingdom,* 43: 1-29.

Southward AJ. 1964. *Limpet Grazing and the Control of Vegetation on Rocky Shores.* Blackwell, Oxford, UK.

Southward AJ. 1967. Recent Changes in Abundance of Intertidal Barnacles in South-West England: A Possible Effect of Climatic Deterioration. *Journal of the Marine Biological Association of the United Kingdom,* 47: 81-95.

Southward AJ. 1980. The Western English Channel - an Inconsistent Ecosystem? *Nature,* 285: 361-366.

Southward AJ. 1991. Forty Years of Changes in Species Composition and Population Density of Barnacles on Rocky Shore near Plymouth. *Journal of the Marine Biological Association of the United Kingdom,* 71: 495-513.

Southward AJ and Boalch GT. 1986. Aspects of Long Term Changes in the Ecosystem of the Western English Channel in Relation to Fish Populations. *In:* Wyatt T and Larraneta MG (eds). *International Symposium on Long Term Changes in Marine Fish Populations, 1986 Vigo*. Instituto Investigaciones Marinas.

Southward AJ, Boalch GT and Maddock L. 1988. Fluctuations in the Herring and Pilchard Fisheries of Devon and Cornwall Linked to Change in Climate since the 16th Century. *Journal of the Marine Biological Association of the United Kingdom,* 68: 423-445.

Southward AJ and Crisp DJ. 1954a. The Distribution of Certain Intertidal Animals around the Irish Coast. *Proceedings of the Royal Irish Academy. Section B: Biological, Geological and Chemical Science,* 57: 1-29.

Southward AJ and Crisp DJ. 1954b. Recent Changes in the Distribution of the Intertidal Barnacles *Chthamalus stellatus* Poli and B*alanus balanoides* L. In the British Isles. *Journal of Animal Ecology,* 23: 163-177.

Southward AJ and Crisp DJ. 1956. Fluctuations in the Distribution and Abundance of Intertidal Barnacles. *Journal of the Marine Biological Association of the United Kingdom,* 35: 211-229.

Southward AJ, Hawkins SJ and Burrows MT. 1995. Seventy Years' Observations of Changes in Distribution and Abundance of Zooplankton and Intertidal Organisms in the Western English Channel in Relation to Rising Sea Temperature. *Journal of Thermal Biology,* 20: 127-155.

Southward AJ, Langmead O, Hardman-Mountford NJ, Aiken J, Boalch GT, Dando PR, Genner MJ, Joint I, Kendall MA, Halliday NC, Harris RP, Leaper R, Mieszkowska N, Pingree RD, Richardson AJ, Sims DW, Smith T, Walne AW and Hawkins SJ 2005. Long-Term Oceanographic and Ecological Research in the Western English Channel. *Advances in Marine Biology,* 47: 1-105.

Southward AJ and Southward EC 1978. Recolonization of Rocky Shores in Cornwall after Use of Toxic Dispersants to Clean up the Torrey Canyon Spill. *Journal of the Fisheries Research Board of Canada,* 35: 682-705.

Stachowicz JJ, Terwin JR, Whitlatch RB and Osman RW. 2002. Linking Climate Change and Biological Invasions: Ocean Warming Facilitates Nonindigenous Species Invasions. *Proceedings of the National Academy of Sciences of the United States of America,* 99: 15497-15500.

Stachowicz JJ, Whitlatch RB and Osman RW. 1999. Species Diversity and Invasion Resistance in a Marine Ecosystem. *Science,* 286: 1577-1579.

Steneck RS and Dethier MN. 1994. A Functional Group Approach to the Structure of Algal-Dominated Communities. *Oikos,* 69: 476-498.

Steneck RS, Graham MH, Bourque BJ, Corbett D, Erlandson JM, Estes JA and Tegner MJ. 2002. Kelp Forest Ecosystems: Biodiversity, Stability, Resilience and Future. *Environmental Conservation,* 29: 436-459.

Stenseth NC, Mysterud A, Ottersen G, Hurrell JW, Chan KS and Lima M. 2002. Ecological Effects of Climate Fluctuations. *Science,* 297: 1292-1296.

Stephenson TA and Stephenson A. 1972. *Life between Tidemarks on Rocky Shores.* W.H.Freeman, San Francisco, USA.

Sueiro MC, Bortolus A and Schwindt E. 2011. Habitat Complexity and Community Composition: Relationships between Different Ecosystem Engineers and the Associated Macroinvertebrate Assemblages. *Helgoland Marine Research,* 65: 467-477.

Sugden HE, Underwood AJ and Hawkins SJ. 2009. The Aesthetic Value of Littoral Hard Substrata and Consideration of Ethical Frameworks for Their Investigation and Conservation. *In:* Wahl M (ed). *In Marine Hard Bottom Communities.* Springer-Verlag, Berlin, Germany.

Sundquist ET. 1993. The Global Carbon Dioxide Budget. *Science, New Series,* 259: 934-941.

Tett SFB, Jones GS, Stoot PA, Hill DC, Mitchell JFB, Allen MR, Ingram WJ, Johns TC, Johnson CE, Jones A, Roberts DL, Sexton DMH and Woodage MJ. 2002. Estimation of Natural and Anthropogenic Contributions to Twentieth Century Temperature Change. *Journal of Geophysical Research,* 107: 4306-4316.

Thom RM and Widdowson TB. 1978. A Resurvey of E. Yale Dawson's 42 Intertidal Algal Transects on the Southern California Mainland after 15 Years. *Bulletin of the Southern California Academy of Sciences,* 77: 1-13.

Thomas CD, Cameron A, Green RE, Bakkenes M, Beaumont LJ, Collingham YC, Erasmus BFN, Siqueira MF, Grainger A, Hannah L, Hughes L, Huntley B, Van Jaarsveld AS, Midgley GF, Miles L, Ortega-Huerta MA, Peterson AT, Phillips OL and Williams SE. 2004. Extinction Risk from Climate Change. *Nature,* 427: 145-148.

Thomas MLH. 1986. A Physically Derived Exposure Index for Marine Shorelines. *Ophelia,* 25: 1-13.

Thompson DW, Wallace JM, Kennedy JJ and Jones PD. 2010. An Abrupt Drop in Northern Hemisphere Sea Surface Temperature around 1970. *Nature,* 467: 444-447.

Thompson GB. 1979. Distribution and Population Dynamics of the Limpet *Patella aspera* (Lamarck) in Bantry Bay. *Journal of Experimental Marine Biology and Ecology,* 40: 115-135.

Thompson RC, Crowe TP and Hawkins SJ. 2002. Rocky Intertidal Communities: Past Environmental Changes, Present Status and Predictions for the Next 25 Years. *Environmental Conservation,* 29: 168-191.

Thompson RC, Norton TA and Hawkins SJ. 2004. Physical Stress and Biological Control Regulate the Producer-Consumer Balance in Intertidal Biofilms. *Ecology,* 85: 1372-1382.

Thompson RC, Robers MF, Norton TA and Hawkins SJ. 2000. Feast or Famine for Intertidal Grazing Molluscs: A Mismatch between Seasonal Variations in Grazing Intensity and the Abundance of Microbial Resources. *Hydrobiologia,* 440: 357-367.

Thompson RC, Wilson BJ, Tobin ML, Hill AS and Hawkins SJ. 1996. Biologically Generated Habitat Provision and Diversity of Rocky Shore Organisms at a Hierarchy of Spatial Scales. *Journal of Experimental Marine Biology and Ecology,* 202: 73-84.

Tittley I, Neto AI, Farnham WF and Parente MI. 2001. Additions to the Marine Algal (Seaweed) Flora of the Azores. *Botanica Marina,* 44: 215-220.

Trenberth KE, Dai A, Rasmussen RM and Parsons DB. 2003. The Changing Character of Precipitation. *Bulletin of the American Meteorological Society,* 84: 1205-1217.

Trenberth KE, Jones PD, Ambenje P, Bojariu R, Easterling D, Klein Tank A, Parker D, Rahimzadeh F, Renwick JA, Rusticucci M, Soden B and Zhai P. 2007. Observations: Surface and Atmospheric Climate Change. *In:* Solomon S, Quin D, Manning M, Chen Z, Marquis M, Averyt KB, Tignor M and Miller HL (eds). *Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change.* Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA.

Trenberth KE and Shea DJ. 2005. Relationships between Precipitation and Surface Temperature. *Geophysical Research Letters,* 32: 1-4.

Trenberth KE and Shea DJ. 2006. Atlantic Hurricanes and Natural Variability in 2005. *Geophysical Research Letters,* 33: 1-4.

Underwood AJ. 1980. The Effects of Grazing by Gastropods and Physical Factors on the Upper Limits of Distribution of Intertidal Macroalgae. *Oecologia,* 46: 201-213.

Underwood AJ. 1991. Beyond Baci: Experimental Designs for Detecting Human Environmental Impacts on Temporal Variations in Natural Populations. *Australian Journal of Marine and Freshwater Research,* 42: 569-587.

Underwood AJ. 1992. Beyond Baci: The Detection of Environmental Impact on Populations in the Real, but Variable, World. *Journal of Experimental Marine Biology and Ecology,* 161: 145-178.

Underwood AJ. 1994. On Beyond Baci: Sampling Designs That Might Reliably Detect Environmental Distrubances. *Ecological Applications,* 4: 3-15.

Underwood AJ and Jernakoff P. 1984. The Effects of Tidal Height, Wave-Exposure, Seasonality and Rocky-Pools on Grazing and the Distribution of Intertidal Macroalgae in New South Wales. *Journal of Experimental Marine Biology and Ecology,* 75: 71-96.

Vergés A, Steinberg PD, Hay ME, Poore AGB, Campbell AH, Ballesteros E, Heck KLJ, Booth DJ, Coleman MA, Feary DA, Figueira W, Langlois T, Marzinelli EM, Mizerek T, Mumby PJ, Nakamura Y, Roughan M, Sebille EV, Gupta AS, Smale DA, Tomas F, Wernberg T and Wilson SK. 2014a. The Tropicalization of Temperate Marine Ecosystems: Climate-Mediated Changes in Herbivory and Community Phase Shifts. *Proceedings of the Royal Society B: Biological Sciences,* 281: 20140846.

Vergés A, Tomas F, Cebrian E, Ballesteros E, Kizilkaya Z, Dendrinos P, Karamanlidis A, Spiegel D and Sala E. 2014b. Tropical Rabbitfish and the Deforestation of a Warming Temperate Sea. *Journal of Ecology,* 102: 1518-1527.

Vermeij GJ. 1973. Morphological Patterns in High-Intertidal Gastropods: Adaptive Strategies and Their Limitations. *Marine Biology,* 20: 319-346.

Vermeij GJ. 2005. Invasion as Expectation: A Historical Fact of Life. *In:* Sax DF, Stachowicz JJ and Gaines SD (eds). *Species Invasions: Insights into Ecology, Evolution, and Biogeography.* Sinauer Associates, Sunderland, USA.

Veron JEN. 2008. Mass Extinctions and Ocean Acidification: Biological Constraints on Geological Dilemmas. *Coral Reefs,* 27: 459-472.

Vogt H and Schramm W. 1991. Conspicuous Decline of *Fucus* in Kiel Bay (Western Baltic): What Are the Causes? *Marine Ecology Progress Series,* 69: 189-194.

Wallenstein FFMM, Neto AI, Álvaro NV and Tittley I. 2008. Subtidal Rocky Shore Communities of the Azores: Developing a Biotope Survey Method. *Journal of Coastal Research,* 24: 244-249.

Walther G-R, Post E, Convey P, Menzel A, Parmesan C, Beebee TJC, Fromentin J-M, Hoegh-Guldberg O and Bairlein F. 2002. Ecological Responses to Recent Climate Change. *Nature,* 416: 389-395.

Wang XL, Zwiers FW and Swail VR. 2004. North Atlantic Ocean Wave Climate Change Scenarios for the Twenty-First Century. *Journal of Climate,* 17: 2368-2383.

Watt CA and Scrosati RA. 2013. Bioengineer Effects on Understory Species Richness, Diversity, and Composition Change Along an Environmental Stress Gradient: Experimental and Mensurative Evidence. *Estuarine, Coastal and Shelf Science,* 123: 10-18.

Weber LI and Hawkins SJ. 2002. Evolution of the Limpet *Patella candei* D'Orbigny (Mollusca, Patellidae) in Atlantic Archipelagos: Human Intervention and Natural Processes. *Biological Journal of the Linnean Society,* 77: 341-353.

Weber LI and Hawkins SJ. 2005. *Patella aspera* and *P. ulyssiponensis*: Genetic Evidence of Speciation in the North-East Atlantic. *Marine Biology,* 147: 153-162.

Wentz FJ, Ricciardulli L, Hilburn K and Mears C. 2007. How Much More Rain Will Global Warming Bring? *Science,* 317: 233-235.

Wernberg T, Russell BD, Moore PJ, Ling SD, Smale DA, Campbell A, Coleman MA, Steinberg PD, Kendrick GA and Connell SD. 2011. Impacts of Climate Change in a Global Hotspot for Temperate Marine Biodiversity and Ocean Warming. *Journal of Experimental Marine Biology and Ecology,* 400: 7-16.

Wernberg T, Smale D and Thomsen MS. 2012. A Decade of Climate Change Experiments on Marine Organisms: Procedures, Patterns and Problems. *Global Change Biology,* 18: 1491-1498.

Wernberg T, Smale DA, Tuya F, Thomsen MS, Langlois TJ, Bettignies T, Bennett S and Rousseaux CS. 2013. An Extreme Climatic Event Alters Marine Ecosystem Structure in a Global Biodiversity Hotspot. *Nature Climate Change,* 3: 78-82.

Wethey DS. 2002. Biogeography, Competition, and Microclimate: The Barnacle *Chthamalus fragilis* in New England. *Integrative and Comparative Biology,* 42: 872-880.

Wethey DS and Woodin SA. 2008. Ecological Hindcasting of Biogeographic Responses to Climate Change in the European Intertidal Zone. *Hydrobiologia,* 606: 139-151.

Wethey DS, Woodin SA, Hilbish TJ, Jones SJ, Lima FP and Brannock PM. 2011. Response of Intertidal Populations to Climate: Effects of Extreme Events Versus Long Term Change. *Journal of Experimental Marine Biology and Ecology,* 400: 132-144.

Wikström SA and Kautsky L. 2007. Structure and Diversity of Invertebrate Communities in the Presence and Absence of Canopy-Forming *Fucus vesiculosus* in the Baltic Sea. *Estuarine, Coastal and Shelf Science,* 72: 168-176.

Williams GA. 1994. The Relationship between Shade and Molluscan Grazing in Structuring Communities on a Moderately-Exposed Tropical Rocky Shore *Journal of Experimental Marine Biology and Ecology,* 178: 79-95.

Williams GA and Morritt D. 1995. Habitat Partitioning and Thermal Tolerance in a Tropical Limpet, *Cellana grata Marine Ecology Progress Series,* 124: 89-103.

Williamson M. 1981. *Island Populations.* Oxford University Press, Oxford, UK.

Wiltshire KH, Kraberg A, Bartsch I, Boersma M, Franke H-D, Freund J, Gebühr C, Gerdts G, Stockmann K and Wichels A. 2010. Helgoland Roads, North Sea: 45 Years of Change. *Estuaries and Coasts,* 33: 295-310.

Wiltshire KH, Malzahn AM, Wirtz K, Greve W, Janisch S, Mangelsdorf P, Manly BFJ and Boersma M. 2008. Resilience of North Sea Phytoplankton Spring Bloom Dynamics: An Analysis of Long-Term Data at Helgoland Roads. *Limnology and Oceanography,* 53: 1294-1302.

Witman JD. 1987. Subtidal Coexistence: Storms, Grazing, Mutualism, and the Zonation of Kelps and Mussels. *Ecological Monographs,* 57: 167-187.

Wolcott TG. 1973. Physiological, Ecology and Intertidal Zonation in Limpets (*Acmaea*): A Critical Look at "Limiting Factors". *The Biological Bulletin,* 145: 389-422.

Wolf J and Woolf DK. 2006. Waves and Climate Change in the North-East Atlantic. *Geophysical Research Letters,* 33: 1-4.

Wolkovich EM, Cook BI, Allen JM, Crimmins TM, Betancourt JL, Travers SE, Pau S, Regetz J, Davies TJ, Kraft NJB, Ault TR, Bolmgren K, Mazer SJ, McCabe GJ, McGill BJ, Parmesan C, Salamin N, Schwartz MD and Cleland EE. 2012. Warming Experiments Underpredict Plant Phenological Responses to Climate Change. *Nature,* 485: 494-497.

Worm B, Barbier EB, Beaumont N, Duffy JE, Folke C, Halpern BS, Jackson JBC, Lotze HK, Micheli F, Palumbi SR, Sala E, Selkoe KA, Stachowicz JJ and Watson R. 2006. Impacts of Biodiversity Loss on Ocean Ecosystem Services. *Science,* 314: 787-790.

Wright JT, Williams SL and Dethier MN. 2004. No Zone Is Always Greener: Variation in the Performance of *Fucus gardneri* Embryos, Juveniles and Adults across Tidal Zone and Season. *Marine Biology,* 145: 1061-1073.

Yamane L and Gilman SE. 2009. Opposite Responses by an Intertidal Predator to Increasing Aquatic and Aerial Temperatures. *Marine Ecology Progress Series,* 393: 27-36.

Yesson C, Bush LE, Davies AJ, Maggs CA and Brodie J. 2015. Large Brown Seaweeds of the British Isles: Evidence of Changes in Abundance over Four Decades. *Estuarine, Coastal and Shelf Science,* 155: 167-175.

Young IR, Zieger S and Babanin AV. 2011. Global Trends in Wind Speed and Wave Height. *Science,* 332: 451-455.

Yund, PO. 2000. How Severe is Sperm Limitation in Natural Populations of Marine Free-Spawners? *Trends in Ecology and Evolution*, 15: 10-13.

Zacherl D, Gaines SD and Lonhart SI. 2003. The Limits to Biogeographical Distributions: Insights from the Northward Range Extension of the Marine Snail, *Kelletia kelletii* (Forbes, 1852). *Journal of Biogeography,* 30: 913-924.

Zardi GI, Nicastro KR, Canovas F, Costa JF, Serrao EA and Pearson GA. 2011. Adaptive Traits Are Maintained on Steep Selective Gradients Despite Gene Flow and Hybridization in the Intertidal Zone. *PLoS One,* 6: e19402.

Zardi GI, Nicastro KR, Serrao EA, Jacinto R, Monteiro CA and Pearson GA. 2015. Closer to the Rear Edge: Ecology and Genetic Diversity Down the Core-Edge Gradient of a Marine Macroalga. *Ecosphere,* 6: 23.

Zhang X, Zwiers FW and Stoot PA. 2006. Multimodel Multisignal Climate Change Detection at Regional Scale. *Journal of Climate,* 19: 4294-4307.

Zwiers FW. 2003. Toward Regional-Scale Climate Change Detection. *Journal of Climate,* 16: 793-797.