PhD in Aquatic Biosciences no. 10 (2013)

UNIVERSITY OF
NORDLAND

Alexander Jüterbock

"Climate change impact on the seaweed *Fucus serratus*, a key foundational species on North Atlantic rocky shores"

“Climate change impact on the seaweed *Fucus Serratus*, a key foundational species on North Atlantic rocky shores”

Alexander Jüterbock

A dissertation for the degree of
Philosophiae Doctor (PhD)

PhD in Aquatic Biosciences no.10 (2013)
Faculty of Biosciences and Aquaculture

PhD in Aquatic Biosciences no. 10 (2013)

Alexander Jüterbock
“Climate change impact on the seaweed *Fucus Serratus*, a key
foundational species on North Atlantic rocky shores”

ISBN: 978-82-93165-09-5

Print: Trykkeriet UiN

University of Nordland
N-8049 Bodø
Tel: +47 75 51 72 00
www.uin.no

Preface

This dissertation is submitted in partial fulfillment of the requirements for the degree of Philosophiae Doctor (PhD) at the Faculty of Biosciences and Aquaculture (FBA), University of Nordland (UiN, Bodø, Norway). The different studies compiled in this dissertation represent original research carried out over a period of three years, from 01.06.2010 to 31.08.2013, as part of the project "Ecological and evolutionary responses to global warming in the seaweed *Fucus serratus*, a key foundational species in the North Atlantic intertidal". The project was funded by the Research Council of Norway (HAVKYST project 196505, 203839, and 216484) to Professor Galice Hoarau.

The project team included the following members:

Alexander Jüterbock, MSc, UiN, PhD student
Galice Hoarau, Professor, UiN, primary supervisor
Jorge M.O. Fernandes, Professor, UiN, co-supervisor
Jeanine L. Olsen, Professor, University of Groningen, The Netherlands, co-supervisor

UNIVERSITETET I
NORDLAND

Alexander Jüterbock

Bodø, June 2013

Acknowledgements

First of all I would like to thank my Ph.D supervisors Galice Hoarau, Jorge Fernandes and Jeanine Olsen (University of Groningen, The Netherlands) for their guidance and support along this project. I am glad for the opportunity to do my Ph.D in the field of marine ecology and am very grateful for the clear structure of the project.

Galice, thank you for your sincere support over the last three years. I highly appreciate your effort in helping me building a network in the field of marine ecology. Thank you for giving me the opportunity to teach and supervise students, for your guidance in the experimental setups and for sharing your knowledge and experience in numerous discussions. I am very grateful for your guidance through the last and most difficult stage of my Ph.D with timely and very helpful advises. I will also not forget enjoyable times skiing, hiking in the mountains and evenings in Valnesfjord. Jorge, thank you for sharing your expertise in the gene expression studies and your help with the data analysis. Jeanine, thank you for your support and motivation and your professional input that enriched this thesis.

I wish to thank the members of my dissertation committee: Christine Maggs, Nicolas Bierne and Kurt Tande for their time and effort they have spent to evaluate this document and for agreeing to participate in the defence of this thesis.

Special thanks to Spyros Kollias. You were a great help in the lab and I appreciate your professional contribution to the RNA related work; and thank you for organizing the coffee! I would also like to acknowledge support by Kurt Tande and Ketil Eiane during my start in Bodø. Ketil, thank you for giving me the opportunity to teach the R course - that was fun. I thank Ove Nicolaisen for the good teamwork in teaching the R course. Thanks also to Jarle Tryti Nordeide for organizing the Ph.D seminars. Furthermore, I would like to thank Henning Reiss, Sünnje Basedow, Ketil Eiane, Cindy Hornaff, Age Mohus and Magne Haakstad for valuable comments and ideas to improve my conference presentations. Thanks to Katrin Reiss for her input on how to structure the thesis discussion. I am also grateful to Bard Ove Karlsen and Truls Moum for giving me the opportunity to contribute to their population genomics studies on Atlantic cod.

Setting up the heat stress experiments was a challenge and I would like to thank those who contributed to its realization: Randi Restad Sjøvik, Franz Allmendingen, Tor Ove Dyping, Morten Krogstad, Steinar Johnson, Kaspar Klaudiussen and Robert Eliassen. Special thanks to Randi for mastering all the organizational challenges, to Morten for organizing the UV-light and to Steinar for taking the underwater light measurements. Some equipment for the experiments was kindly provided by Mark Powell and Dalia Dahle.

I would like to thank Kevin Klingan, Marion Skog Nilsen and Renate Fretheim Karlsen for introducing me to the lab environment when I started my Ph.D. Further, thank you Renate for your great help in the lab throughout the last three years. Many thanks to Florence Perera for the HMS work and lab organization and to Ellen Sirnes and Liv Johansen for help with ordering.

I also don't want to forget all the unsung heroes of the library and administration - thank you for all your efforts!

I cannot thank enough Jim Coyer (Cornell University, USA) for his contribution in so many ways. Jim, thank you for helping me sampling in Spain, for your great help in the microsatellite work and for the days you spent in the dark and cold wetlab to run the heat stress experiments. Thank you also for your patience with going through my messy first drafts, for your thorough comments and ideas that significantly improved the quality of the entire dissertation. Also, thanks for your motivating words.

In 2011, I visited Phycology the Phycology Research Group of Olivier De Clerck at the Ghent University in Belgium. I would like to thank Heroen Verbruggen and Lennert Tyberghein for organizing this stay. Lennert, thank you for introducing me to the world of Niche Modeling, for your time, patience, and for many valuable discussions during my stay. Heroen, thank you for your support and your professional input in the Niche Modeling work. Further thanks to Klaas Pauly and Olivier De Clerck for sharing their knowledge and ideas.

I also would like to thank my Diploma thesis supervisor, Gabriele Gerlach (University of Oldenburg, Germany). Gabi, I will always be grateful for your guidance through the early stages of my career as a biologist.

Great thanks to the British Phycological Society for the Irene Menton Price award at the 60th Annual Winter Meeting in 2012. It was a great motivation.

I acknowledge financial support from the Research Council of Norway (HAVKYST project 196505, 203839, 216484, and the FoU funds). I would like to thank the following publishers, who kindly allowed permission for the reprint of their copyrighted figures: The National Academy of Sciences (USA), Springer, and John Wiley and Sons.

I am very grateful to my friends and colleagues for all the enjoyable moments we shared in and out of work: Sünnje Basedow, Maren Mommens, Cindy Hornaff, Michael Weinert, Spyros Kollias, Marol Tomprou, Arvind Sundaram, Priya Balasubramanian, Anna Abramova, Irina Zhulay, Hin Hoarau, Binoy Rajan, Teshome Bizuayehu, Carlos Lanes, Carlo Lazado, Kazue and Miyuki Nagasawa, Andrea Bozman, Henning und Katrin Reiss, Marloes Poortvliet, Philipp Krämer, Anusha Dhanasiri, Catarina Campos, Silje Svendsen, and April

Snøfrid Kleppe. I would like to single out: Maren, thank you for helping me moving; Cindy, Sünnje, Spyros, Henning, Michael and Katrin for their support and motivation in the end phase (sorry for that I was so unsociable in the end period).

I further would like to thank my sister and her family for many enjoyable moments during my often too short visits in southern Germany over these years.

I thank my girlfriend, Irina Smolina. Irina, you might have missed your name throughout the acknowledgements because it would fit in many places. I thank you for your help in setting up and suffering through the heat-stress experiments. Also, thank you for your input to and proofreading of my thesis while weathering storms during your trans-Atlantic cruise. You have been my rock throughout the last period of writing and I would like to thank you for all the great moments we shared - thank you for all your love.

I am very grateful to my parents, who always encouraged me and supported me throughout my life. Thank you for always being there, holding a peaceful place to where I can come back and recharge.

Contents

List of Figures

Abbreviations

Adh	Alcohol Dehydrogenase
AFLP	Amplified Fragment Length Polymorphism
cDNA	Complementary DNA
Dissox	Dissolved Oxygen
DNA	Desoxyribonucleic Acid
ENM	Ecological Niche Modeling
EST	Expressed Sequence Tag
GHG	Greenhouse Gas
GIS	Geographic Information System
GtC	Gigaton of Carbon
H	Heterozygosity
HSP	Heat Shock Protein
HSR	Heat Shock Response
IPCC	Intergovernmental Panel on Climate Change
LGM	Last Glacial Maximum
mtDNA	Mitochondrial DNA
NADP	Nicotinamide Adenine Dinucleotide Phosphate
N_e	Effective Population Size
NGS	Next Generation Sequencing
PCR	Polymerase Chain Reaction
PI_{Abs}	Absolute Photosynthetic Performance Index ppm
ppm	
PS	Photosystem
RNA	Ribonucleic Acid
SAT	Surface Air Temperature
SDM	Species Distribution Modeling
SNP	Single Nucleotide Polymorphism
SRES	Special Report on Emission Scenarios (Nakicenovic *et al.*, 2000)
SST	Sea Surface Temperature

List of papers

Paper I **Jueterbock A.**, Tyberghein L., Verbruggen H., Coyer J.A., Olsen J.L., Hoarau G. (2013)
Climate change impact on seaweed meadow distribution in the North Atlantic rocky intertidal
Ecology and Evolution 3 (5), 1356-1373

Paper II **Jueterbock A.**, Kollias S., Smolina I., Fernandes J.M.O., Coyer J.A., Olsen J.L., Hoarau G.
Thermal stress resistance of the brown alga *Fucus serratus* along the North-Atlantic coast: acclimatization potential to climate change
Submitted to *Marine Genomics*

Paper III **Jueterbock A.**, Kollias S., Coyer J.A., Olsen J.L., Hoarau G.
A decade of climate change on North Atlantic rocky shores - can the seaweed *Fucus serratus* adapt to rising temperatures?
Manuscript

Abstract

Atmospheric CO_2 concentration has increased rapidly since the 18th century Industrial Revolution, leading to global climate change. The planet is now facing an evolutionary turning point with drastic ecosystem shifts. For a species, the extinction risk under climate change depends on its potential to respond via: 1) distributional range shifts; 2) phenotypic plasticity; and 3) adaptation. Coastal ecosystems in general, and intertidal systems in particular, are likely to be profoundly affected by climate change. Most marine intertidal species exist close to their upper temperature tolerance limits and due to their high sensitivity to rising temperatures, their responses can be considered as early warning signals for the impact of climate change. On temperate rocky shores, responses of foundational seaweed species to climate change can influence the entire intertidal ecosystem. Fucoid algae (Heterokontophyta; Phaeophyta) are crucial ecosystem engineer species, forming the vast majority of the rocky intertidal biomass throughout the North Atlantic, providing food and shelter for numerous invertebrates and fishes but also buffering the community from environmental changes. Accordingly, the overall objective of this dissertation was to identify the impact of climate change on seaweed meadows in the North-Atlantic rocky intertidal with focus on the brown canopy-forming macroalga *Fucus serratus*.

Under climate change scenarios, Ecological Niche Model predictions suggest that habitat-provisioning key species on North-Atlantic rocky shores (*Fucus serratus*, *Fucus vesiculosus*, and *Ascophyllum nodosum*) will shift northwards as an assemblage or "unit". The models predict that Arctic shores in Canada, Greenland, and Spitsbergen will become suitable for all three species by 2100. Shores south of 45° North will become unsuitable for at least two of the three focal species on both the Northwest- and Northeast-Atlantic coasts by 2200. These predictions, however, do not take plastic and adaptive responsiveness into account.

To assess the plastic response of *F. serratus* in four populatins spanning the species' distribution range (Norway, Denmark, Brittany and Spain), the photosynthetic performance and transcriptomic up-regulation of heat shock protein genes was measured in common-garden heat stress experiments. Both stress indicators revealed population-specific differences. In all four populations, photosynthetic performance were significantly reduced at temperatures ≥ 24 °C (predicted to be reached in France and Spain by 2200), but the Danish and Spanish populations showed highest heat-stress resilience. However, the constitutively high hsp gene expression levels of the Spanish population are likely to impede a heat stress response to stressful high temperatures.

To investigate the adaptive responsiveness, a temporal and spatial genome scan approach was used in *F. serratus*. Thirty one microsatellite loci were genotyped in order to identify outlier loci (putatively under selection), changes in effective population size, and changes in genetic diversity over the past decade in four populations (Norway, Denmark, Brittany, and Spain). The Brittany and Spanish populations showed highest evolutionary change with a proportion of 23% and 13% outlier loci, respectively. One EST-linked locus was a consistent outlier between populations from cold (Norway) versus warm (Denmark, France and Spain) thermal regimes and between temporal samples separated by one decade. The Norwegian and Spanish populations had an $Ne<50$, while the Brittany population was of highest and temporally stable $Ne(\leq 210)$ and genetic diversity. Over the past decade, the Spanish population suffered significant loss in allelic richness and an abundance decline of about 90%.

In summary, both the physiological acclimatization potential and the adaptive capacity of the southern edge of *F. serratus* are likely insufficient to prevent its predicted extinction. Its extinction from rocky shores in southern Europe will likely trigger major ecological changes in the entire associated ecosystem. The stable population size and high genetic diversity in the Brittany population of *F. serratus* suggest that it may prevent its predicted extinction. The work in this thesis illustrates the potential of a multidisciplinary approach, integrating modeling, experiments, and population genetics in order to investigate the ecological and evolutionary responses of a key species to global warming. This highlights the need for integrative studies in order to further understand and predict the effect of climate change on natural ecosystems.

1 Introduction

Climate change

Atmospheric CO_2 concentration varied substantially in historic times but burning of fossil fuels since the 18th century Industrial Revolution increased it rapidly from a pre-industrial level of 280 ppm to >380 ppm (Feely *et al.*, 2004; Sabine *et al.*, 2004). In May 2013, CO_2 levels have hit the 400 ppm mark (http://blog.algore.com/2013/05/400_ppm.html) and are now at least 100 ppm higher than they have been within the last 740,000 years (Petit *et al.*, 1999; Augustin *et al.*, 2004; Hoegh-Guldberg *et al.*, 2007) (Fig. 1). This increase in CO_2 concentration has had far ranging consequences for our planet, from rising of global temperature (Keller, 2009), alteration of precipitation pattern (Trenberth *et al.*, 2007) and ocean acidification (Hoegh-Guldberg *et al.*, 2007; Turley & Findlay, 2009). The resulting global environmental change has become one of the major challenges facing human society. .

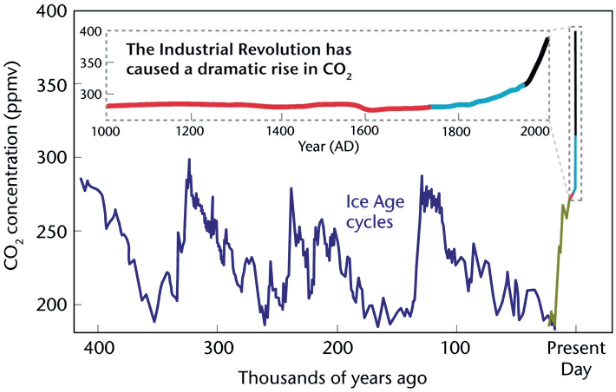
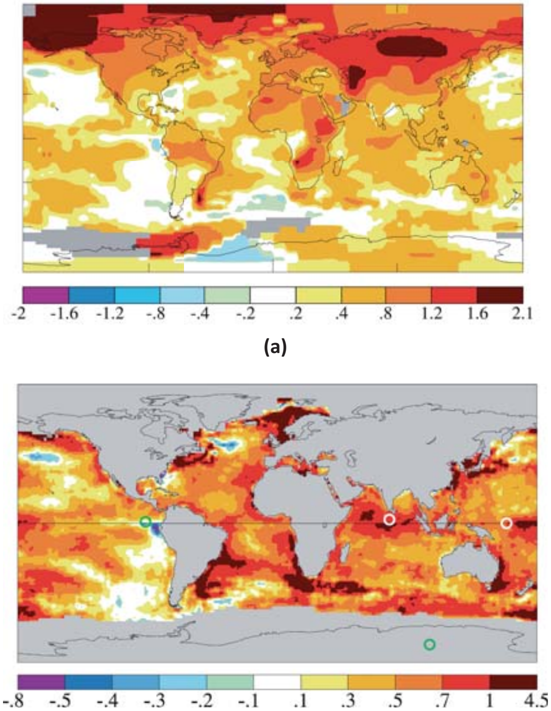


Figure 1: Changes in the atmospheric CO_2 concentration over the past 400,000 years. The inset shows the rapid rise in CO_2 to 380 ppm since the Industrial Revolution in the 18th century. From http://www.metoffice.gov.uk/, contains public sector information licensed under the Open Government Licence v1.0.

Recent warming

CO_2 is a greenhouse gas (GHG), whereby increasing concentrations trap solar radiation and consequently, have increased the global average surface air temperature by about 1 °C during the 20th century (Thompson *et al.*, 2008), and up to 2.1 °C in the Arctic (Fig. 2a). Concomitantly, the average global ocean temperature increased by 0.5 °C during the 20th century (Thompson *et al.*, 2008) (0.9 °C in the upper 700 m, Domingues *et al.*, 2008) and currently (2001 - 2005 average) ranks among the highest levels recorded during the past 1.4 million years (Hansen *et al.*, 2006). In general, the Atlantic Ocean has warmed faster (Trenberth *et al.*, 2007; Lee *et al.*, 2011) and to greater depths (Barnett *et al.*, 2005) than the Pacific or the Indian Oceans. More specifically, sea surface temperature (SST) increased by 4.5 °C in the Northeast-Atlantic (Fig. 2b). Moreover, the frequency and intensity of warm thermal extremes has increased (reviewed in Easterling *et al.*, 2000; Trenberth *et al.*, 2007). Summer warm extremes have increased by about 10% since the 1960's to 1970's in China and Europe (Yan *et al.*, 2002; Klein Tank & Können, 2003; Alexander *et al.*, 2006) and the European heat waves in summer 2003 and 2010 (Beniston & Stephenson, 2004; Shär & Jendritzky, 2004; Barriopedro *et al.*, 2011) caused major community shifts and local species extinctions (e.g. Garrabou *et al.*, 2009; Sorte *et al.*, 2010a).



(a)

(b)

Figure 2: Mean surface (**a**, relative to 1951 - 1980, global mean=0.54 °C) and sea surface (**b**, relative to 1870 - 1900) temperature anomaly (°C) for 2001 - 2005. Reprinted from Hansen *et al.* (2006, Fig. 1 (a) and Fig. 3 (b)) with permission from the National Academy of Sciences, U.S.A.

Climate change predictions

Since increasing atmospheric GHG concentrations are the main cause of climate change, it is possible to predict further changes under different GHG emission scenarios. The Intergovernmental Panel on Climate Change (IPCC) released a set of six SRES (Special Report on Emission Scenarios) emission scenario groups (Nakicenovic *et al.*, 2000) of which three illustrative marker scenarios were chosen to develop climate change projections in the IPCC Fourth Assessment Report (Meehl *et al.*, 2007): B1, A1B and A2.

B1 Scenario B1 is the most eco-friendly of the three scenarios, as it assumes worldwide initiation of vigorous programs to attain environmental and economical sustainability (Nakicenovic *et al.*, 2000). Thus, predicted GHG emissions are lowest under the B1 scenario (Meehl *et al.*, 2007) with a peak in CO_2 emissions of ca. 12 gigaton of carbon GtC) yr^{-1} by 2050 (Fig. 3), coinciding with an expected peak in human population size (Nakicenovic *et al.*, 2000). CO_2 concentrations are predicted to reach ca. 550 ppm in 2100 and global mean temperatures are predicted to rise by almost 2 °C (Fig. 3) until 2100 with local maxima in surface temperature increase of up to 4.5 °C in the Arctic (Fig. 4).

A1B Scenario The A1B scenario is based on rapid economic and technological development with a balanced use of the available energy sources (Nakicenovic *et al.*, 2000). Predicted GHG emissions fall between the emissions of the B1 and the A2 scenarios (Meehl *et al.*, 2007). As for the B1 scenario , human population size (Nakicenovic *et al.*, 2000) and CO_2 emissions are expected to peak in ca. 2050 with 13 GtC yr^{-1} (Fig. 3). CO_2 concentrations will reach 700 ppm in 2100 and global mean temperatures will rise by ca. 3 °C (Fig. 3) with local maxima in surface temperature increase of up to 7 °C in the Arctic (Fig. 4).

A2 Scenario The A2 scenario assumes a continuous human population growth and is based on a fragmented and regionally oriented economy (Nakicenovic *et al.*, 2000). Predicted GHG emissions are highest under the A2 scenario (Meehl *et al.*, 2007) with CO_2 emissions rising continuously up to ca. 28 GtC yr^{-1} in 2100 (Fig.3). CO_2 concentrations will reach maxima of ca. 880 ppm and global mean temperature is predicted to rise by ca. 4 °C until 2100 (Fig.3) with local maxima in surface temperature increase of up to 8 °C in the Arctic (Fig. 4).

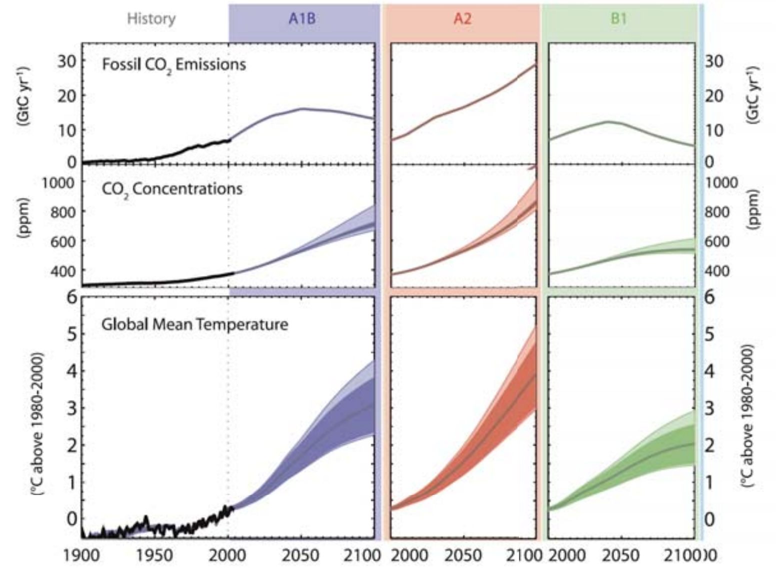


Figure 3: Multi-model mean of fossil CO_2 emissions, CO_2 concentrations and global mean temperature projections (dark shade: ±1 standard deviation) of 19 models. Light shade: change in standard deviation with lower/higher than medium carbon cycle feedbacks for the three illustrative SRES marker scenarios B1 (low emissions), A1B (medium emissions) and A2 (high emissions). Adapted from Meehl *et al.* (2007, Fig. 10.26).

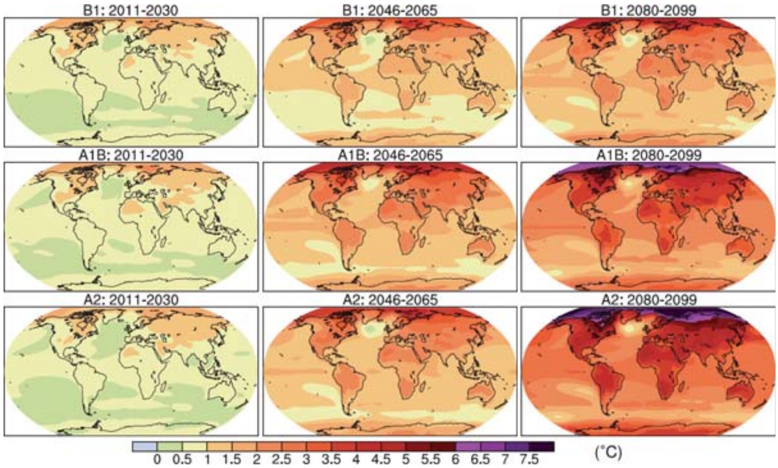
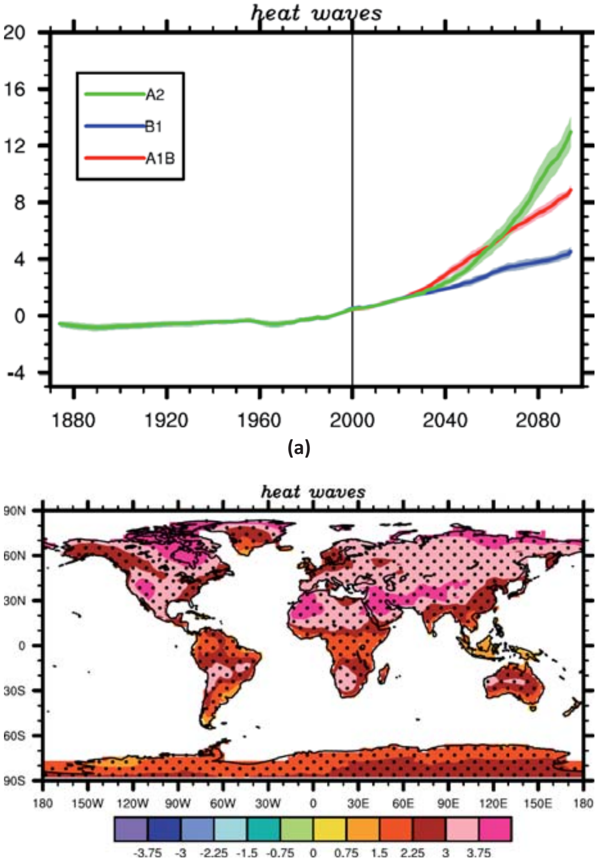


Figure 4: Multi-model mean of annual mean surface warming (surface air temperature change, °C) for the scenarios B1 (top), A1B (middle) and A2 (bottom), and three time periods, 2011 to 2030 (left), 2046 to 2065 (middle) and 2080 to 2099 (right). Anomalies are relative to the average of the period 1980 to 1999. Figure with full legend reprinted from Meehl *et al.* (2007, Fig. 10.8).

Besides increasing mean temperatures, the SRES scenarios further predict an increase in the frequency and intensity of heat waves over the coming century (Meehl *et al.*, 2007), (Fig. 5). Heat waves such as the European Heat Waves in 2003 and 2010 are predicted to become 5 to 10 times more probable over the next 40 years due to increasing daily temperature variability in the northern hemisphere (Barriopedro *et al.*, 2011).



(a)

(b)

Figure 5: Global average changes (terrestrial) of the heat wave duration index. The index is defined as the maximum period of at least 5 consecutive days with maximum temperature higher by at least 5 °C than the climatological norm for the same calendar day from nine global coupled climate models; **(a)** Temporal change from 1870 to 2090 under the three SRES scenarios B1 (low emissions), A1B (medium emissions) and A2 (high emissions) with inter-model variability shown as one standard deviation of the ensemble mean by the shaded regions, and **(b)** spatial patterns of change under the SRES scenario A1B. Reproduced from Tebaldi *et al.* (2006, Fig. 2, and Fig. 3) with permission from Springer.

Ecological and evolutionary responses to global warming

Numerous studies show that species are responding coherently to anthropogenic climate change (Hughes, 2000; Parmesan & Yohe, 2003; Root *et al.*, 2003; Parmesan, 2006; Rosenzweig *et al.*, 2008) suggesting that the planet faces an evolutionary turning point with drastic ecosystem shifts and mass extinctions (Barnosky *et al.*, 2011). Based on a temperature rise of 1.8-2.0 °C until 2050, 15% - 37% of species were predicted to become extinct in a region covering 20% of the earth's terrestrial surface (Thomas *et al.*, 2004). Nevertheless, extinction risk under climate change depends on a species' potential to rapidly respond via: 1) distributional range shifts (moving into habitats with optimal thermal conditions); 2) phenotypic plasticity (acclimatizing phenotypically/physiologically to increasing temperatures); and 3) adaptation (evolving genetically through the positive selection of alleles providing an advantage in warmer climates) (Reusch & Wood, 2007; Bijlsma & Loeschcke, 2012) (Fig. 6).

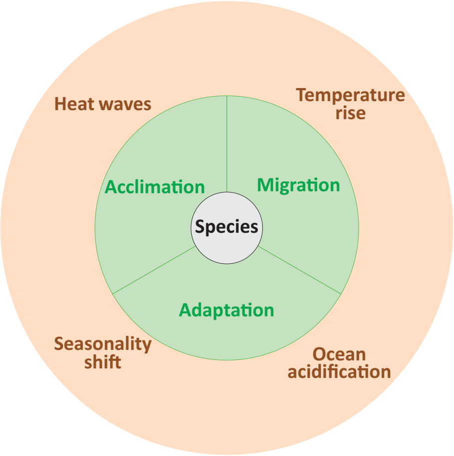


Figure 6: Climate change impact and species responses. A species failing to respond to the impacts of climate change (heat waves, ocean acidification, etc.) in any of the three potential pathways (migration, acclimation and adaptation) is threatened with extinction.

Distributional range shift

Climate is one of the main factors shaping species range limits (Parmesan & Yohe, 2003; Thomas, 2010) and to track predicted climate change, species must shift at rates of 30 to 50 km per decade (Davis & Shaw, 2001). A global warming related range shift into cooler habitats has been well documented during the 20th century for a broad range of taxonomic and functional groups in both the marine and the terrestrial environment (e.g. alpine herbs, trees, butterflies, birds, mammals, zooplankton and intertidal invertebrates) (Walther *et al.*, 2002; Parmesan & Yohe, 2003; Hickling *et al.*, 2006; Parmesan, 2006; Sorte *et al.*, 2010a). Marine species shifted over an order of magnitude faster (190 km per decade (Sorte *et al.*, 2010a)) than terrestrial species (6.1 km per decade poleward and 6.1 m per decade uphill, Parmesan & Yohe, 2003) with maxima of about 24 km per decade in European butterflies (Parmesan *et al.*, 1999) and 250 km per decade in marine calanoid copepods (Beaugrand *et al.*, 2002; Beaugrand *et al.*, 2009). Rapid distributional shift through individual migration, however, is only possible for species of high mobility. For sedentary and sessile species lacking larvae that can drift with ocean currents over long distances, range shifts require several generations and involve local population extinctions along the species' warm low-latitude edge and colonization of new habitats along their expanding cold high latitude (poleward) edge (Parmesan *et al.*, 1999; Davis & Shaw, 2001; Thomas *et al.*, 2001; Hampe & Petit, 2005; Aitken *et al.*, 2008).

Phenotypic plasticity

Individuals are able to alter their phenotype to changing climatic conditions, through physiological, behavioral or morphological adjustments (Parmesan, 2006; Pörtner & Farrell, 2008). Most of the recorded climate-change related phenotypic adjustments over the 20th century have not been to rising temperatures directly, but to climate-change related seasonality shifts in temperate and polar regions, such as an earlier onset of spring and a prolonged growing season (Bradshaw & Holzapfel, 2006; Parmesan, 2006; Meehl *et al.*, 2007; Bradshaw & Holzapfel, 2008). A global meta-analysis (including in total 172 species of herbs, shrubs, trees, birds, butterflies and amphibians) revealed that phenological spring events like budding, flowering, spring migration, nesting or breeding, have advanced by an average of 2.3 days decade^{-1} (Parmesan & Yohe, 2003). Another meta-analysis including about 700 species revealed an average advancement of 5.1 $\pm$0.1 (standard error) days decade^{-1} over the second half of the 20th century with a maximum of 24 days earlier decade^{-1} for the onset of breeding of the common murre *Uria aalge* in North America (Root *et al.*, 2003). In marine species, phenological changes ranged up to >1 week decade^{-1} (6 weeks within 45 years) and thus, were considerably faster than the average shift of several days in terrestrial species (Edwards, 2009).

Acclimatization is a key mechanism by which organisms can cope with rapid environmental changes and thermal extremes like heat waves, since it occurs within the lifetime of an individual. However, an organism's plasticity is limited within its reaction norm (De Jong, 2005) and thermal changes beyond these limits are lethal.

Adaptation

While phenotypic plasticity can provide a rapid but limited response to climate change, genetic adaptation is the only long-term solution to perpetually rising temperatures (Bijlsma & Loeschcke, 2012). Real evidence for genetic adaptation to climate change is rare and many responses that had been reported to be evolutionary adaptive were often based on non-genetic data and thus could have actually been phenotypically plastic changes (Gienapp *et al.*, 2008). Although seemingly small changes at the molecular level can lead to temperature-adaptive changes in protein function (Somero, 2010), the evolution of increased heat tolerance in response to global warming has not been reported yet (Bradshaw & Holzapfel, 2006; Kordas *et al.*, 2011).

However, as southern climates move northwards, evidence for genetic adaptation to climate change related seasonality shifts is emerging (Bradshaw & Holzapfel, 2006, 2008). For example, in response to earlier spruce cone production, the spring date of parturition (date of giving birth) of the Yukon red squirrel *Tamiasciurus hudsonicus* shifted within 10 years at a rate (13%) that was partly explained by evolutionary change (Réale *et al.*, 2003; Berteaux *et al.*, 2004). Over a 24-year period, the critical photoperiod leading to diapause in the pitcher-plant mosquito (*Wyeomyia smithii*) shifted to shorter day-lengths in response to a prolonged growing season (Bradshaw & Holzapfel, 2001). Another study revealed that, over an 18-year period, the egg hatching date of the winter moth (*Operophtera brumata*) shifted (by genetic change) towards later days in spring to synchronize with the appearance of the first leaves on its food plant *Quercus robur* (Van Asch *et al.*, 2013).

Some of the best examples of genetic changes in response to climate change are the northward shifts of southern warm-adapted genotypes in *Drosophila* species (Gienapp *et al.*, 2008), including recent changes in the frequencies of alcohol dehydrogenase (Adh) alleles (Umina *et al.*, 2005) and chromosomal rearrangements (Levitan, 2003; Levitan & Etges, 2005; Balanya *et al.*, 2006). All of these examples show that evolutionary responses can be rapid, but given the speed of recent climate change, it is questionable whether the adaptive capacity of most organisms is sufficiently high to track predicted climate change (Davis & Shaw, 2001; Hoegh-Guldberg *et al.*, 2007).

Adaptive responsiveness to rapid environmental change relies on the standing level of adaptive genetic variation as new beneficial mutations are likely too seldom to play a role for rapid adaptation (Orr & Unckless, 2008; Teotónio *et al.*, 2009). Thereby, genetic diversity depends on the effective population size (N_e) (Palstra & Ruzzante, 2008), defined as the size of an ideal population in which all individuals reproduce equally and that undergoes the same rate of genetic drift as the real population (Charlesworth, 2009). If N_e is low, genetic drift plays a predominant role and further erodes genetic diversity through stochastic fixation or loss of allelic variations (Palstra & Ruzzante, 2008; Charlesworth, 2009). Thus, populations of low N_e can suffer inbreeding depression through increased homozygosity and thus expression of deleterious recessive alleles (Reed, 2005; Palstra & Ruzzante, 2008; Fox & Reed, 2011; Bijlsma & Loeschcke, 2012). Accordingly, endangered populations revealed congruently a relatively small N_e (Palstra & Ruzzante, 2008) and inbreeding was found to increase extinction risk in butterfly populations (e.g. Saccheri *et al.*, 1998; Nieminen *et al.*, 2001). High sensitivity to genetic drift further makes selection effectively neutral and consequently impedes adaptive responses and lowers the potential to persist under environmental change (Charlesworth, 2009; Bijlsma & Loeschcke, 2012).

Analyzing climate change responses

To assess the extinction risk of a species under climate change, it is essential to investigate its responses to rising temperatures (e.g. Williams *et al.*, 2008; Sorte *et al.*, 2010a; Sorte *et al.*, 2011). The investigation of each of the three major climate change responses (distributional shift, phenotypic plasticity, and adaptation) requires different approaches. The following three sections introduce well-established methods that were used in this dissertation to 1) predict distributional shifts, 2) assess the physiological temperature tolerance, and 3) identify putatively genetically adaptive responses to climate change.

Predicting distributional shifts

Niche modeling is a powerful approach to predict the geographic space providing suitable habitat for a species and it has been used to predict distributional range shifts under climate change. Two fundamentally different modeling approaches have been proposed (Kearney, 2006).

The "mechanistic" niche modeling approach is based on a species' physiological characteristics and projects its fundamental ecological niche by mapping its fitness into geographic space (Kearney & Porter, 2009). Such approach was for example used to predict the future distribution of the cane toad *Bufo marinus* by 2050 in Australia under the climate change scenario SRES B1 (see section 1) (Kearney *et al.*, 2008). A major drawback of the mechanistic approach is that its implementation requires extensive knowledge on a species' physiology and life history (Angilletta, 2009) and generally estimates the fundamental niche of a single population so that regional niche space variation is not taken into account (Pearson & Dawson, 2003; Kearney & Porter, 2009).

In contrast, the "correlative" niche modeling approach (also called "Ecological Niche Modeling" (ENM) or "Species Distribution Modeling" (SDM) (Elith & Leathwick, 2009; Kearney & Porter, 2009)) is based on a species' geographic distribution and the environmental conditions at its occurrence sites (reviewed in Guisan & Zimmermann, 2000; Elith & Leathwick, 2009) and projects the realized niche of a species by mapping habitat suitability into geographic space (Fig. 7). GIS rasters/grids of environmental factors that are involved in setting a species' geographic range limits (e.g. temperature and salinity for marine species) are used to identify its realized niche space (the set of conditions providing suitable habitat). This habitat suitability is then projected back into geographic space, which is represented by GIS rasters containing for each pixel (and thus location), one value for each of the selected environmental conditions. In the projected distribution, those pixels with most suitable conditions are identified as areas providing highest habitat suitability. The model is then evaluated by assessing the congruence between projected habitat suitability and actual occurrence (Elith & Leathwick, 2009). If habitat suitability predictions are continuous, they can be converted to a binary map sharply discriminating suitable from non-suitable habitat by selecting a threshold based on present-day species distribution (see Fig. 7).

This approach has been widely used to predict distributional range shifts under climate change scenarios (Thuiller, 2003; Dormann, 2007; Elith *et al.*, 2010; Austin & Van Niel, 2011), ranging from marine macrophytes (Alahuhta *et al.*, 2011) and marine fishes (Perry *et al.*, 2005) to terrestrial plant and bird species (Thuiller, 2004; Schwartz *et al.*, 2006; Wiens *et al.*, 2009). For this purpose, the realized niche space of a species is projected back into geographic space, which is based on GIS rasters with the future states of the selected environmental conditions as they were predicted from climate change scenarios (Fig. 7).

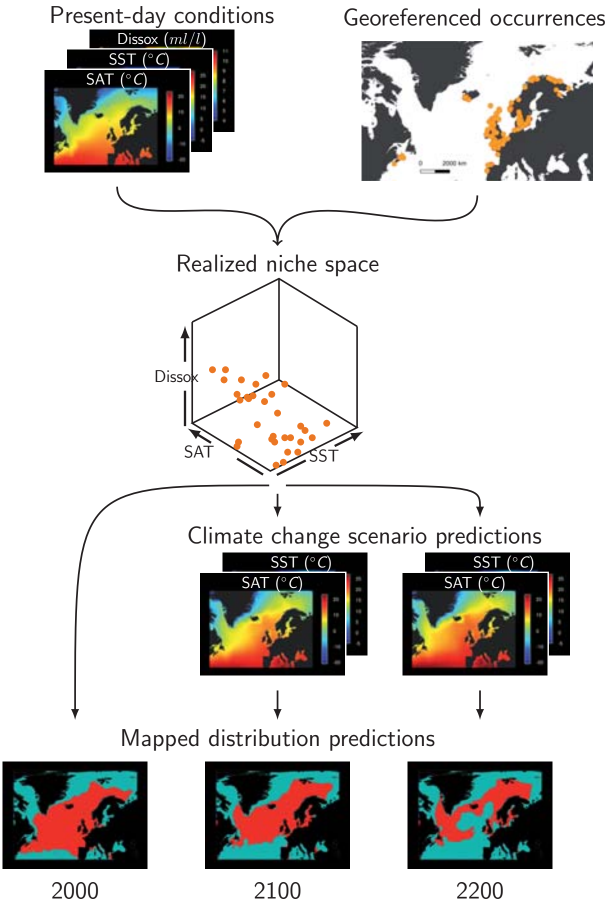


Figure 7: Prediction of species range shifts under climate change with correlative Ecological Niche Models. Geo-referenced occurrence sites and GIS rasters of environmental conditions (in this example, the following layers were used: Dissox, Dissolved oxygen; SAT, surface air temperature; SST, sea surface temperature) were used to identify a species' realized niche space (set of suitable environmental conditions). Habitat suitability was then projected into geographic space and transferred to a binary response (discriminating suitable (red) from non-suitable (blue) habitat) by applying a threshold (map in the lower left under present-day (2000) conditions). The projected habitat suitability evaluated the fit of the model to the species' occurrence records. The species' realized niche space was further used to project its habitat suitability under future environmental conditions, represented by GIS maps that were predicted from climate change scenarios. Based on Elith & Leathwick (2009, Fig. 1).

Assessing the physiological temperature tolerance

Investigating the physiological temperature tolerance of a species over its distributional range can reveal patterns of local thermal adaptation and identifies areas where predicted climate change will exceed tolerance limits and thus enforce range shifts (Hofmann & Todgham, 2010). Two responses at the molecular level (one specific for photosynthetic organisms) are commonly used to assess an organism's temperature tolerance (summarized in Fig. 8): 1) the transcriptional up-regulation of heat shock proteins and 2) the drop in photosynthetic performance.

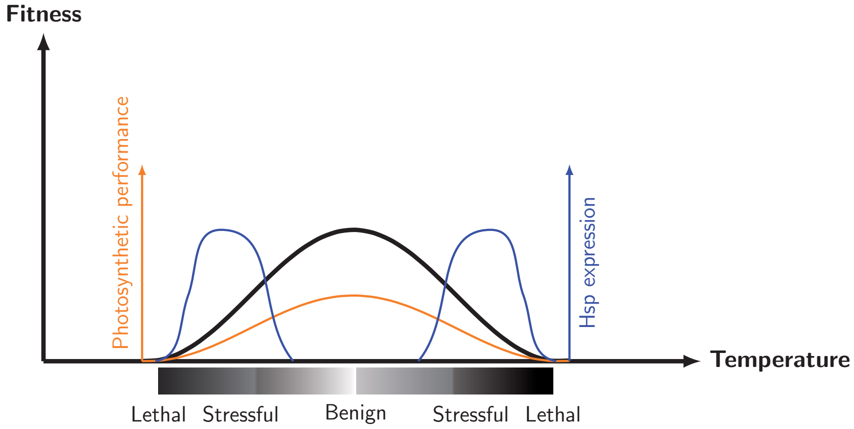


Figure 8: Physiological responses that assess temperature tolerance limits. An organism's decrease in fitness from benign to stressful/lethal conditions (indicated by the bar under the x-axis) is paralleled by a decrease in photosynthetic performance. In contrast, the expression of HSP proteins is initiated under stressful conditions. HSP expression levels rise with increasing stress and reach a peak before decreasing again towards the lethal limits. Modified from Sørensen & Loeschcke (2007, Fig. 1).

A universal molecular response to temperature stress is the transcriptional upregulation of inducible heat shock proteins HSPs (also called the heat shock response HSR) that act as molecular chaperones and protect the cell from detrimental effects of denatured or aggregated proteins (Feder & Hofmann, 1999; Tomanek, 2008; Hofmann & Todgham, 2010). The high conservation of HSP genes across many species and their response to different kinds of environmental stress (e.g. dehydration or osmotic stress) qualifies them as universal stress biomarkers (Feder & Hofmann, 1999; Lewis *et al.*, 1999). Some of the main functions of commonly investigated HSPs, such as protein stabilization, refolding and degradation (Feder & Hofmann, 1999; Wang *et al.*, 2004) are summarized in Fig. 9. Although an organism experiencing heat stress acclimatizes to warmer temperatures by overexpressing HSPs, the HSR is limited by cytotoxic effects and the energetic costs involved in ATP-dependent chaperoning functions (reviewed in Feder & Hofmann, 1999; Dahlhoff, 2004; Sørensen & Loeschcke, 2007).

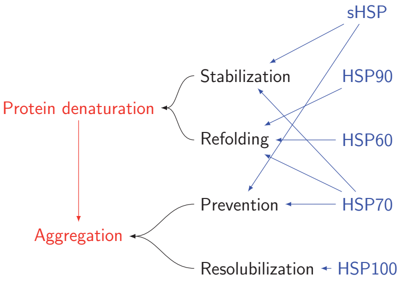


Figure 9: Network of heat-shock protein (HSP) functions under heat stress. Denatured and aggregated proteins (red) are the main targets of different heat-induced HSP classes (blue) that have complementary and partly overlapping functions (black). Protein resolubilization and refolding are ATP-dependent processes. Aggregated proteins that cannot be resolubilized or refolded are degraded by protease. HSP70 and HSP90 further contribute to the heat-induced transcription activation of other stress-response proteins and HSPs. Based on Wang *et al.* (2004).

HSP expression levels allow to assess physiological temperature tolerance limits and a species' vulnerability to climate change. For example, expression levels of the 70 kDa HSP (HSP70) revealed patterns of local thermal acclimation across the distributional range of the purple sea urchin (*Strongylocentrotus purpuratus*) (Osovitz & Hofmann, 2005) and indicated that southern edge populations of the dogwhelk *Nucella canaliculata* are under highest climate change risk (Sorte & Hofmann, 2004). Species from thermally stable environments generally lack a HSR and while species from moderately variable environments (<10 °C) up-regulate HSPs only under extraordinarily high temperatures, those from highly variable environments (>20 °C) induce a HSR frequently and in response to temperatures they normally experience throughout the day (Tomanek, 2008, 2010). The common lack of HSP expression in species from very stable environments (e.g. Antarctic species La Terza *et al.*, 2001; Clark *et al.*, 2008b; Clark & Peck, 2009, but see Clark *et al.*, 2008a) makes them vulnerable to smallest temperature changes and thus to climate change (but see Buckley & Somero, 2009). Also species from highly variable environments (e.g. marine intertidal) are living close to their upper temperature tolerance limits but due to a different reason: the thermal difference between experienced temperatures and upper temperatures that allow for HSP expression is small (Tomanek, 2010). Thus, although marine intertidal species live in a thermally highly variable environment, their low acclimation potential to further rising temperatures could make them most vulnerable to global climate change (Tomanek, 2008; Somero, 2010; Tomanek, 2010).

Since photosynthesis is especially sensitive to high temperatures (Berry & Bjorkman, 1980; Zhang & Sharkey, 2009; Stefanov *et al.*, 2011), a decrease in photosynthetic performance under heat-stress can indicate the thermal tolerance limits of photosynthetic organisms (Fig. 8). High temperatures have a negative effect on electron transport (Berry

& Bjorkman, 1980; Weis, 1982; Wise *et al.*, 2004) and carbon metabolism (decreased CO_2 uptake) in the photosynthetic apparatus (Weis & Berry, 1988; Salvucci & Crafts-Brandner, 2004; Sharkey, 2005). Photosystem (PS) II was found to be most heat sensitive (Havaux, 1993; Maxwell & Johnson, 2000; Rokka *et al.*, 2000). The less efficient the absorbed light energy can be used for photosynthesis, the more heat and chlorophyll a fluorescence is emitted from the two photosynthetic reaction centers (P680 in PS II and P700 in PS I) (Schreiber *et al.*, 1994; Baker, 2008) (Fig. 10).

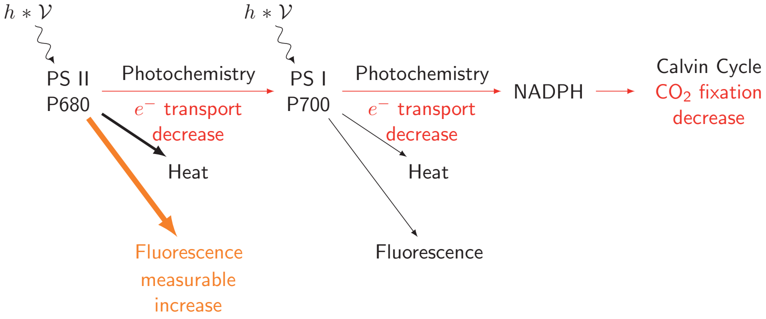


Figure 10: Effect of heat stress on photosynthesis. Light activation energy ($h * \mathcal{V}$) in the reaction centers of photosystem (PS) I and PS II is used for photochemical work and emitted in form of heat and chlorophyll a-fluorescence. Photochemical work results in the reduction of $NADP^+$ to NADPH, which is required for carbon fixation in the Calvin Cycle. Thermal stress has a negative effect on the electron transport and carbon fixation in the photosynthetic apparatus, thus reducing the energy used for photochemical work. In consequence, chlorophyll a fluorescence increases and the amount of increase under different temperatures predicts temperature tolerance. Based on Oxborough (2004); Baker (2008); and Schreiber *et al.* (1994).

A reduction in photosynthetic performance leading to increased chlorophyll a fluorescence (predominantly in PS II (Schreiber *et al.*, 1994; Bussotti *et al.*, 2010)), can be recorded with a fluorometer, by measuring the increase in fluorescence upon illumination of a dark adapted leaf (called the Kautsky effect (Kautsky (1960) in Maxwell & Johnson (2000)). Measurements at certain steps during this fluorescence transient (OJIP curve, Fig. 11) are then extracted (reviewed in Maxwell & Johnson, 2000; Baker, 2008; Bussotti *et al.*, 2010; Stefanov *et al.*, 2011). The first measurement F_0 obtained after switching on the measuring light (step O in the OJIP fluorescence transient, Fig. 11), refers to the minimal chlorophyll fluorescence when all reaction centers are opened in a dark-adapted leaf (all quinone acceptors are completely oxidized and can accept electrons). Subsequently, a saturating light pulse is applied, and while the reaction centers are closing (all quinone acceptors get reduced and become unable to accept any further electrons), chlorophyll fluorescence increases to its maximum value F_m (step P in the OJIP fluorescence transient, Fig. 11) (Maxwell & Johnson, 2000).

A widely used fluorescence parameter to estimate the maximum quantum yield of PS II (a proxy measure of photosynthesis) and thus to assess the physiological condition, is

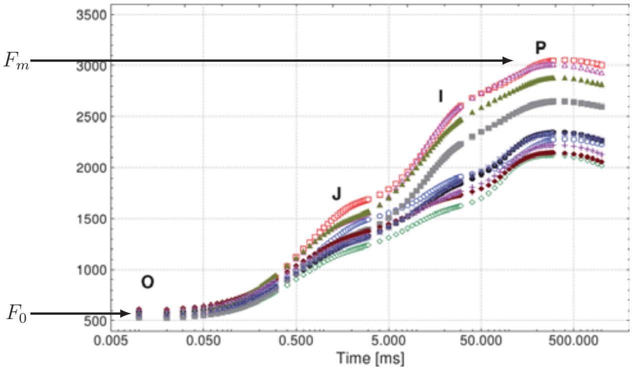


Figure 11: The OJIP curve of fluorescence transient upon illumination of a dark adapted leave over a period of 500 ms. Fluorescence measurements, taken at step O (F_0) and P (F_m) are common measures used to assess photosynthetic performance. The physiological processes at these steps and further details are described in the text. Adapted from Bussotti *et al.* (2010, Fig. 1).

the F_v/F_m ratio $F_v/F_m = (F_m - F_0)/F_m$ (Maxwell & Johnson, 2000; Bussotti *et al.*, 2010). This ratio decreases under heat stress, due to an increase in F_0 (and thus decrease in F_v) chlorophyll a fluorescence (Berry & Bjorkman, 1980). However, it was actually found to remain rather stable under stress (Živčák *et al.*, 2008; Bussotti *et al.*, 2010; Martínez *et al.*, 2012); and a more sensitive stress indicator, the performance index PI_{Abs} was introduced (Strasser *et al.*, 2000). This index measures the overall photosynthetic performance by combining three parameters (Živčák *et al.*, 2008; Bussotti *et al.*, 2010; Stefanov *et al.*, 2011): 1) the density of reaction centers, 2) the electron transport at the onset of illumination, and 3) the maximum energy flux reaching the reaction center in PS II. Like F_v/F_m, PI_{Abs} can be directly derived from fluorescence measurements along the OJIP curve (described in Živčák *et al.*, 2008; Bussotti *et al.*, 2010).

To identify if phenotypic or physiological differences between populations are based on genetic differences and thus putative local adaptations requires reciprocal transplant experiments or a common garden setup (reviewed in Kawecki & Ebert, 2004) where individuals from different environments are kept under the same environmental conditions in the field (reciprocal transplant experiment) or the laboratory (common garden experiment). Acclimation to these conditions over a given time period shall minimize phenotypic variation that is not based on genetic differentiation.

Identifying genetic adaptation

Two alternative approaches allow to assess the molecular basis of thermal adaptation (reviewed in Vasemagi & Primmer, 2005; Reusch & Wood, 2007; Hansen *et al.*, 2012):

1) in the spatial approach, allele frequencies are compared between populations living in cold versus warm conditions. 2) in the temporal approach, allele frequency shifts are identified between retrospective temporal samples of individuals exposed relative to individuals not exposed to the "new" environment (Reusch & Wood, 2007). The spatial approach (landscape genetics/genomics approach (Joost *et al.*, 2007; Manel *et al.*, 2010)) can only give indirect evidence for genetic changes that might be adaptive under climate change (Reusch & Wood, 2007) but remains the only choice if temporal samples are not available. The availability of historical retrospective samples of otoliths or dried scales have allowed, for example, to investigate adaptive genomic responses to natural and fisheries- or farming-induced selection in Atlantic cod (e.g. Nielsen *et al.*, 2009; Therkildsen *et al.*, 2013), brown trout (Hansen *et al.*, 2010) and Atlantic salmon (Bourret *et al.*, 2011). However, as natural selection usually involves simultaneous changes in multiple environmental factors, it is difficult to correlate adaptive responses with the selective agent it responded to (e.g. Orsini *et al.*, 2012).

Ideally, the two approaches are combined to increase confidence in the association between adaptive genetic regions and environmental factors. Thus, genomic regions identified to be adaptive in contrasting thermal environments and over a time period of thermal change are likely to play a role in thermal adaptation. For example, a recent study on the ecological model *Daphnia* combined genome scans in spatial and temporal samples with genome scans on individuals from experimental evolution studies and thus identified genetic regions that likely played a role in the adaptation to land use, fish predation or parasitism (Orsini *et al.*, 2012).

A common approach to identify genetic responses to environmental change is to use whole genome scans for outlier loci (e.g. microsatellites, SNPs or AFLPs) that are closely linked to and hitchhike (Smith & Haigh, 1974) with loci under selection (Fig. 12). This approach has also been called "hitch-hiking-mapping" since it identifies chromosomal regions that are closely linked to loci responding to directional selection (Vasemagi & Primmer, 2005). Outlier loci are characterized by extraordinary allele frequency patterns differing from patterns of genetic drift and gene flow, which affect all loci in a genome (Smith & Haigh, 1974; Luikart *et al.*, 2003; Vasemagi & Primmer, 2005).

The allele frequency patterns of loci under directional selection differ from those under balancing selection. Loci under directional selection rapidly spread throughout a population, causing a "selective sweep" (increasing frequency of favorable alleles and closely linked genomic regions, Fig. 13) that is characterized by a decrease in genetic variation (commonly measured as heterozygosity H) and high genetic differentiation between retrospective temporal samples (commonly measured by the genetic differentiation index F_{ST} (Nei, 1972)) (Luikart *et al.*, 2003; Hartl & Clark, 2007) (Fig. 12).

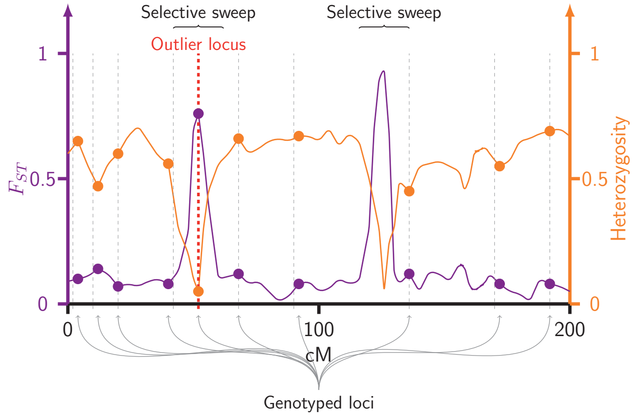


Figure 12: Genome scan for outlier loci. Samples from different selection regimes are genotyped for genetic markers (e.g. microsatellites, SNPs or AFLPs) that are dispersed throughout the genome of the target species. The y-axis shows the genetic distance along a certain genomic region in centimorgans (CM). For each marker, the genetic differentiation (based on the fixation index F_{ST} (Nei, 1972)) and changes in genetic variation (heterozygosity *H*) between the two samples are analyzed. Selective sweeps (Fig. 13) are characterized by extraordinarily high and low *H* values. In this simplified example, only one of the two regions under selection was detected with the selected markers.

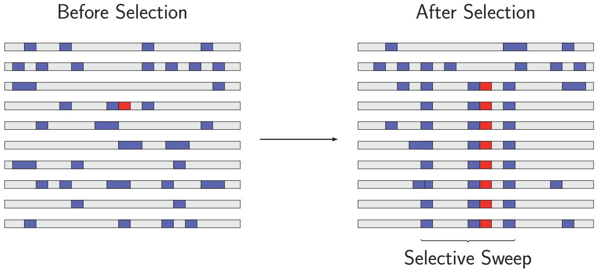


Figure 13: Selective sweep. An adaptive mutation (red) appeared in a certain genomic region (long gray bars) in 1 out of 10 population samples. The frequency of this allele increased rapidly in the population and was found in eight of ten samples after few generations. Selectively neutral loci (blue) hitchhike with the adaptive locus if they are closely linked to it through small physical distances and thus low recombination frequencies. Reproduced from Vitti *et al.* (2012, Fig. 1) with permission from the National Academy of Sciences, U.S.A.

In contrast, balancing selection favors several alleles and is characterized by high genetic diversity and low genetic differentiation between retrospective temporal samples. Multiple-marker-based neutrality tests to compare locus-specific heterozygosity H to the degree of differentiation (F_{ST}) are now implemented in software packages such as Arlequin (Excoffier & Lischer, 2010) (see Fig. 14 for an example result), Bayescan (url: http://www-leca.ujf-grenoble.fr/logiciels.htm) or FDist, differing in their neutrality model setup (Vitalis *et al.*, 2001; Luikart *et al.*, 2003; Vasemagi & Primmer, 2005). In the search for "selective sweeps", the probability to "hit" a genomic region under selection increases with the number of genetic markers used. Once identified, annotation of outliers allows to trace genes in the adaptive process and thus, to understand how populations adapt to environmental change (e.g. Galindo *et al.*, 2010; Coyer *et al.*, 2011).

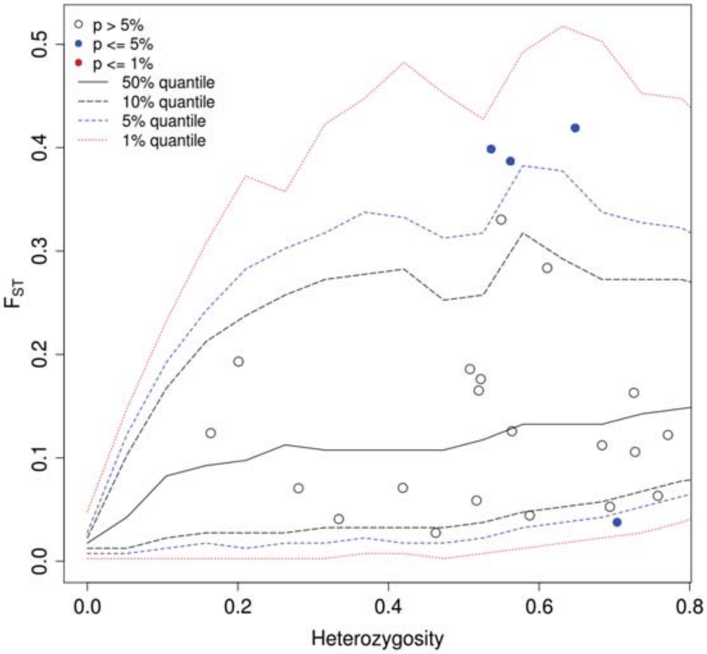


Figure 14: Example outcome of the program ARLEQUIN ver. 3.5 (Excoffier & Lischer, 2010) for the identification of outlier loci. Each dot represents the relation between the fixation index F_{ST} and the heterozygosity level H for a single locus. The lines are based on simulations and indicate upper/lower levels of neutral genetic divergence that can be expected to arise by genetic drift between the compared pair of populations. The three blue dots falling above the upper 95% quantile null distribution threshold (dashed blue line) represent loci that are putatively under positive selection. The blue dot falling below the 5% quantile null distribution threshold represents a locus that is putatively under balancing selection.

However, outliers identified with genome scans on spatially separated samples do not necessarily have to be adaptive to the environmental factor that differs between the samples. Following the argumentation of Bierne *et al.* (2011), as spatial outliers often occur at a frequency of 5-10% of the investigated loci and hitchhiking regions around adaptive genes are generally not bigger than 5 kb (<0.003% of the genome) (reviewed in Bierne *et al.*, 2011), thousands of genes throughout the genome would have to be adaptive to a certain environmental factor. Instead of being adaptive, most of these outliers could reflect intrinsic genetic incompatibilities (Bierne *et al.*, 2011). Genetic incompatibilities appear to be frequent and as they act as gene flow barriers that often get trapped by and coupled with extrinsic barriers imposed by divergent selection, they can mimic adaptive allele frequency shifts over the contrasting environments of the investigated populations (Bierne *et al.*, 2011). Consequently, spatial genome scans must be complemented by temporal genome scans and experimental approaches to confirm the adaptive value of identified outlier loci.

Climate change impact on North-Atlantic rocky shores

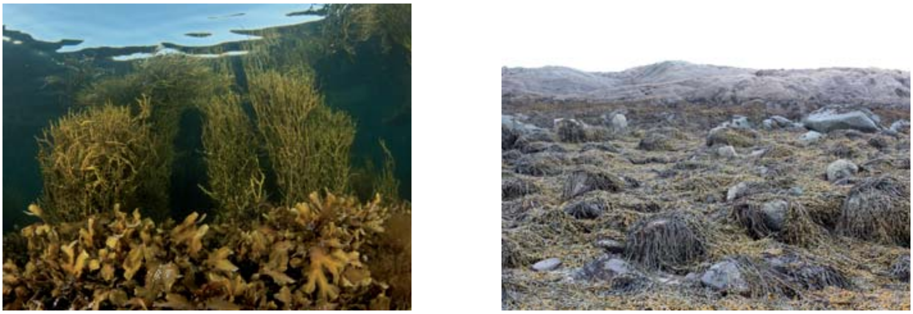
The sensitivity of marine intertidal species to climate change

Climate change responses are particularly pronounced in marine ecosystems (Southward *et al.*, 1995; Hoegh-Guldberg & Bruno, 2010; Sorte *et al.*, 2010b) (section 1,1). The rapid poleward shift of pelagic species in response to climate change (section 1) is favored by their generally high dispersal potential and adaptation to a stable thermal environment (stenothermality) (Beaugrand *et al.*, 2009; Edwards, 2009; Sorte *et al.*, 2010b). In contrast, environmental variability is thought to increase genetic diversity and thus enhance a population's ability to cope with future environmental change (Padilla-Gamino & Carpenter, 2007; Pespeni *et al.*, 2013). Thus, one might expect that marine intertidal species are adapted to high thermal stress and thus, may cope with the predicted temperature increase, given the extreme temperature variations they experience in their natural habitat. However, most intertidal species actually live close to their upper temperature tolerance limits and their acclimation potential to further rising temperatures is specifically low (Somero, 2005; Helmuth *et al.*, 2006; Somero, 2010; Tomanek, 2010). Even a small temperature increase can be lethal and may explain why the climate-change related poleward shift was also higher in intertidal than in terrestrial species (Southward *et al.*, 1995; Helmuth *et al.*, 2006; Wethey & Woodin, 2008; Sorte *et al.*, 2010b). Due to their high sensitivity to rising temperatures, responses of marine intertidal species can thus be considered as early warning signals for the impact of climate change (Helmuth *et al.*, 2006).

The key role of seaweeds in the rocky intertidal

Climate change responses by foundation species can affect an entire ecological community (Sanford, 1999; Kordas *et al.*, 2011). On temperate rocky shores, canopy-forming seaweeds (Fig. 15) are foundational species (sensu Dayton (1972)) (Christie *et al.*, 2009; Wahl *et al.*, 2011; Harley *et al.*, 2012), as they: 1) increase the habitable surface by a factor of four (Boaden, 1996), 2) support a complex food web with food and habitat (Carss

& Elston, 2003; Gollety *et al.*, 2010), and 3) protect a broad range of associated species against visual predators, desiccation stress, and high temperature and salinity fluctuations (Chapman, 1995; Dijkstra *et al.*, 2012).



(a) The habitat-forming seaweeds *Ascophyllum nodosum* (top) and *Fucus serratus* (bottom) during high-tide.

(b) Rocky shore during low tide, covered with *Ascophyllum nodosum*.

Figure 15: Canopy-forming seaweeds - foundational key species on North-Atlantic rocky shores; **(a)** reprinted from Jueterbock *et al.* (2013, Fig. 1).

The distribution of marine seaweeds is usually directly limited by their temperature tolerance (Breeman, 1988; Eggert, 2012; Sunday *et al.*, 2012) and thus closely follows SST isotherms (Lüning *et al.*, 1990). Over the 21st century, isotherms are predicted to shift up to 600 km northward under the SRES IPCC scenario A2 (see section 1) (Hansen *et al.*, 2006)), and will likely cause drastic range shifts of temperate seaweeds on a global scale (Müller *et al.*, 2009; Wernberg *et al.*, 2011). For example, on the shores of Southwest- and Southeast-Australia, up to 25% of the diverse temperate seaweed flora is predicted to retreat beyond the availability of rocky substrate and may become extinct within the 21st century (Wernberg *et al.*, 2011).

The poleward shift of canopy-forming seaweeds can have a profound impact on the rocky shore community. For example, the disappearance of habitat-providing macroalgae was generally followed by a loss of biodiversity and the appearance of large open substrate only partially covered by more stress-resistant crustose algae or red algal turf (Sagarin *et al.*, 1999; Worm *et al.*, 1999; Schiel *et al.*, 2004; Connell, 2005; Lilley & Schiel, 2006; Schiel & Lilley, 2007, 2011). Thus, if North-Atlantic rocky shore communities will undergo substantial changes over the next centuries depends largely on the fate of predominant seaweed species under predicted climate change.

Predominant macroalgae on North-Atlantic rocky shores

North-Atlantic shores provide suitable habitat for canopy-forming seaweed meadows predominantly in the temperate region (Van den Hoek, 1975) (Fig. 16). To the north (Arctic region), canopy-forming species largely disappear from the intertidal and are primarily confined to the subtidal (Van den Hoek, 1975; Wiencke & Amsler, 2012). On the other hand, to the south (the tropics) herbivores become increasingly predominant and canopy-forming algae get replaced by green algae and crustose red algae of smaller growth-forms (Van den Hoek, 1975; Lüning *et al.*, 1990).

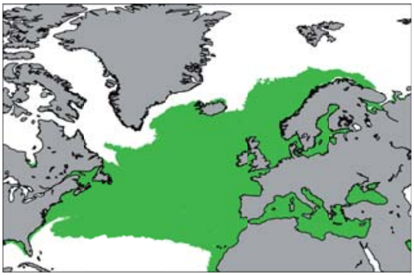


Figure 16: The temperate North-Atlantic region (green), that is delimited to the north by the 15 °C summer and to the south by the 20 °C winter isotherm.

The 15 °C summer SST isotherm separates the warm- from the cold-temperate region in the North-Atlantic (Van den Hoek, 1975) and its recent shift of 330 km northwards from 1985 to 2000 (McMahon & Hays, 2006) (Fig. 17), demonstrates that a seemingly small rise in Atlantic SST (0.4 °C - 1.6 °C over the past 50 - 60 years (Hansen *et al.*, 2006)) can have a huge impact on species whose distributional range limits are set by SST isotherms.

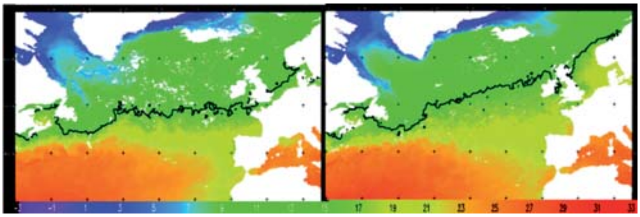


Figure 17: Position of the 15 °C SST isotherm in August 1985 (left) and 2000 (right), indicating a northward shift of 330 km. Reprinted from McMahon & Hays (2006) with permission from John Wiley and Sons.

The predominant seaweeds inhabiting the rocky intertidal/shallow subtidal of the North-Atlantic temperate regions are *Fucus serratus*, *F. vesiculosus* and *Ascophyllum nodosum* (Fig. 18). The southern distribution limit of *F. vesiculosus* retreated over the past 30 years approximately 11° latitude (1,250 km) northwards (Nicastro *et al.*, 2013). Southern-edge populations of other macroalgal species responded similarly with a recent northward shift of more than 100 km; 180 km since 1971 in the case of *Chrondrus crispus* (Lima *et al.*, 2007; Provan & Maggs, 2012) and 150 km for *Laminaria hyperborea* and other kelp species presumably due to ceased upwelling of cool water in 2008 (Müller *et al.*, 2009; Müller *et al.*, 2010). Moreover, rear edge populations of *A. nodosum* suffered enhanced mortality and invested increasingly in reproductive output at the expense of growth in northern Portugal (Araújo *et al.*, 2011).


(a) *Fucus serratus* **(b)** *Fucus vesiculosus* **(c)** *Ascophyllum nodosum*

Figure 18: Three of the most predominant canopy-forming seaweeds on temperate North-Atlantic rocky shores.

The canopy-forming seaweed *Fucus serratus*

Fucus serratus depends on SST isotherms and thus, provided an excellent model for identifying the impact of global warming on North-Atlantic rocky shores. It is a perennial (3 - 4 years), dioecious seaweed in the lower intertidal of North-Atlantic rocky shores and reproduces annually with a generation time of 1 - 2 years (Coyer *et al.*, 2006). Adult stages lack air bladders and thus sink if not attached to flotsam or jetsam and fertilized gametes generally settle <12 m from their parental sites (Arrontes, 1993, 2002). The low dispersal capacity of *F. serratus* explains its small panmictic unit of 0.5 - 2 km (Coyer *et al.*, 2003) and its slow natural dispersal rate of 0.2 - 0.6 km per year (Coyer *et al.*, 2006; Brawley *et al.*, 2009).

On the East-Atlantic coast, the distribution of *F. serratus* extends from the White Sea (Lüning *et al.*, 1990) south to Northern Portugal (Arrontes, 1993; Pearson *et al.*, 2009; Viejo *et al.*, 2011; Martínez *et al.*, 2012) with distributional gaps in the southern North Sea and in the Bay of Biscay where rocky substrate is lacking (Van den Hoek, 1975; Lüning *et al.*, 1990) (Fig. 19). On the West-Atlantic coast, human shipping activities facilitated the introduction of *F serratus* to Nova Scotia from Europe at least twice in the late 1860s (Brawley *et al.*, 2009; Johnson *et al.*, 2012). It was further introduced to Iceland from southern Norway during the 19th century and from Iceland to the Faroes in the late 20th century (Coyer *et al.*, 2006).

(a) Occurrence sites **(b)** Sampling sites **(c)** Ancient glacial refugia

Figure 19: Distribution and sampling sites of *F. serratus* in the Northeast-Atlantic intertidal. Occurrence sites **(a)** reflect the present-day distribution of this seaweed. Sampling sites for this dissertation **(b)** cover the species' latitudinal range of distribution and include two ancient glacial refugia **(c)**.

During the last glacial maximum (LGM, ca. 18 to 20 kya), *F. serratus* was restricted to three major glacial refugia: the Northwest-Iberian Peninsula, Southwest-Ireland and the Hurdle-deep region off the coast of Brittany (France) (Coyer *et al.*, 2003; Hoarau *et al.*, 2007) (Fig. 19, 20). While ancient refugial populations persisted over a long time-period that allowed for the evolution of a high and unique genetic diversity and thus adaptability (Hampe & Petit, 2005; Maggs *et al.*, 2008; Diekmann & Serrao, 2012), this is only true for the latter two refugia of *F. serratus* (Coyer *et al.*, 2003; Hoarau *et al.*, 2007). In contrast, the North-Iberian edge populations lost most of their genetic diversity over thermally induced cycles of extinction and recolonization (Coyer *et al.*, 2003).

Southern range-edge populations of the North-Iberian refugium are highly vulnerable to increasing temperatures. Here, *F. serratus* is present only in the northwest, an upwelling region of cool deep water. Consequently, *F. serratus* has two southern distributional limits: one in northern Spain and the other in northern Portugal. In northern Spain, sea surface temperatures reach 22 °C and although below the lethal limit of *F. serratus* (25 °C (Lüning, 1984; Lüning *et al.*, 1990)), the high temperatures inhibit growth, physiological performance and reproductive capacity (Arrontes, 1993, 2002; Viejo *et al.*, 2011; Martínez *et al.*, 2012). Over the past decade, a previously abundant population on the Spanish north-coast (in Ribadeo) became almost extinct (see Fig. 21), providing a case example for the dynamics of *F. serratus* populations along the Cantabrian shore.

In northern Portugal, upwelling events keep sea surface temperatures below 15 °C, but increasing air-temperature stress depressed the upper zonational boundary limit of *F. serratus* (Pearson *et al.*, 2009). Maladaptation to heat stress at this second southern range boundary was indicated by reduced heat stress resilience and an increased heat shock response compared to a population from the species' mid-range of distribution on the southwest coast of the UK (Pearson *et al.*, 2009). This suggests that the acclima-

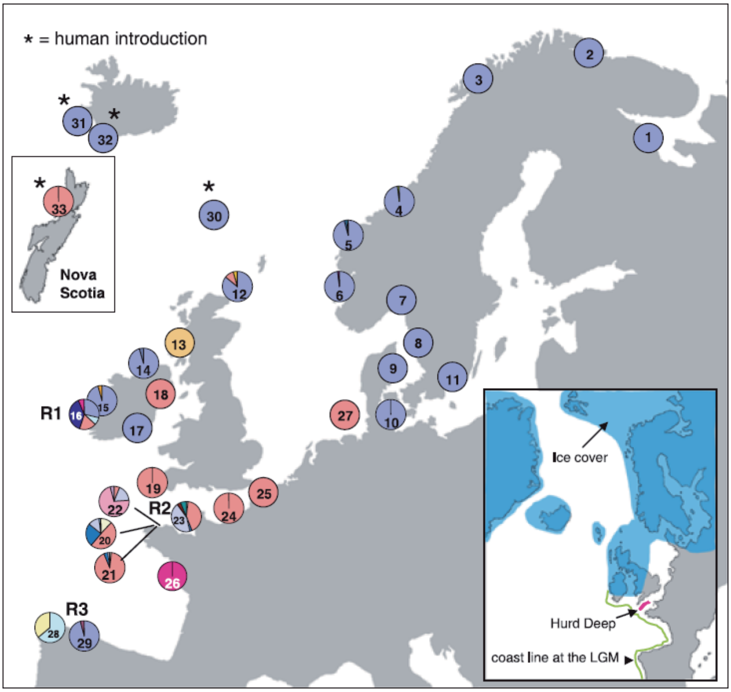


Figure 20: Glacial refugia of *Fucus serratus*. Three potential refugia (R1-R3) in Southwest-Ireland, Brittany (France) and the North-Iberian Peninsula are identified. The pie charts represent the spatial distribution (sampling sites indicated by numbers) of different mtDNA haplotypes (encoded by different colors). The small inset shows the ice cover (blue) and coastline (green) as it was expected at the last glacial maximum (18 - 20 kya). Reprinted from Hoarau *et al.* (2007, Fig. 1) with permission from John Wiley and Sons.

(a) 1999

(b) 2010

Figure 21: Abundance decline of *Fucus serratus* at its southern distributional edge in northern Spain (Ribadeo). The coverage of *F. serratus*, recorded in **(a)** 1999 and **(b)** 2010 declined by about 90% over an 11-year period. Reproduced from Jueterbock *et al.* (2013, Fig. S6).

tion potential of *F. serratus* may be insufficient to prevent the extinction of its southern distributional edge on the North-Iberian Peninsula.

Main objectives

The overall objective of this dissertation was to identify the impact of climate change on seaweed meadows in the North-Atlantic intertidal. The specific aims were to:

- **Paper I**: Predict the distributional shift of predominant macroalgae from the temperate North Atlantic rocky intertidal based on climate change projections.
- **Paper II**: Identify the acclimation potential of the seaweed *F. serratus* to increasing temperatures based on two stress indicators: the photosynthetic performance and the expression of heat shock protein genes.
- **Paper III**: Identify adaptive genetic changes in the seaweed *F. serratus* in response to North-Atlantic warming over the past decade and assess its adaptive potential to further environmental change.

The investigations in **paper II** and **III** were based on four populations that cover the entire latitudinal range of *F. serratus* in the East-Atlantic (Fig. 19): 1) Northern Norway (Kirkenes), close to the species' northern distribution limit; 2) Denmark (Blushøy); 3) Brittany (Roscoff), an ancient refugial population of high genetic diversity (Coyer *et al.*, 2003; Hoarau *et al.*, 2007); and 4) Spain (Ribadeo), the southern edge and ancient refugial population of low genetic diversity (Coyer *et al.*, 2003; Hoarau *et al.*, 2007). Besides differing in biogeographic history, these populations further represent different thermal regimes. Norway represents a cold thermal regime characterized by an annual temperature range (2 ° - 13 °C) that overlaps only partly with the range at the French (8 ° - 18 °C) and barely with the range at the Spanish (12 ° - 21 °C) locations, both representing warm thermal regimes. The Danish location experiences highest thermal variability with annual temperatures ranging from ca. 1°C to 21°C.

2 Discussion

Main contributions

Climate change in the North Atlantic involves rapid warming (Müller *et al.*, 2009; Lee *et al.*, 2011) and increasing numbers of heat waves (Schär *et al.*, 2004; Barriopedro *et al.*, 2011). Both events challenge the plastic and adaptive responding potential of marine species, especially those species inhabiting the rocky intertidal (Somero, 2010; Tomanek, 2010). On temperate rocky shores, responses of foundational seaweed species to climate change can influence the entire intertidal ecosystem (Christie *et al.*, 2009; Harley *et al.*, 2012). Accordingly, the overall objective of this dissertation was to identify the impact of climate change on seaweed meadows in the North-Atlantic rocky intertidal with focus on the brown canopy-forming macroalga *Fucus serratus*. My first aim (**paper I**) was to identify regions where climate change will have a major impact on the future distribution of seaweed meadows and their associated community along North-Atlantic shores. Additionally, I aimed to identify if the predominant seaweeds will shift as a coherent species assemblage or if the shift will only involve a subset of component species. My second aim (**paper II**) was built on these predictions and assessed how thermal tolerance of the predominant seaweed *F. serratus* varies spatially and could mitigate the predicted extinction from its southern-most distribution (Iberian Peninsula). My third specific aim (**paper III**) was to identify evolutionary changes in *F. serratus* at the molecular level over the past decade and to assess the adaptive potential of four populations along the East-Atlantic shore. My key findings, visualized in Figure 22, were:

- **Paper I**: Under climate change projections, Ecological Niche Modeling (ENM) suggests that suitable seaweed habitat will emerge along Arctic shores and that seaweed meadows will disappear from shores south of 45°latitude North by 2200. The predominant North-Atlantic seaweeds will likely shift as a coherent species assemblage.

- **Paper II**: Low heat stress resilience in France and reduced responsiveness (in terms of *hsp* gene expression) to further increasing temperatures in northern Spain indicate that the plasticity of *F. serratus* might be insufficient to prevent its extinction from ancient glacial refugia along its southern distributional edge.

- **Paper III**: Genetic changes over the past decade were highest in the southern ancient glacial refugia of *F. serratus* and included a putatively adaptive outlier locus. The effective population sizes (N_e) were generally low thus potentially reducing the species' adaptive capacity. Furthermore, loss of genetic diversity and inbreeding depression may threaten its Spanish southern edge with extinction. Only the ancient glacial refugium in France has likely sufficient evolutionary potential to persist under climate change.

Regions under change

Seaweeds are foundational species (e.g. Christie *et al.*, 2009; Harley *et al.*, 2012) and can help mediating the impact of climate change on the associated rocky shore community. Consequently, the most significant shifts will likely occur in warm-temperate North-Atlantic regions where seaweed-meadows are predicted to disappear and in Arctic regions where suitable seaweed habitat is predicted to emerge before 2200 (**paper I**). The extent to which these predictions will be realized depends largely on two factors that the ENM analysis did not address: the species' plastic and adaptive responding potential (addressed for *F. serratus* in **paper II** and **III**). The responses of the four *F. serratus* populations are likely representative for the species' mid-range and range-edge populations, as the genetic characteristics (**paper III**) reflect the species' biogeographic history and are in agreement with earlier findings (Coyer *et al.*, 2003; Hoarau *et al.*, 2007).

Extinction risk at the southern edge

The southern range limit of *F. serratus* in the North-Iberian Peninsula was predicted to become extinct by 2100 if its adaptive and plastic responsiveness is low (**paper I**). An adaptive genetic shift over the past decade in the Spanish population was indicated by the presence of numerous outlier loci (13 %, **paper III**). However, this response to selection involved high costs (Orr & Unckless, 2008; Palstra & Ruzzante, 2008; Bell & Gonzalez, 2009) as abundance declined by 90% (Figure S6 in **paper I**), and allelic richness declined significantly (**paper III**). Because of its small effective population size, the Spanish population may have low adaptive potential to further environmental change and inbreeding may occur (Palstra & Ruzzante, 2008; Charlesworth, 2009; Bijlsma & Loeschcke, 2012) (**paper III**). My data agree closely with other Spanish southern edge populations of *F. serratus* showing low fitness (Arrontes, 2002; Viejo *et al.*, 2011; Martínez *et al.*, 2012) and support the hypothesis that high constitutive *hsp* gene expression is a precautionary protection against chronic warm temperature stress and impedes heat stress response to further thermal stress (Tomanek, 2008; Somero, 2010; Tomanek, 2010) (**paper II**). In conclusion, it is likely that *F. serratus* has insufficient plastic and adaptive potential to prevent its predicted extinction from the North-Iberian Peninsula within the next 200 years (**paper I**). The southern edge populations of *F. serratus* merit a special conserva-

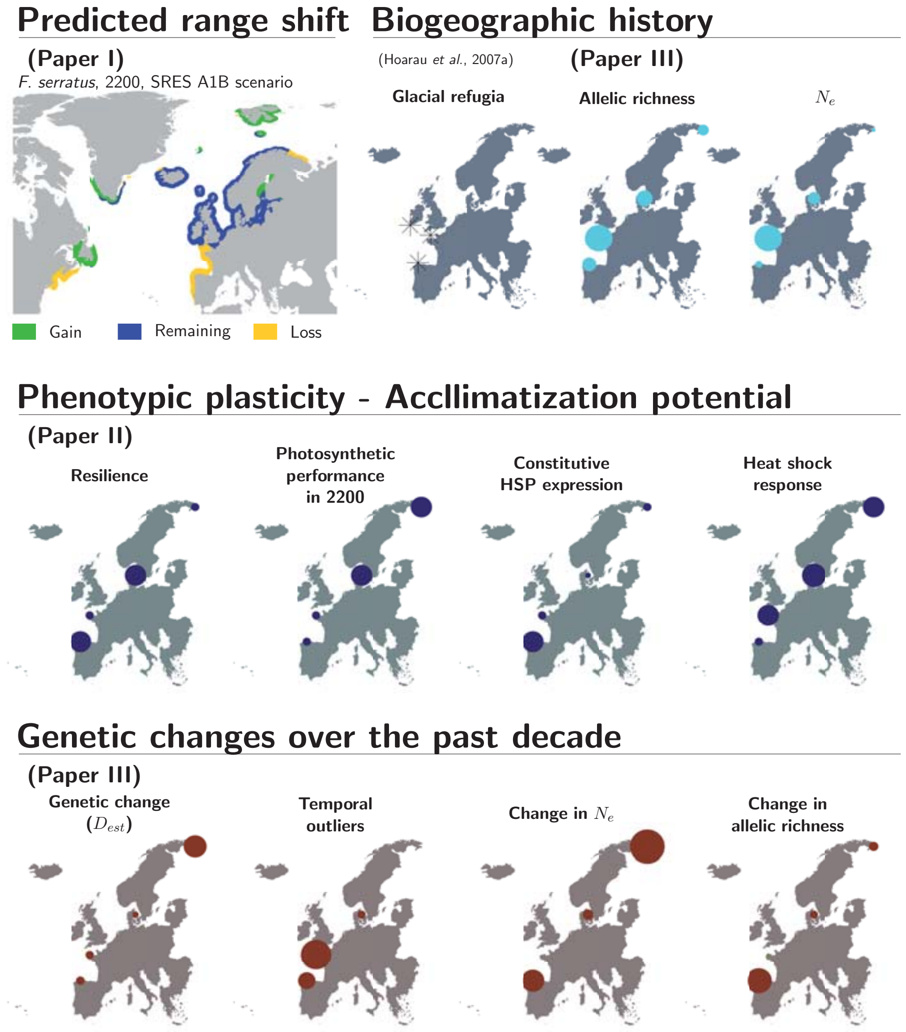


Figure 22: Key findings of the three thesis-associated papers on climate change responses of the seaweed *F. serratus*. **Paper II** and **III** are based on the same four sampling locations indicated by the dots along the East-Atlantic shore. The locations of ancient glacial refugia are based on Hoarau *et al.* (2007). The size of the dots representing the major findings of **paper II** are not quantitative but interpretative and aim to summarize differences in the populations' heat stress response visually (bigger dots indicate "more" or "better"). 'Photosynthetic performance in 2200' indicates the performance at maximum SST predicted for year 2200. The summarized findings of **paper III** and the present-day effective population-size (N_e) and allelic richness (mean number of alleles per locus) are based on quantitative results. Changes in N_e and allelic richness over the past decade are relative to values of the older samples (collected around 2000). The changes were too small in the Brittany population to be depicted.

tion effort, particularly because of strong local differentiation (Coyer *et al.*, 2003), in order to protect its genetic distinctiveness (Hoarau *et al.*, 2007) and potentially high regional among-population diversity (Hampe & Petit, 2005; Diekmann & Serrao, 2012; Neiva *et al.*, 2012).

Extinction risk in Brittany

F. serratus was predicted to become extinct south of Great Britain by 2200 (**paper I**) and thus, lose its ancient glacial refugium in Brittany. Brittany displayed the highest genetic diversity (**paper III**), a characteristic shared by ancient refugial populations of various other North-Atlantic species with the same biogeographic history (reviewed in Maggs *et al.*, 2008). High genetic variation is generally associated with increased adaptive potential (Teotónio *et al.*, 2009; Bijlsma & Loeschcke, 2012), which may account for the high proportion of temporal outlier loci (**paper III**). Nevertheless, the Brittany population did not show increased resilience to heat stress (**paper II**), a potential problem as physiologically stressful temperatures (≥ 24 °C) are predicted by 2200 (**paper II**). High effective population size and genetic diversity (**paper III**) suggest that Brittany is less sensitive to genetic drift effects (Palstra & Ruzzante, 2008; Charlesworth, 2009) and might have sufficient adaptive and/or plastic potential to prevent its predicted extinction under climate change (**paper I**). The Brittany region could serve as a source for adaptive rescue (Bell & Gonzalez, 2009, 2011; Bijlsma & Loeschcke, 2012) of the species' threatened southern edge and the genetic diversity of *F. serratus* in this region may enhance resilience of the entire seaweed-associated community (Hughes *et al.*, 2008) (as it was found for seagrass beds (Hughes & Stachowicz, 2004; Reusch *et al.*, 2005; Procaccini *et al.*, 2007; Ehlers *et al.*, 2008)). Consequently, it is important to track the fitness state of *F. serratus* in the Brittany region in order to initiate effective conservation measures.

Performance in the Kattegat

The annual temperature range at the Danish sampling site (20 °C) was much higher than at the other three sampling sites (9 °C - 11 °C) (**paper II** and **III**). Adaptation to increased thermal variability could explain its increased heat stress resilience (recovery from up to 32 °C, **paper II**) in a manner similar to that displayed by the red alga *Asparagopsis taxiformis*, which showed increased photosynthetic acclimatization potential in populations from an environment with increased thermal variability (Padilla-Gamino & Carpenter, 2007). Although, highly speculative, increased physiological acclimation potential (**paper II**) could dampen selective pressure (relaxed selection (Snell-Rood *et al.*, 2010)) and might explain why its adaptive response was reduced (less outlier loci) compared to the Brittany and Spanish populations (Fig. 22, **paper III**).

Colonization potential in Arctic regions

Arctic regions (Canada, Greenland and Spitsbergen) were predicted to provide suitable habitat for temperate seaweeds by the end of the 21st century (**paper I**). The ability of temperate seaweeds to colonize Arctic rocky shores, however, may be hindered by the polar photoperiod of up to six months of darkness. The Norwegian northern edge population of *F. serratus* displayed low genetic diversity and effective population size (**paper III**), suggesting that its adaptive potential to "new" environmental conditions may be low (Palstra & Ruzzante, 2008; Bijlsma & Loeschcke, 2012). Although evolutionary change played a major role in range shifts resulting from historical climate change (Davis & Shaw, 2001; Thomas *et al.*, 2001), leading edge populations are characterized by low genetic diversity (Pauls *et al.*, 2013, and references therein). Their survival is often enhanced by the 'surfing' of favorable mutations that can rapidly increase in frequency over iterated founder events (Klopfstein *et al.*, 2006; Excoffier & Ray, 2008; McInerny *et al.*, 2009). Thus, the low genetic diversity of *F. serratus*' northern edge populations does not necessarily inhibit adaptation to the environmental conditions on Arctic shores. Arctic shores of Greenland and Svalbard may be reached by *A. nodosum* and *F. vesiculosus*, as they bear flotation vesicles, and accordingly show long-distance dispersal across the Atlantic (John, 1974; Van den Hoek, 1987; Olsen *et al.*, 2010). In contrast, long-distance dispersal of *F. serratus* to Iceland and Canada was mediated by human shipping transport (Coyer *et al.*, 2006; Brawley *et al.*, 2009; Johnson *et al.*, 2012), as it lacks flotation vesicles and sinks if not attached to flotsam or jetsam (discussed in **paper I**). Thus, arctic colonists of *F. serratus* may not be located at the species' northern edge, but within European harbors with frequent shipping traffic to the northern polar regions.

Climate change responses

Climate change involves multiple simultaneous stressors

Climate change involves simultaneous changes of various biotic and abiotic factors that can strongly affect marine communities (Harley *et al.*, 2006; Wahl *et al.*, 2011; Harley *et al.*, 2012). For example, changing biotic interactions can trigger major community reorganizations, as demonstrated by numerous examples of 'phase shifts' in which removal of a key species allows another species to become dominant (Estes & Duggins, 1995; Nyström *et al.*, 2000). How the warm-temperate community will change under a scenario that integrates both the positive impact of increasing SST and the negative impact of ocean acidification on calcified herbivores is still poorly understood (reviewed in Harley *et al.*, 2012). The ENM analysis, however, identified SST derivatives as most important predictors for the geographic distribution of our focal seaweed species (**paper I**). As their distributional ranges were mainly limited by temperature, the seaweeds were predicted to follow the northward isotherm shift as a coherent assemblage (**paper I**). Thus, for seaweeds that strongly depend on SST isotherms (Breeman, 1988; Eggert, 2012), ENMs being based on temperature changes (**paper I**) can indeed provide a first good approximation of climate change induced niche shifts (Pearson & Dawson, 2003; Araújo & Guisan, 2006).

Heat stress tolerance depends on several environmental factors and the intrinsic acclimation potential. A meta-analysis revealed that the effect of multiple abiotic stressors on *Fucus* spp. can be additive, synergistic or antagonistic (Wahl *et al.*, 2011). For example, hyper-salinity was found to increase heat stress tolerance of fucoid embryos (antagonistic effect) (Li & Brawley, 2004). Long-term heat stress experiments, moreover, might reveal higher tolerance limits than those recorded under acute heat stress exposure as the study organisms are allowed to acclimatize gradually and thus top shift their heat tolerance to future conditions (Somero, 2010). A realistic heat wave may follow a temperature increase of 1 °C - 2 °C day^{-1} from 19 °C to 26 °C, followed by a stress period of 3 weeks at 26 °C (Franssen *et al.*, 2011), based on the temperature profile recorded during the Heat Wave in summer 2003 (Reusch *et al.*, 2005). In contrast, **paper II** and previous heat stress experiments on *F. serratus* were focused on acute temperature stress (Lüning, 1984; Ireland *et al.*, 2004; Pearson *et al.*, 2009; Pearson *et al.*, 2010). These single-factor common garden experiments, however, identified ecotypic differentiation in the thermal tolerance of *F. serratus* and thus are of great value to assess spatial variation in the extinction risk when temperature is the predominant dynamic environmental factor (**paper II**, Pelini *et al.*, 2012).

Accordingly, the temporal outlier loci (identified in **paper III**) could have responded to various other environmental changes than temperature, particularly as the North-Atlantic is a region that has experienced high human impact over the past decade, such as chemical pollution, eutrophication, ocean acidification and UV radiation (Halpern *et al.*, 2008). Although all of these factors affect seaweed fitness (e.g. Altamirano *et al.*, 2003; Porzio *et al.*, 2011; Wahl *et al.*, 2011), the ENMs have shown that temperature is the most important abiotic factor for the three focal seaweeds in **paper I**. Increasing grazing pressure on South-European shores (Southward *et al.*, 1995; Hawkins *et al.*, 2008; Harley *et al.*, 2012) (discussed in **paper I**) may be another selection pressure that could explain the high proportion of temporal outlier loci in the southern range of *F. serratus* (**paper III**).

One locus (F19), however, revealed spatial and temporal signatures of selection that, in combination, increased confidence that temperature was likely a major selective force. Thus, combined spatio-temporal genome scan approaches can be a powerful strategy to single out loci affected by specific selection pressures under a multitude of environmental changes (Orsini *et al.*, 2012). However, to ultimately confirm the association of evolutionary changes at the molecular level with specific selective agents requires complementary investigations in the field and lab.

Capturing heat-stress protection at the cellular level

Besides heat shock proteins, metabolic and cell membrane adjustments can have heat protective functions (Feder & Hofmann, 1999; Sørensen & Loeschcke, 2007; Eggert, 2012). For example, the transcriptomic heat-stress response of the red alga *Chondrus crispus* (assessed via cDNA microarrays) revealed that major resource allocations and genes encoding detoxifying enzymes also were involved in warm temperature acclimation (Collén *et al.*, 2007). Furthermore, EST libraries of heat-shocked *F. serratus* and *F. vesiculosus* also identified expression of genes implicated in photoprotection (Pearson *et al.*, 2010). Thus, *hsp* gene expression per se does not necessarily indicate the thermotolerance of a physiological process within an organism. Moreover, transcriptional *hsp* gene expression may not directly correlate with the presence of functional heat-stress proteins, owing to post-transcriptional and -translational gene-regulation mechanisms (Feder & Walser, 2005; Halbeisen *et al.*, 2008). Thus, assessment of the heat stress response (HSR) in three *hsp* genes was complemented with measurements of photosynthetic performance (**paper II**). These measurements served as control for the potential activity of other stress-protective mechanisms that could explain unexpected *hsp* gene expression patterns. As photosynthesis is especially sensitive to high temperatures (Berry & Bjorkman, 1980; Zhang & Sharkey, 2009; Stefanov *et al.*, 2011) it may integrate the effect of temperature on an organism's total metabolism. Thus, physiological temperature tolerance limits and a species' vulnerability to climate change are ideally assessed by measuring complementary stress indicators, like *hsp* gene expression and photosynthetic performance or growth (Eggert, 2012).

Heat stress tolerance can differ between life stages

Juvenile stages are often more susceptible than adult individuals (e.g. Brawley & Johnson, 1991; Schiel & Foster, 2006). For example, while *F. serratus* tolerates temperatures between 0 °C and 25 °C (Lüning *et al.*, 1990) in the adult stage, growth of juvenile stages is inhibited at temperatures $>$18 °C (Arrontes, 1993). The thermal tolerance of *F. serratus* was assessed in adult individuals (**paper II**) as juveniles are difficult to raise in the lab. Consequently, temperatures at which I found significant stress in the adult stage (≥ 24 °C in all four populations, **paper II**) could indeed prevent successful recruitment of juvenile stages. At the Spanish and French sampling sites, where water temperatures were predicted to frequently reach 24 °C by 2200 (**paper II**), *F. serratus* and *F. vesiculosus* may thus experience a rapid abundance decline (confirming our predictions in **paper I**) as they rely on nearly annual recruitment with a generation time of 1 - 2 years (e.g. Coyer *et al.*, 2007). Consequently, also selective pressures may be highest on the juvenile life stage. Thus, besides a combined spatio-temporal genome scan approach (**paper III**), another promising approach to identify outlier loci playing a putative role in thermal adaptation, would be to track allele frequency shifts in genetic markers during larval development under heat stress. This approach revealed, for example, adaptive genetic responses in sea urchin larvae in response to seawater acidification (Pespeni *et al.*, 2013).

3 Future perspectives

Integrative niche modeling approach

ENMs are an appropriate approach to predict range shifts of seaweeds under climate change, as their range limits generally correlate directly with SST isotherms (Breeman, 1988; Lüning *et al.*, 1990; Eggert, 2012). Nevertheless, these models can only give a first rough approximation of future distributions as they do not take biological aspects or the eco-evolutionary responding potential of the focal species into account (Parmesan & Yohe, 2003; Hijmans & Graham, 2006; Araújo & Luoto, 2007; Thuiller *et al.*, 2008; Lavergne *et al.*, 2010)

I investigated the physiological acclimatization potential (**paper II**) and adaptive responsiveness (**paper III**) of *F. serratus* to identify if these could prevent its predicted extinction from shores south of Great Britain (**paper I**). However, instead of discussing how eco-evolutionary responses could alter the predicted shift of correlative niche models, the ultimate aim is to integrate information on a species' plasticity, adaptability, dispersal potential, and biotic interactions into a single forecasting approach (Moore *et al.*, 2007; Lavergne *et al.*, 2010) (Figure 23). Although the need for an integrative approach is well recognized (e.g. Pearson & Dawson, 2003; Guisan & Thuiller, 2005; Guisan *et al.*, 2006; Lavergne *et al.*, 2010; Sinclair *et al.*, 2010), implementation is largely unexplored and lacks consensus.

ENMs or correlative niche models can incorporate species interactions. For example, the distribution of shrublands (habitat) and host plants (food) were considered biotic variables in the niche models of endangered bird and butterfly species (Prestion *et al.*, 2008). Ecotypic differentiation and regional niche space variation also was included in correlative model predictions by partitioning the models regionally (Murphy & Lovett-Doust, 2007). Mechanistic approaches (see section 1) have great potential to incorporate evolutionary changes (Angilletta, 2009; Kearney & Porter, 2009), as pioneering studies demonstrate (e.g. Kearney *et al.*, 2008, 2009; Kramer *et al.*, 2010). Both the correlative and mechanistic approach were used to predict range shifts under climate change (Thuiller, 2003; Crozier & Dwyer, 2006; Dormann, 2007; Buckley, 2008; Elith *et al.*, 2010; Austin & Van Niel, 2011) and could be combined in an integrative forecasting approach (Kearney & Porter, 2009; Morin & Thuiller, 2009; Mokany & Ferrier, 2011). Also promising is a hierarchical modeling framework where correlative niche models build the framework at the largest spatial scale at which climate can be considered the dominant niche-limiting factor, while biotic interactions and dispersal become important at more local scales (Pearson & Dawson, 2003; Guisan & Thuiller, 2005). Implementing these approaches is a chal-

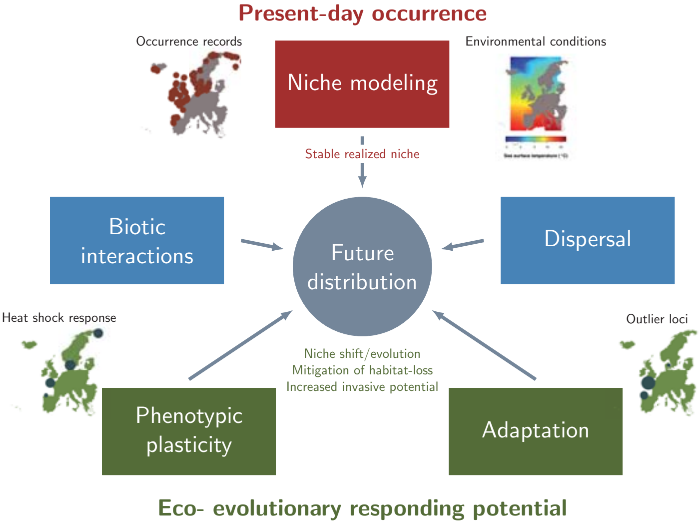


Figure 23: Integrative niche modeling approach. Combining the potential of correlative and mechanistic niche model approaches to incorporate plastic and adaptive responses as well as dispersal capacity and biotic interactions of species provides a promising integrative forecasting approach to predict species range shifts under climate change more realistically.

lenging task but will certainly improve the power of niche models to predict range shifts and to assess species extinction risks under climate change with more realistic assumptions.

Next generation sequencing opens the 'omics-era for non-model species

A first step in relating the outlier loci identified in **paper III** to functional biological changes and to ultimately identify their evolutionary importance, would be to assemble a reference genome (Vasemagi & Primmer, 2005) in order to identify the genomic position and the genetic surroundings of the outliers. The genome sequence of the filamentous brown alga *Ectocarpus siliculosus* was recently published (Cock *et al.*, 2010a,b). However, because of the large phylogenetic distance among different taxa of brown algae (heterokontophyta) (Keeling *et al.*, 2005), it is likely to vary significantly from the *Fucus* genome and thus, of limited value for genomic studies on *Fucus*. *De novo* sequencing of non-model species genomes has become possible at a relatively low-cost with the advent of Next Generation Sequencing (NGS Metzker, 2010) (reviewed in Stapley *et al.*, 2010; Ekblom & Galindo, 2011). Assembling the *Fucus* genome (ca. 1,100 Mbp (Peters *et al.*, 2004)) will be easier from hermaphroditic selfers such as *F. distichus* as the intra-individual genetic variation is lower compared to dioecious outcrossers, such as *F. ser-*

ratus. However, it will take much effort and time to identify the functional value of the expressed genome part before we can relate differences at the molecular level to functional differences and confirm their adaptive value.

The biggest contribution of NGS for evolutionary studies on non-model species is that it allows genotyping of thousands of genetic markers in parallel, primarily by identifying SNPs (Slate *et al.*, 2009). High coverage genomic scans provide a picture of allele frequency variations throughout the genome in high resolution and less likely to miss evolutionary important genomic responses (Gilad *et al.*, 2009; Stapley *et al.*, 2010; Ekblom & Galindo, 2011). NGS approaches were first applied to non-model organisms in 2007 (Toth *et al.*, 2007; Ekblom & Galindo, 2011) and recently identified loci underlying ecotypic differentiation in whitefish species *Coregonus* spp. (Renaut *et al.*, 2010), the apple maggot fly *Rhagoletis pomonella* (Schwarz *et al.*, 2009) and the marine snail *Littorina saxatilis* (Galindo *et al.*, 2010). NGS is becoming a crucially important technique for identifying evolutionary important variation at the molecular level in non-model organisms.

Another valuable approach using NGS is RNA-seq or whole transcriptome profiling, which identifies gene regulation patterns at the transcriptomic level (Wang *et al.*, 2009; Valerio *et al.*, 2010; Hornett & Wheat, 2012). While a quantitative real-time PCR (qPCR) approach (**paper II**) was sufficient to identify expression patterns of predefined candidate genes, RNA-seq tracks regulatory variation over the entire transcriptome and identifies new candidate genes that may play a key role in stress tolerance and local adaptation (Ekblom & Galindo, 2011). RNA-seq involves sequencing of thousands of EST transcripts from cDNA (reverse transcribed mRNA) libraries to quantify regulatory variation at each transcript with high precision (Gilad *et al.*, 2009; Wang *et al.*, 2009). For example, this approach identified divergent gene expression patterns during heat stress recovery in the foundation species *Zostera marina* suggesting local thermal adaptation (Franssen *et al.*, 2011). An alternative to quantifying gene expression to identify putatively adaptive genes, is to screen the sequenced reads for transcripts with a high proportion of non-synonymous substitutions, as it was done in cichlid fishes (Elmer *et al.*, 2010) and lake whitefish species pairs (Renaut *et al.*, 2010). Although RNA-seq involves certain bias in gene-expression quantification (owing to base-composition or read length or introduced during library preparation or read-mapping) (Gilad *et al.*, 2009; Ekblom & Galindo, 2011), it is a promising approach to understand transcriptomic gene regulation and the molecular basis of local adaptation. Certainly, NGS can bring us a step closer to answer the fundamental question of which genes and associated biological functions are involved in rapid adaptive responses (e.g. Stinchcombe & Hoekstra, 2007; Ekblom & Galindo, 2011) and more specifically, if and how seaweeds might keep pace with anthropogenic climate change.

4 Conclusions

Over the next two centuries, climate change is predicted to have a major impact on the rocky intertidal ecosystems of the North Atlantic with the disappearance of the major canopy forming fucoids along their southern distributional range and the opening of new habitat in the Arctic. Effective population size and genetic diversity will be the keys to their adaptive and plastic potential and subsequent persistence under climate change. For marine macroalgae, glacial refugia are often characterized by high genetic variation. These diversity hot spots, such as the Brittany area, are likely to play again a crucial role in the persistence of these species. However, at the southern edge of the seaweed *F. serratus*, both the species' physiological acclimatization potential and the adaptive capacity are likely insufficient to prevent its predicted extinction. Extinction of *F. serratus* and other fucoids from rocky shores in southern Europe will undoubtedly trigger major ecological changes in the entire associated ecosystem. The work in this thesis illustrates the potential of a multidisciplinary approach to investigate the ecological and evolutionary responses of a key species to global warming. This highlights the need for integrative studies in order to further understand and predict the effect of climate change on natural ecosystems.

5 References

Aitken SN, Yeaman S, Holliday JA, Wang T, & Curtis-McLane S (2008). Adaptation, migration or extirpation: climate change outcomes for tree populations. *Evol. Appl.* **1**, 95–111.

Alahuhta J, Heino J, & Luoto M (2011). Climate change and the future distributions of aquatic macrophytes across boreal catchments. *J. Biogeogr.* **38**, 383–393.

Alexander LV, Zhang X, Peterson TC, Caesar J, Gleason B, Klein Tank AMG, *et al.* (2006). Global observed changes in daily climate extremes of temperature and precipitation. *J. Geophys. Res. - Atm.* **111**.

Altamirano M, Flores-Moya A, Kuhlenkamp R, & Figueroa FL (2003). Stage-dependent sensitivity to ultraviolet radiation in zygotes of the brown alga *Fucus serratus*. *Zygote*, **11**, 101–106.

Angilletta MJ (2009). Thermal adaptation: a theoretical and empirical synthesis. New York: Oxford University Press.

Araújo MB & Guisan A (2006). Five (or so) challenges for species distribution modelling. *J. Biogeogr.* **33**, 1677–1688.

Araújo MB & Luoto M (2007). The importance of biotic interactions for modelling species distributions under climate change. *Glob. Ecol. Biogeogr.* **16**, 743–753.

Araújo R, Serrão EA, Sousa-Pinto I, & berg P (2011). Phenotypic differentiation at southern limit borders: The case study of two fucoid macroalgal species with different life-history traits. *J. Phycol.* **47**, 451–462.

Arrontes J (1993). The nature of the distributional boundary of *Fucus serratus* on the north shore of Spain. *Mar. Ecol. Prog. Ser.* **93**, 183–193.

Arrontes J (2002). Mechanisms of range expansion in the intertidal brown alga *Fucus serratus* in northern Spain. *Mar. Biol.* **141**, 1059–1067.

Augustin L, Barbante C, Barnes PR, Barnola JM, Bigler M, Castellano E, *et al.* (2004). Eight glacial cycles from an Antarctic ice core. *Nature*, **429**, 623–628.

Austin MP & Van Niel KP (2011). Improving species distribution models for climate change studies: variable selection and scale. *J. Biogeogr.* **38**, 1–8.

Baker NR (2008). Chlorophyll fluorescence: a probe of photosynthesis *in vivo*. *Annu. Rev. Plant Biol.* **59**, 89–113.

Balanya J, Oller JM, Huey RB, Gilchrist GW, & Serra L (2006). Global genetic change tracks global climate warming in *Drosophila subobscura*. *Science*, **313**, 1773–1775.

Barnett TP, Pierce DW, AchutaRao KM, Gleckler PJ, Santer BD, Gregory JM, *et al.* (2005). Penetration of human-induced warming into the world's oceans. *Science*, **309**, 284–287.

Barnosky AD, Matzke N, Tomiya S, Wogan GO, Swartz B, Quental TB, *et al.* (2011). Has the Earth's sixth mass extinction already arrived? *Nature*, **471**, 51–57.

Barriopedro D, Fischer EM, Luterbacher J, Trigo RM, & García-Herrera R (2011). The hot summer of 2010: redrawing the temperature record map of Europe. *Science*, **332**, 220–224.

Beaugrand G, Luczak C, & Edwards M (2009). Rapid biogeographical plankton shifts in the North Atlantic Ocean. *Glob. Change Biol.* **15**, 1790–1803.

Beaugrand G, Reid PC, Ibanez F, Lindley JA, & Edwards M (2002). Reorganization of North Atlantic marine copepod biodiversity and climate. *Science*, **296**, 1692–1694.

Bell G & Gonzalez A (2009). Evolutionary rescue can prevent extinction following environmental change. *Ecol. Lett.* **12**, 942–948.

Bell G & Gonzalez A (2011). Adaptation and evolutionary rescue in metapopulations experiencing environmental deterioration. *Science*, **332**, 1327–1330.

Beniston M & Stephenson D (2004). Extreme climatic events and their evolution under changing climatic conditions. *Glob. Planet Change*, **44**, 1–9.

Berry J & Bjorkman O (1980). Photosynthetic response and adaptation to temperature in higher plants. *Annu. Rev. Plant Physiol.* **31**, 491–543.

Berteaux D, Reale D, McAdam AG, & Boutin S (2004). Keeping pace with fast climate change: can arctic life count on evolution? *Integr. Comp. Biol.* **44**, 140–151.

Bierne N, Welch J, Etienne L, Bonhomme F, & David P (2011). The coupling hypothesis: why genome scans may fail to map local adaptation genes. *Mol. Ecol.* **20**, 2044–2072.

Bijlsma R & Loeschcke V (2012). Genetic erosion impedes adaptive responses to stressful environments. *Evol. Appl.* **5**, 117–129.

Boaden PJS (1996). Habitat provision for meiofauna by *Fucus serratus* epifauna with particular data on the flatworm *Monocelis lineata*. *Mar. Ecol.* **17**, 67–75.

Bourret V, O'Reilly P, Carr J, Berg P, & Bernatchez L (2011). Temporal change in genetic integrity suggests loss of local adaptation in a wild Atlantic salmon (*Salmo salar*) population following introgression by farmed escapees. *Heredity*, **106**, 500–510.

Bradshaw WE & Holzapfel CM (2001). Genetic shift in photoperiodic response correlated with global warming. *Proc. Natl. Acad. Sci.* **98**, 14509–14511.

Bradshaw WE & Holzapfel CM (2006). Climate change - evolutionary response to rapid climate change. *Science*, **312**, 1477–1478.

Bradshaw WE & Holzapfel CM (2008). Genetic response to rapid climate change: it's seasonal timing that matters. *Mol. Ecol.* **17**, 157–66.

Brawley SH, Coyer JA, Blakeslee AMH, Hoarau G, Johnson LE, Byers JE, *et al.* (2009). Historical invasions of the intertidal zone of Atlantic North America associated with distinctive patterns of trade and emigration. *Proc. Natl. Acad. Sci.* **106**, 8239–8244.

Brawley SH & Johnson LE (1991). *Survival of fucoid embryos in the intertidal zone depends upon developmental stage and habitat*.

Breeman AM (1988). Relative importance of temperature and other factors in determining geographic boundaries of seaweeds: experimental and phenological evidence. *Helgol. Mar. Res.* **42**, 199–241.

Buckley BA & Somero GN (2009). cDNA microarray analysis reveals the capacity of the cold-adapted Antarctic fish *Trematomus bernacchii* to alter gene expression in response to heat stress. English. *Polar Biol.* **32**, 403–415.

Buckley LB (2008). Linking traits to energetics and population dynamics to predict lizard ranges in changing environments. English. *Am. Nat.* **171**,

Bussotti F, Desotgiu R, Pollastrini M, & Cascio C (2010). The JIP test: a tool to screen the capacity of plant adaptation to climate change. *Scand. J. Forest Res.* **25**, 43–50.

Carss DN & Elston DA (2003). Patterns of association between algae, fishes and grey herons *Ardea cinerea* in the rocky littoral zone of a Scottish sea loch. *Estuar. Coast. Shelf Sci.* **58**, 265–277.

Chapman ARO (1995). Functional ecology of fucoid algae: twenty-three years of progress. *Phycologia*, **34**, 1–32.

Charlesworth B (2009). Effective population size and patterns of molecular evolution and variation. *Nat. Rev. Genet.* **10**, 195–205.

Christie H, Norderhaug KM, & Fredriksen S (2009). Macrophytes as habitat for fauna. *Mar. Ecol. Prog. Ser.* **396**, 221–233.

Clark MS, Fraser KP, & Peck LS (2008a). Antarctic marine molluscs do have an HSP70 heat shock response. English. *Cell Stress Chaperones*, **13**, 39–49.

Clark M, Fraser K, & Peck L (2008b). Lack of an HSP70 heat shock response in two Antarctic marine invertebrates. English. *Polar Biol.* **31**, 1059–1065.

Clark M & Peck L (2009). HSP70 Heat shock proteins and environmental stress in Antarctic marine organisms: a mini-review. *Mar. Genomics*, **2**, 11–18.

Cock JM, Coelho SM, Brownlee C, & Taylor AR (2010a). The *Ectocarpus* genome sequence: insights into brown algal biology and the evolutionary diversity of the eukaryotes. *New Phytol.* **188**, 1–4.

Cock JM, Sterck L, Rouze P, Scornet D, Allen AE, Amoutzias G, *et al.* (2010b). The *Ectocarpus* genome and the independent evolution of multicellularity in brown algae. *Nature*, **465**, 617–621.

Collén J, Guisle-Marsollier I, Léger JJ, & Boyen C (2007). Response of the transcriptome of the intertidal red seaweed *Chondrus crispus* to controlled and natural stresses. *New Phytol.* **176**, 45–55.

Connell SD (2005). Assembly and maintenance of subtidal habitat heterogeneity: synergistic effects of light penetration and sedimentation. *Mar. Ecol. Prog. Ser.* **289**, 53–61.

Coyer JA, Hoarau G, Pearson G, Mota C, Juterbock A, Alpermann T, *et al.* (2011). Genomic scans detect signatures of selection along a salinity gradient in populations of the intertidal seaweed *Fucus serratus* on a 12 km scale. *Mar. Genomics*, **4**, 41–49.

Coyer JA, Hoarau G, Skage M, Stam WT, & Olsen JL (2006). Origin of *Fucus serratus* (Heterokontophyta, Fucaceae) populations in Iceland and the Faroes: a microsatellite-based assessment. *Eur. J. Phycol.* **41**, 235–246.

Coyer JA, Hoarau G, Stam WT, & Olsen JL (2007). Hybridization and introgression in a mixed population of the intertidal seaweeds *Fucus evanescens* and *F. serratus*. *J. Evol. Biol.* **20**, 2322–2333.

Coyer JA, Peters AF, Stam WT, & Olsen JL (2003). Post-ice age recolonization and differentiation of *Fucus serratus* L. (Phaeophyceae, Fucaceae) populations in Northern Europe. *Mol. Ecol.* **12**, 1817–1829.

Crozier L & Dwyer G (2006). Combining population-dynamic and ecophysiological models to predict climate-induced insect range shifts. *Am. Nat.* **167**, 853–866.

Dahlhoff EP (2004). Biochemical indicators of stress and metabolism: applications for marine ecological studies. *Annu. Rev. Physiol.* **66**. PMID: 14977401, 183–207.

Davis MB & Shaw RG (2001). Range shifts and adaptive responses to quaternary climate change. *Science*, **292**, 673–679.

Dayton P (1972). . *Proceedings of the Colloquium on Conservation Problems*. Ed. by B Parker. Lawrence, Kansas: Allen Press. Chap. Towards an understanding of community resilience and the potential effects of enrichment to the benthos at McMurdo Sound, Antarctica, 81–96.

De Jong G (2005). Evolution of phenotypic plasticity: patterns of plasticity and the emergence of ecotypes. *New Phytol.* **166**, 101–118.

Diekmann OE & Serrao EA (2012). Range-edge genetic diversity: locally poor extant southern patches maintain a regionally diverse hotspot in the seagrass *Zostera marina*. *Mol. Ecol.* **21**, 1647–1657.

Dijkstra JA, Boudreau J, & Dionne M (2012). Species-specific mediation of temperature and community interactions by multiple foundation species. *Oikos*, **121**, 646–654.

Domingues CM, Church JA, White NJ, Gleckler PJ, Wijffels SE, Barker PM, *et al.* (2008). Improved estimates of upper-ocean warming and multi-decadal sea-level rise. *Nature*, **453**, 1090–1093.

Dormann CF (2007). Promising the future? Global change projections of species distributions. *Basic Appl. Ecol.* **8**, 387–397.

Easterling DR, Meehl GA, Parmesan C, Changnon SA, Karl TR, & Mearns LO (2000). Climate extremes: observations, modeling, and impacts. *Science*, **289**, 2068–2074.

Edwards M (2009). . *Climate change: observed impacts on planet Earth*. Ed. by TM Letcher. Oxford: Elsevier Science. Chap. Sea life (pelagic and planktonic ecosystems) as an indicator of climate and global change, 233–251.

Eggert A (2012). . *Seaweed Biology: Novel Insights into Ecophysiology, Ecology and Utilization*. Ed. by C Wiencke & K Bischof. Berlin, Germany: Springer-Verlag. Chap. Seaweed responses to temperature, 47–66.

Ehlers A, Worm B, & Reusch TBH (2008). Importance of genetic diversity in eelgrass *Zostera marina* for its resilience to global warming. *Mar. Ecol. Prog. Ser.* **355**, 1–7.

Ekblom R & Galindo J (2011). Applications of next generation sequencing in molecular ecology of non-model organisms. *Heredity*, **107**, 1–15.

Elith J, Kearney M, & Phillips S (2010). The art of modelling range-shifting species. *Methods in Ecology and Evolution*, **1**, 330–342.

Elith J & Leathwick JR (2009). Species distribution models: ecological explanation and prediction across space and time. English. *Annu. Rev. Ecol. Evol. Syst.* **40**, 677–697.

Elmer KR, Fan S, Gunter HM, Jones JC, Boekhoff S, Kuraku S, *et al.* (2010). Rapid evolution and selection inferred from the transcriptomes of sympatric crater lake cichlid fishes. *Mol. Ecol.* **19**, 197–211.

Estes JA & Duggins DO (1995). Sea otters and kelp forests in Alaska: generality and variation in a community ecological paradigm. *Ecol. Monogr.* **65**, 75–100.

Excoffier L & Lischer HEL (2010). Arlequin suite ver 3. 5: a new series of programs to perform population genetics analyses under Linux and Windows. *Mol. Ecol. Resour.* **10**, 564–567.

Excoffier L & Ray N (2008). Surfing during population expansions promotes genetic revolutions and structuration. *Trends Ecol. Evol.* **23**, 347–351.

Feder ME & Hofmann GE (1999). Heat-shock proteins, molecular chaperones, and the stress response: evolutionary and ecological physiology. *Annu. Rev. Physiol.* **61**, 243–282.

Feder ME & Walser JC (2005). The biological limitations of transcriptomics in elucidating stress and stress responses. *J. Evol. Biol.* **18**, 901–910.

Feely RA, Sabine CL, Lee K, Berelson W, Kleypas J, Fabry VJ, *et al.* (2004). Impact of anthropogenic CO on the CaCO system in the oceans. *Science*, **305**, 362–366.

Fox CW & Reed DH (2011). Inbreeding depression increases with environmental stress: an experimental study and meta-analysis. *Evolution*, **65**, 246–258.

Franssen SU, Gu J, Bergmann N, Winters G, Klostermeier UC, Rosenstiel P, *et al.* (2011). Transcriptomic resilience to global warming in the seagrass *Zostera marina*, a marine foundation species. *Proc. Natl. Acad. Sci.* **108**, 19276–19281.

Galindo J, Grahame JW, & Butlin RK (2010). An EST-based genome scan using 454 sequencing in the marine snail *Littorina saxatilis*. *J. Evol. Biol.* **23**, 2004–2016.

Garrabou J, Coma R, Benoussan N, Bally M, Chevaldonné P, Cigliano M, *et al.* (2009). Mass mortality in Northwestern Mediterranean rocky benthic communities: effects of the 2003 heat wave. *Glob. Change Biol.* **15**, 1090–1103.

Gienapp P, Teplitsky C, Alho JS, Mills JA, & Merila J (2008). Climate change and evolution: disentangling environmental and genetic responses. English. *Mol. Ecol.* **17**, 167–178.

Gilad Y, Pritchard JK, & Thornton K (2009). Characterizing natural variation using next-generation sequencing technologies. *Trends Genet.* **25**, 463–471.

Gollety C, Riera P, & Davoult D (2010). Complexity of the food web structure of the *Ascophyllum nodosum* zone evidenced by a delta C-13 and delta N-15 study. *J. Sea Res.* **64**, 304–312.

Guisan A & Zimmermann NE (2000). Predictive habitat distribution models in ecology. *Ecol. Modell.* **135**, 147–186.

Guisan A, Lehmann A, Ferrier S, Austin M, Overton JMC, Aspinall R, *et al.* (2006). Making better biogeographical predictions of species' distributions. *J. Appl. Ecol.* **43**, 386–392.

Guisan A & Thuiller W (2005). Predicting species distribution: offering more than simple habitat models. *Ecol. Lett.* **8**, 993–1009.

Halbeisen R, Galgano A, Scherrer T, & Gerber A (2008). Post-transcriptional gene regulation: from genome-wide studies to principles. English. *Cell. Mol. Life Sci.* **65**, 798–813.

Halpern BS, Walbridge S, Selkoe KA, Kappel CV, Micheli F, D'Agrosa C, *et al.* (2008). A global map of human impact on marine ecosystems. *Science*, **319**, 948–952.

Hampe A & Petit RJ (2005). Conserving biodiversity under climate change: the rear edge matters. *Ecol. Lett.* **8**, 461–467.

Hansen J, Sato M, Ruedy R, Lo K, Lea DW, & Medina-Elizade M (2006). Global temperature change. *Proc. Natl. Acad. Sci. U.S.A.* **103**, 14288–93.

Hansen MM, Meier K, & Mensberg KLD (2010). Identifying footprints of selection in stocked brown trout populations: a spatio-temporal approach. *Mol. Ecol.* **19**, 1787–1800.

Hansen MM, Olivieri I, Waller DM, Nielsen EE, & Group TGW (2012). Monitoring adaptive genetic responses to environmental change. *Mol. Ecol.* **21**, 1311–1329.

Harley CDG, Anderson KM, Demes KW, Jorve JP, Kordas RL, Coyle TA, *et al.* (2012). Effects of climate change on global seaweed communities. *J. Phycol.* **48**, 1064–1078.

Harley CDG, Randall Hughes A, Hultgren KM, Miner BG, Sorte CJB, Thornber CS, *et al.* (2006). The impacts of climate change in coastal marine systems. *Ecol. Lett.* **9**, 228–241.

Hartl DL & Clark AG (2007). Principles of population genetics. 4th. S5R3-6: Sinauer Associates.

Havaux M (1993). Characterization of thermal damage to the photosynthetic electron transport system in potato leaves. *Plant Sci.* **94**, 19–33.

Hawkins SJ, Moore PJ, Burrows MT, Poloczanska E, Mieszkowska N, Herbert RJH, *et al.* (2008). Complex interactions in a rapidly changing world: responses of rocky shore communities to recent climate change. *Clim. Res.* **37**, 123–133.

Helmuth B, Mieszkowska N, Moore P, & Hawkins SJ (2006). Living on the edge of two changing worlds: forecasting the responses of rocky intertidal ecosystems to climate change. *Annu. Rev. Ecol. Evol. Syst.* **37**, 373–404.

Hickling R, Roy DB, Hill JK, Fox R, & Thomas CD (2006). The distributions of a wide range of taxonomic groups are expanding polewards. *Glob. Change Biol.* **12**, 450–455.

Hijmans RJ & Graham CH (2006). The ability of climate envelope models to predict the effect of climate change on species distributions. *Glob. Change Biol.* **12**, 2272–2281.

Hoarau G, Coyer JA, Veldsink JH, Stam WT, & Olsen JL (2007). Glacial refugia and recolonization pathways in the brown seaweed *Fucus serratus*. *Mol. Ecol.* **16**, 3606–3616.

Hoegh-Guldberg O & Bruno JF (2010). The impact of climate change on the world's marine ecosystems. *Science*, **328**, 1523–1528.

Hoegh-Guldberg O, Mumby P, Hooten A, Steneck R, Greenfield P, Gomez E, *et al.* (2007). Coral reefs under rapid climate change and ocean acidification. *Science*, **318**, 1737–1742.

Hofmann GE & Todgham AE (2010). Living in the now: physiological mechanisms to tolerate a rapidly changing environment. *Annu. Rev. Physiol.* **72**, 127–145.

Hornett E & Wheat C (2012). Quantitative RNA-Seq analysis in non-model species: assessing transcriptome assemblies as a scaffold and the utility of evolutionary divergent genomic reference species. *BMC Genomics*, **13**, 361.

Hughes AR, Inouye BD, Johnson MTJ, Underwood N, & Vellend M (2008). Ecological consequences of genetic diversity. *Ecol. Lett.* **11**, 609–623.

Hughes AR & Stachowicz JJ (2004). Genetic diversity enhances the resistance of a seagrass ecosystem to disturbance. *Proc. Natl. Acad. Sci. U.S.A.* **101**, 8998–9002.

Hughes L (2000). Biological consequences of global warming: is the signal already apparent? *Trends Ecol. Evol.* **15**, 56–61.

Ireland HE, Harding SJ, Bonwick GA, Jones M, Smith CJ, & Williams JHH (2004). Evaluation of heat shock protein 70 as a biomarker of environmental stress in *Fucus serratus* and *Lemna minor*. *Biomarkers*, **9**, 139–155.

John DM (1974). New records of *Ascophyllum nodosum* (L.) Le Jol. from the warmer parts of the Atlantic Ocean. *J. Phycol.* **10**, 243–244.

Johnson LE, Brawley SH, & Adey WH (2012). Secondary spread of invasive species: historic patterns and underlying mechanisms of the continuing invasion of the European rockweed *Fucus serratus* in eastern North America. *Biol. Invasions*, **14**, 79–97.

Joost S, Bonin A, Bruford MW, Després L, Conord C, Erhardt G, *et al.* (2007). A spatial analysis method (SAM) to detect candidate loci for selection: towards a landscape genomics approach to adaptation. *Mol. Ecol.* **16**, 3955–3969.

Jueterbock A, Tyberghein L, Verbruggen H, Coyer JA, Olsen JL, & Hoarau G (2013). Climate change impact on seaweed meadow distribution in the North Atlantic rocky intertidal. *Ecol. Evol.* **3**, 1356–1373.

Kawecki TJ & Ebert D (2004). Conceptual issues in local adaptation. *Ecol. Lett.* **7**, 1225–1241.

Kearney M (2006). Habitat, environment and niche: what are we modelling? *Oikos*, **115**, 186–191.

Kearney M, Phillips BL, Tracy CR, Christian KA, Betts G, & Porter WP (2008). Modelling species distributions without using species distributions: the cane toad in Australia under current and future climates. *Ecography*, **31**, 423–434.

Kearney M & Porter W (2009). Mechanistic niche modelling: combining physiological and spatial data to predict species' ranges. *Ecol. Lett.* **12**, 334–350.

Kearney M, Porter WP, Williams C, Ritchie S, & Hoffmann AA (2009). Integrating biophysical models and evolutionary theory to predict climatic impacts on species' ranges: the dengue mosquito *Aedes aegypti* in Australia. *Funct. Ecol.* **23**, 528–538.

Keeling PJ, Burger G, Durnford DG, Lang BF, Lee RW, Pearlman RE, *et al.* (2005). The tree of eukaryotes. *Trends Ecol. Evol.* **20**, 670–676.

Keller CF (2009). Global warming: a review of this mostly settled issue. English. *Stoch. Environ. Res. Risk Assess.* **23**, 643–676.

Klein Tank AMG & Können GP (2003). Trends in indices of daily temperature and precipitation extremes in Europe, 1946--99. *J. Clim.* **16**, 3665–3680.

Klopfstein S, Currat M, & Excoffier L (2006). The fate of mutations surfing on the wave of a range expansion. *Mol. Biol. Evol.* **23**, 482–490.

Kordas RL, Harley CDG, & O'Connor MI (2011). Community ecology in a warming world: The influence of temperature on interspecific interactions in marine systems. *J. Exp. Mar. Biol. Ecol.* **400**, 218–226.

Kramer K, Degen B, Buschbom J, Hickler T, Thuiller W, Sykes MT, *et al.* (2010). *Forest Ecology and Management*, **259**. The ecology and silviculture of beech: from gene to landscape, 2213–2222.

La Terza A, Papa G, Miceli C, & Luporini P (2001). Divergence between two Antarctic species of the ciliate *Euplotes*, *E*. *focardii* and *E*. *nobilii*, in the expression of heat-shock protein 70 genes. *Mol. Ecol.* **10**, 1061–1067.

Lavergne S, Mouquet N, Thuiller W, & Ronce O (2010). Biodiversity and climate change: integrating evolutionary and ecological responses of species and communities. *Annual Review of Ecology Evolution, and Systematics*, **41**, 321–350.

Lee SK, Park W, van Sebille E, Wang C, Enfield DB, Yeager S, *et al.* (2011). What caused the significant increase in Atlantic Ocean heat content since the mid-20th century? *Geophys. Res. Lett.* **38**.

Letcher TM, ed. (2009). Climate change: observed impacts on planet Earth. Oxford: Elsevier Science.

Levitan M (2003). Climatic factors and increased frequencies of `southern' chromosome forms in natural populations of *Drosophila robusta*. *Evol. Ecol. Res.* **5**, 597–604.

Levitan M & Etges WJ (2005). Climate change and recent genetic flux in populations of *Drosophila robusta*. *BMC Evol. Biol.* **5**.

Lewis S, Handy RD, Cordi B, Billinghurst Z, & Depledge MH (1999). Stress proteins (HSP's): methods of detection and their use as an environmental biomarker. *Ecotoxicology*, **8** (5). 10.1023/A:1008982421299, 351–368.

Li R & Brawley S (2004). Improved survival under heat stress in intertidal embryos (*Fucus* spp.) simultaneously exposed to hypersalinity and the effect of parental thermal history. *Mar. Biol.* **144**, 205–213.

Lilley SA & Schiel DR (2006). Community effects following the deletion of a habitat-forming alga from rocky marine shores. *Oecologia*, **148**, 672–681.

Lima FP, Ribeiro PA, Queiroz N, Hawkins SJ, & Santos AM (2007). Do distributional shifts of northern and southern species of algae match the warming pattern? *Glob. Change Biol.* **13**, 2592–2604.

Luikart G, England PR, Tallmon D, Jordan S, & Taberlet P (2003). The power and promise of population genomics: from genotyping to genome typing. *Nat. Rev. Genet.* **4**, 981–994.

Lüning K (1984). Temperature tolerance and biogeography of seaweeds - the marine algal flora of Helgoland (North-Sea) as an example. *Helgol. Meersunters.* **38**, 305–317.

Lüning K, Yarish C, & Kirkman H (1990). Seaweeds: their environment, biogeography, and ecophysiology. New York: John Wiley. 527 pp.

Maggs CA, Castilho R, Foltz D, Henzler C, Jolly MT, Kelly J, *et al.* (2008). Evaluating signatures of glacial refugia for North Atlantic benthic marine taxa. *Ecology*, **89**, 108–122.

Manel S, Joost S, Epperson BK, Holderegger R, Storfer A, Rosenberg MS, *et al.* (2010). Perspectives on the use of landscape genetics to detect genetic adaptive variation in the field. *Mol. Ecol.* **19**, 3760–3772.

Martínez B, Arenas F, Rubal M, Burgués S, Esteban R, García-Plazaola I, *et al.* (2012). Physical factors driving intertidal macroalgae distribution: physiological stress of a dominant fucoid at its southern limit. *Oecologia*, **170**, 341–353.

Maxwell K & Johnson GN (2000). Chlorophyll fluorescence - a practical guide. *J. Exp. Bot.* **51**, 659–668.

McInerny G, Turner J, Wong H, Travis J, & Benton T (2009). How range shifts induced by climate change affect neutral evolution. *Proc. R. Soc. London, Ser. B*, **276**, 1527–1534.

McMahon CR & Hays GC (2006). Thermal niche, large-scale movements and implications of climate change for a critically endangered marine vertebrate. *Glob. Change Biol.* **12**, 1330–1338.

Meehl GA, Stocker TF, Collins WD, Friedlingstein P, Gaye AT, Gregory JM, *et al.* (2007). Global Climate Projections. *Climate Change 2007: the physical science basis: contribution of working group I to the fourth assessment report of the intergovernmental panel on climate change*. Ed. by S Solomon, D Qin, M Manning, Z Chen, M Marquis, KB Averyt, *et al.* Cambridge, United Kingdom and New York, NY, USA: Cambridge University Press. Chap. Global Climate Projections, 749–846.

Metzker ML (2010). Sequencing technologies—the next generation. *Nat. Rev. Genet.* **11**, 31–46.

Mokany K & Ferrier S (2011). Predicting impacts of climate change on biodiversity: a role for semi-mechanistic community-level modelling. English. *Divers. Distrib.* **17**, 374–380.

Moore P, Hawkins SJ, & Thompson RC (2007). Role of biological habitat amelioration in altering the relative responses of congeneric species to climate change. *Mar. Ecol. Prog. Ser.* **334**, 11–19.

Morin X & Thuiller W (2009). Comparing niche-and process-based models to reduce prediction uncertainty in species range shifts under climate change. *Ecology*, **90**, 1301–1313.

Müller R, Laepple T, Bartsch I, Wiencke C, *et al.* (2009). Impact of oceanic warming on the distribution of seaweeds in polar and cold-temperate waters. *Bot. Mar.* **52**, 617–638.

Müller R, Bartsch I, Laepple T, & Wiencke C (2010). . *Biology of polar benthic algae*. Ed. by C Wiencke. Berlin, Boston: Walter de Gruyter. Chap. Impact of oceanic warming on the distribution of seaweeds in polar and cold-temperate waters, 237–270.

Murphy HT & Lovett-Doust J (2007). Accounting for regional niche variation in habitat suitability models. *Oikos*, **116**, 99–110.

Nakicenovic N, Alcamo J, Davis G, de Vries B, Fenhann J, Gaffin S, *et al.* (2000). IPCC 2000: Special report on emissions scenarios: a special report of Working Group III of the Intergovernmental Panel on Climate Change. Cambridge, UK: Cambridge University Press.

Nei M (1972). Genetic distance between populations. *Am. Nat.* **106**, 283–292.

Neiva J, Pearson GA, Valero M, & Serrao EA (2012). Drifting fronds and drifting alleles: range dynamics, local dispersal and habitat isolation shape the population structure of the estuarine seaweed *Fucus ceranoides*. *J. Biogeogr.* **39**, 1167–1178.

Nicastro KR, Zardi GI, Teixeira S, Neiva J, Serrao EA, & 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.

Nielsen EE, Hemmer-Hansen J, Poulsen NA, Loeschcke V, Moen T, Johansen T, *et al.* (2009). Genomic signatures of local directional selection in a high gene flow marine organism, the Atlantic cod (*Gadus morhua*). *BMC Evol. Biol.* **9**.

Nieminen M, Singer MC, Fortelius W, Schöps K, & Hanski I (2001). Experimental confirmation that inbreeding depression increases extinction risk in butterfly populations. *Am. Nat.* **157**, 237–244.

Nyström M, Folke C, & Moberg F (2000). Coral reef disturbance and resilience in a human-dominated environment. *Trends Ecol. Evol.* **15**, 413–417.

Olsen JL, Zechman FW, Hoarau G, Coyer JA, Stam WT, Valero M, *et al.* (2010). The phylogeographic architecture of the fucoid seaweed *Ascophyllum nodosum*: an intertidal 'marine tree' and survivor of more than one glacial-interglacial cycle. *J. Biogeogr.* **37**, 842–856.

Orr HA & Unckless RL (2008). Population extinction and the genetics of adaptation. *Am. Nat.* **172**, 160–169.

Orsini L, Spanier KI, & De Meester L (2012). Genomic signature of natural and anthropogenic stress in wild populations of the waterflea *Daphnia magna*: validation in space, time and experimental evolution. *Mol. Ecol.* **21**, 2160–2175.

Osovitz CJ & Hofmann GE (2005). Thermal history-dependent expression of the *hsp70* gene in purple sea urchins: biogeographic patterns and the effect of temperature acclimation. *J. Exp. Mar. Biol. Ecol.* **327**, 134–143.

Oxborough K (2004). Imaging of chlorophyll a fluorescence: theoretical and practical aspects of an emerging technique for the monitoring of photosynthetic performance. *J. Exp. Bot.* **55**, 1195–1205.

Padilla-Gamino JL & Carpenter RC (2007). Seasonal acclimatization of *Asparagopsis taxiformis* (Rhodophyta) from different biogeographic regions. *Limnol. Oceanogr.* **52**, 833–842.

Palstra FP & Ruzzante DE (2008). Genetic estimates of contemporary effective population size: what can they tell us about the importance of genetic stochasticity for wild population persistence? *Mol. Ecol.* **17**, 3428–3447.

Parmesan C (2006). Ecological and evolutionary responses to recent climate change. *Annu. Rev. Ecol. Evol. Syst.* **37**, 637–69.

Parmesan C, Ryrholm N, Stefanescu C, Hill J, Thomas C, Descimon H, *et al.* (1999). Poleward shifts in geographical ranges of butterfly species associated with regional warming. *Nature*, **399**, 579–583.

Parmesan C & Yohe G (2003). A globally coherent fingerprint of climate change impacts across natural systems. *Nature*, **421**, 37–42.

Pauls SU, Nowak C, Bálint M, & Pfenninger M (2013). The impact of global climate change on genetic diversity within populations and species. *Mol. Ecol.* **22**, 925–946.

Pearson GA, Lago-Leston A, & Mota C (2009). Frayed at the edges: selective pressure and adaptive response to abiotic stressors are mismatched in low diversity edge populations. *J. Ecol.* **97**, 450–462.

Pearson GA, Hoarau G, Lago-Leston A, Coyer JA, Kube M, Reinhardt R, *et al.* (2010). An expressed sequence tag analysis of the intertidal brown seaweeds *Fucus serratus* (L.) and *F. vesiculosus* (L.) (Heterokontophyta, Phaeophyceae) in response to abiotic stressors. *Mar. Biotechnol.* **12**, 195–213.

Pearson RG & Dawson TP (2003). Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? *Glob. Ecol. Biogeogr.* **12**, 361–371.

Pelini SL, Diamond SE, MacLean H, Ellison AM, Gotelli NJ, Sanders NJ, *et al.* (2012). Common garden experiments reveal uncommon responses across temperatures, locations, and species of ants. *Ecol. Evol.* **2**, 3009–3015.

Perry AL, Low PJ, Ellis JR, & Reynolds JD (2005). Climate change and distribution shifts in marine fishes. *Science*, **308**, 1912–1915.

Pespeni MH, Sanford E, Gaylord B, Hill TM, Hosfelt JD, Jaris HK, *et al.* (2013). Evolutionary change during experimental ocean acidification. *Proc. Natl. Acad. Sci.* **110**, 6937–6942.

Peters AF, Marie D, Scornet D, Kloareg B, & Mark Cock J (2004). Proposal of *Ectocarpus siliculosus* (Ectocarpals, Phaeophyceae) as a model organism for brown algal genetics and genomics. *J. Phycol.* **40**, 1079–1088.

Petit JR, Jouzel J, Raynaud D, Barkov N, Barnola JM, Basile I, *et al.* (1999). Climate and atmospheric history of climate and atmospheric history the past 420,000 years from the Vostok ice core, Antarctica. *Nature*, **399**, 429–436.

Pörtner H & Farrell A (2008). Physiology and climate change. *Science*, **322**, 690–692.

Porzio L, Buia MC, & Hall-Spencer JM (2011). Effects of ocean acidification on macroalgal communities. *J. Exp. Mar. Biol. Ecol.* **400**, 278–287.

Prestion KL, Rotenberry JT, Redak RA, & Allen MF (2008). Habitat shifts of endangered species under altered climate conditions: importance of biotic interactions. *Glob. Change Biol.* **14**, 2501–2515.

Procaccini G, Olsen JL, & Reusch TB (2007). Contribution of genetics and genomics to seagrass biology and conservation. *Journal of Experimental Marine Biology and Ecology*, **350**, 234–259.

Provan J & Maggs CA (2012). Unique genetic variation at a species' rear edge is under threat from global climate change. *Proc. R. Soc. London, Ser. B*, **279**, 39–47.

Réale D, Berteaux D, McAdam AG, & Boutin S (2003). Lifetime selection on heritable life-history traits in a natural population of red squirrels. *Evolution*, **57**, 2416–2423.

Reed DH (2005). Relationship between population size and fitness. *Conserv. Biol.* **19**, 563–568.

Renaut S, Nolte AW, & Bernatchez L (2010). Mining transcriptome sequences towards identifying adaptive single nucleotide polymorphisms in lake whitefish species pairs (*Coregonus* spp. Salmonidae). *Mol. Ecol.* **19**, 115–131.

Reusch T, Ehlers A, Hammerli A, & Worm B (2005). Ecosystem recovery after climatic extremes enhanced by genotypic diversity. English. *Proc. Natl. Acad. Sci. U.S.A.* **102**, 2826–2831.

Reusch TBH & Wood TE (2007). Molecular ecology of global change. English. *Mol. Ecol.* **16**, 3973–3992.

Rokka A, Aro E, Herrmann R, Andersson B, & Vener A (2000). Dephosphorylation of photosystem II reaction center proteins in plant photosynthetic membranes as an immediate response to abrupt elevation of temperature. *Plant Physiol.* **123**, 1525–1536.

Root TL, Price JT, Hall KR, Schneider SH, Rosenzweig C, & Pounds JA (2003). Fingerprints of global warming on wild animals and plants. *Nature*, **421**, 57–60.

Rosenzweig C, Karoly D, Vicarelli M, Neofotis P, Wu Q, Casassa G, *et al.* (2008). Attributing physical and biological impacts to anthropogenic climate change. *Nature*, **453**, 353–357.

Sabine CL, Feely RA, Gruber N, Key RM, Lee K, Bullister JL, *et al.* (2004). The oceanic sink for anthropogenic CO. *Science*, **305**, 367–371.

Saccheri I, Kuussaari M, Kankare M, Vikman P, Fortelius W, & Hanski I (1998). Inbreeding and extinction in a butterfly metapopulation. *Nature*, **392**, 491–494.

Sagarin RD, Barry JP, Gilman SE, & Baxter CH (1999). Climate-related change in an intertidal community over short and long time scales. *Ecol. Monogr.* **69**, 465–490.

Salvucci ME & Crafts-Brandner SJ (2004). Relationship between the heat tolerance of photosynthesis and the thermal stability of Rubisco activase in plants from contrasting thermal environments. *Plant Physiol.* **134**, 1460–1470.

Sanford E (1999). Regulation of keystone predation by small changes in ocean temperature. *Science*, **283**, 2095–2097.

Schär C, Vidale PL, Lüthi D, Frei C, Häberli C, Liniger MA, *et al.* (2004). The role of increasing temperature variability in European summer heatwaves. *Nature*, **427**, 332–336.

Schiel DR & Foster MS (2006). The population biology of large brown seaweeds: ecological consequences of multiphase life histories in dynamic coastal environments. *Annu. Rev. Ecol. Evol. Syst.* **37**, 343–372.

Schiel DR & Lilley SA (2007). Gradients of disturbance to an algal canopy and the modification of an intertidal community. *Mar. Ecol. Prog. Ser.* **339**, 1–11.

Schiel DR & Lilley SA (2011). Impacts and negative feedbacks in community recovery over eight years following removal of habitat-forming macroalgae. *J. Exp. Mar. Biol. Ecol.* **407**, 108–115.

Schiel DR, Steinbeck JR, & Foster MS (2004). Ten years of induced ocean warming causes compreshensive changes in marine benthic communities. *Ecology*, **85**, 1833–1839.

Schreiber U, Bilger W, & Neubauer C (1994). Chlorophyll fluorescence as a nonintrusive indicator for rapid assessment of *in vivo* photosynthesis. English. *Ecophysiology of Photosynthesis*. Ed. by ED Schulze & M Caldwell. Vol. 100. Springer Study Edition. Berlin, Heidelberg: Springer, 49–70.

Schwartz MW, Iverson LR, Prasad AM, Matthews SN, & O'Connor RJ (2006). Predicting extinctions as a result of climate change. *Ecology*, **87**, 1611–1615.

Schwarz D, Robertson H, Feder J, Varala K, Hudson M, Ragland G, *et al.* (2009). Sympatric ecological speciation meets pyrosequencing: sampling the transcriptome of the apple maggot *Rhagoletis pomonella*. *BMC Genomics*, **10**, 633.

Shär C & Jendritzky G (2004). Climate change: hot news from summer 2003. *Nature*, **432**.

Sharkey TD (2005). Effects of moderate heat stress on photosynthesis: importance of thylakoid reactions, rubisco deactivation, reactive oxygen species, and thermotolerance provided by isoprene. *Plant Cell Environ.* **28**, 269–277.

Sinclair SJ, White MD, & Newell GR (2010). How useful are species distribution models for managing biodiversity under future climates. *Ecology and Society*, **15**, 8.

Slate J, Gratten J, Beraldi D, Stapley J, Hale M, & Pemberton J (2009). Gene mapping in the wild with SNPs: guidelines and future directions. English. *Genetica*, **136**, 97–107.

Smith JM & Haigh J (1974). The hitch-hiking effect of a favorable gene. *Genet. Res*, **23**, 23–35.

Snell-Rood EC, Van Dyken JD, Cruickshank T, Wade MJ, & Moczek AP (2010). Toward a population genetic framework of developmental evolution: the costs, limits, and consequences of phenotypic plasticity. *BioEssays*, **32**, 71–81.

Solomon S, Qin D, Manning M, Chen Z, Marquis M, Averyt KB, *et al.*, eds. (2007). Cambridge, United Kingdom and New York, NY, USA: Cambridge University Press.

Somero GN (2005). Linking biogeography to physiology: evolutionary and acclimatory adjustments of thermal limits. *Front. Zool.* **2**.

Somero GN (2010). The physiology of climate change: how potentials for acclimatization and genetic adaptation will determine 'winners' and 'losers'. *J. Exp. Biol.* **213**, 912–920.

Sørensen JG & Loeschcke V (2007). Studying stress responses in the post-genomic era: its ecological and evolutionary role. *J. Bioscience*, **32**, 447–456.

Sorte CJB, Fuller A, & Bracken MES (2010a). Impacts of a simulated heat wave on composition of a marine community. *Oikos*, **119**, 1909–1918.

Sorte CJB & Hofmann GE (2004). Changes in latitudes, changes in aptitudes: *Nucella canaliculata* (Mollusca : Gastropoda) is more stressed at its range edge. *Mar. Ecol. Prog. Ser.* **274**, 263–268.

Sorte CJB, Williams SL, & Carlton JT (2010b). Marine range shifts and species introductions: comparative spread rates and community impacts. *Glob. Ecol. Biogeogr.* **19**, 303–316.

Sorte CJ, Jones SJ, & Miller LP (2011). Geographic variation in temperature tolerance as an indicator of potential population responses to climate change. *J. Exp. Mar. Biol. Ecol.* **400**, 209–217.

Southward AJ, Hawkins SJ, & 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. *J. Therm. Biol.* **20**, 127–155.

Stapley J, Reger J, Feulner PGD, Smadja C, Galindo J, Ekblom R, *et al.* (2010). Adaptation genomics: the next generation. *Trends Ecol. Evol.* **25**, 705–712.

Stefanov D, Petkova V, & Denev ID (2011). Screening for heat tolerance in common bean (*Phaseolus vulgaris* L.) lines and cultivars using JIP-test. *Sci. Hortic.* **128**, 1–6.

Stinchcombe J & Hoekstra H (2007). Combining population genomics and quantitative genetics: finding the genes underlying ecologically important traits. *Heredity*, **100**, 158–170.

Strasser R, Srivastava A, Tsimilli-Michael M, *et al.* (2000). . *Probing photosynthesis: Mechanisms, regulation and adaptation*. Ed. by M Yunus, U Pathre, & P Mohanty. London: Taylor and Francis. Chap. The fluorescence transient as a tool to characterize and screen photosynthetic samples, 445–483.

Sunday JM, Bates AE, & Dulvy NK (2012). Thermal tolerance and the global redistribution of animals. *Nat. Clim. Chang.* **2**, 686–690.

Tebaldi C, Hayhoe KC, Arblaster JM, & Meehl GA (2006). Going to the extremes. English. *Clim. Change*, **79** (3-4), 185–211.

Teotónio H, Chelo IM, Bradić M, Rose MR, & Long AD (2009). Experimental evolution reveals natural selection on standing genetic variation. *Nat. Genet.* **41**, 251–257.

Therkildsen NO, Hemmer-Hansen J, Als TD, Swain DP, Morgan MJ, Trippel EA, *et al.* (2013). Microevolution in time and space: SNP analysis of historical DNA reveals dynamic signatures of selection in Atlantic cod. *Mol. Ecol.* **22**, 2424–2440.

Thomas CD (2010). Climate, climate change and range boundaries. *Divers. Distrib.* **16**, 488–495.

Thomas CD, Bodsworth EJ, Wilson RJ, Simmons AD, Davies ZG, Musche M, *et al.* (2001). Ecological and evolutionary processes at expanding range margins. *Nature*, **411**, 577–581.

Thomas CD, Cameron A, Green RE, Bakkenes M, Beaumont LJ, Collingham YC, *et al.* (2004). Extinction risk from climate change. *Nature*, **427**, 145–147.

Thompson DWJ, Kennedy JJ, Wallace JM, & Jones PD (2008). A large discontinuity in the mid-twentieth century in observed global-mean surface temperature. *Nature*, **453**, 646–649.

Thuiller W (2003). BIOMOD - optimizing predictions of species distributions and projecting potential future shifts under global change. *Glob. Change Biol.* **9**, 1353–1362.

Thuiller W (2004). Patterns and uncertainties of species' range shifts under climate change. *Glob. Change Biol.* **10**, 2020–2027.

Thuiller W, Albert C, Araújo MB, Berry PM, Cabeza M, Guisan A, *et al.* (2008). Predicting global change impacts on plant species' distributions: Future challenges. *Perspectives in Plant Ecology, Evolution and Systematics*, **9**, 137–152.

Tomanek L (2008). The importance of physiological limits in determining biogeographical range shifts due to global climate change: the heat-shock response. *Physiol. Biochem. Zool.* **81**, 709–717.

Tomanek L (2010). Variation in the heat shock response and its implication for predicting the effect of global climate change on species' biogeographical distribution ranges and metabolic costs. English. *J. Exp. Biol.* **213**, 971–979.

Toth AL, Varala K, Newman TC, Miguez FE, Hutchison SK, Willoughby DA, *et al.* (2007). Wasp gene expression supports an evolutionary link between maternal behavior and eusociality. *Science*, **318**, 441–444.

Trenberth KE, Jones PD, Ambenje P, Bojariu R, Easterling D, Klein Tank A, *et al.* (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*. Ed. by S Solomon, D Qin, M Manning, Z Chen, M Marquis, KB Averyt, *et al.* Cambridge, United Kingdom and New York, NY, USA: Cambridge University Press. Chap. Observations: Surface and Atmospheric Climate Change.

Turley C & Findlay HS (2009). . *Climate change: observed impacts on planet Earth*. Ed. by TM Letcher. Oxford: Elsevier Science. Chap. Ocean acidification as an indicator for climate change, 367–390.

Umina PA, Weeks AR, Kearney MR, McKechnie SW, & Hoffmann AA (2005). A rapid shift in a classic clinal pattern in *Drosophila* reflecting climate change. *Science*, **308**, 691–693.

Valerio C, Claudia A, Italia DF, & Alfredo C (2010). Uncovering the complexity of transcriptomes with RNA-seq. *J. Biomed. Biotechnol.* **2010**.

Van Asch M, Salis L, Holleman LJM, van Lith B, & Visser ME (2013). Evolutionary response of the egg hatching date of a herbivorous insect under climate change. *Nature Clim. Change*, **3**, 244–248.

Van den Hoek C (1975). Phytogeographic provinces along the coasts of the northern Atlantic Ocean. *Phycologia*, **14**, 317–330.

Van den Hoek C (1987). The possible significance of long-range dispersal for the biogeography of seaweeds. *Helgol. Meersunters.* **41**, 261–272.

Vasemagi A & Primmer CR (2005). Challenges for identifying functionally important genetic variation: the promise of combining complementary research strategies. *Mol. Ecol.* **14**, 3623–3642.

Viejo RM, Martínez B, Arrontes J, Astudillo C, & Hernández L (2011). Reproductive patterns in central and marginal populations of a large brown seaweed: drastic changes at the southern range limit. *Ecography*, **34**, 75–84.

Vitalis R, Dawson K, & Boursot P (2001). Interpretation of variation across marker loci as evidence of selection. *Genetics*, **158**, 1811.

Vitti JJ, Cho MK, Tishkoff SA, & Sabeti PC (2012). Human evolutionary genomics: ethical and interpretive issues. *Trends Genet.* **28**, 137–145.

Wahl M, Jormalaineny V, Erikssonz BK, Coyer JA, Molis M, Schubert H, *et al.* (2011). Stress ecology in *Fucus*: abiotic, biotic and genetic interactions. *Advances in Marine Biology*. Ed. by M Lesser. Oxford: Academic Press, 37–105.

Walther GR, Post E, Convey P, Menzel A, Parmesan C, Beebee TJC, *et al.* (2002). Ecological responses to recent climate change. *Nature*, **416**, 389–395.

Wang W, Vinocur B, Shoseyov O, & Altman A (2004). Role of plant heat-shock proteins and molecular chaperones in the abiotic stress response. *Trends Plant Sci.* **9**, 244–252.

Wang Z, Gerstein M, & Snyder M (2009). RNA-Seq: a revolutionary tool for transcriptomics. *Nat. Rev. Genet.* **10**, 57–63.

Weis E (1982). Influence of light on the heat sensitivity of the photosynthetic apparatus in isolated spinach chloroplasts. *Plant Physiol.* **70**, 1530.

Weis E & Berry J (1988). Plants and high temperature stress. *Symposia of the Society for Experimental Biology*. Vol. 42, 329–346.

Wernberg T, Russell BD, Thomsen MS, Gurgel CFD, Bradshaw CJ, Poloczanska ES, *et al.* (2011). Seaweed communities in retreat from ocean warming. *Curr. Biol.* **21**, 1828–1832.

Wethey DS & Woodin SA (2008). Ecological hindcasting of biogeographic responses to climate change in the European intertidal zone. *Hydrobiologia*, **606**, 139–151.

Wiencke C & Amsler CD (2012). Seaweeds and their communities in polar regions. *Seaweed Biology*. Ed. by C Wiencke & K Bischof. Vol. 219. Ecological Studies. Berlin Heidelberg: Springer, 265–291.

Wiens J, Stralberg D, Jongsomjit D, Howell C, & Snyder M (2009). Niches, models, and climate change: assessing the assumptions and uncertainties. *Proc. Natl. Acad. Sci.* **106**, 19729–19736.

Williams SE, Shoo LP, Isaac JL, Hoffmann AA, & Langham G (2008). Towards an integrated framework for assessing the vulnerability of species to climate change. *PLoS Biol.* **6**, e325.

Wise RR, Olson AJ, Schrader SM, & Sharkey TD (2004). Electron transport is the functional limitation of photosynthesis in field-grown *Pima* cotton plants at high temperature. *Plant Cell Environ.* **27**, 717–724.

Worm B, Lotze HK, Boström C, Engkvist R, Labanauskas V, & Sommer U (1999). Marine diversity shift linked to interactions among grazers, nutrients and propagule banks. *Mar. Ecol. Prog. Ser.* **185**, 309–314.

Yan Z, Jones P, Davies T, Moberg A, Bergström H, Camuffo D, *et al.* (2002). Trends of extreme temperatures in Europe and China based on daily observations. English. *Clim. Change*, **53** (1-3), 355–392.

Zhang R & Sharkey TD (2009). Photosynthetic electron transport and proton flux under moderate heat stress. *Photosynth. Res.* **100**, 29–43.

Živčák M, Brestič M, Olšovská K, & Slamka P (2008). Performance index as a sensitive indicator of water stress in *Triticum aestivum* L. *Plant Soil Environ.* **54** (4), 133–139.