UNIVERSIDADE DO ALGARVE
FACULDADE DE CIÊNCIAS E TECNOLOGIA

MARINE FOUNDATION SPECIES
SHIFTING RANGES AND GENETIC BASELINES

JORGE MANUEL FERREIRA DE ASSIS

TESE PARA A OBTENÇÃO DO GRAU DE DOUTOR NO RAMO DE CIÊNCIAS DO MAR,
ESPECIALIDADE DE PROCESSOS E ECOSSISTEMAS MARINHOS

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DECLARAÇÃO DE AUTORIA DE TRABALHO:

Declaro ser o autor deste trabalho, que é original e inédito. Autores e trabalhos consultados estão devidamente citados no texto e constam da listagem de referências incluídas.

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APOIO

A presente tese teve o apoio da Fundação para a Ciência e Tecnologia (FCT), através da bolsa SFRH / BD / 65702 / 2009 e dos projetos EDGES PTDC/AAC-CLI/109108/2008, EXTANT EXCL/AAG-GLO/0661/2012 e MEGIKELP PTDC/MAR/65461/2006, bem como da EDP – Energias de Portugal que apoiou o projeto FINDKELP.

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MARINE FOUNDATION SPECIES SHIFTING RANGES AND GENETIC BASELINES

ABSTRACT

This thesis revealed the most importance factors shaping the distribution, abundance and genetic diversity of four marine foundation species. Environmental conditions, particularly sea temperatures, nutrient availability and ocean waves, played a primary role in shaping the spatial distribution and abundance of populations, acting on scales varying from tens of meters to hundreds of kilometres. Furthermore, the use of Species Distribution Models (SDMs) with biological records of occurrence and high-resolution oceanographic data, allowed predicting species distributions across time. This approach highlighted the role of climate change, particularly when extreme temperatures prevailed during glacial and interglacial periods. These results, when combined with mtDNA and microsatellite genetic variation of populations allowed inferring for the influence of past range dynamics in the genetic diversity and structure of populations. For instance, the Last Glacial Maximum produced important shifts in species ranges, leaving obvious signatures of higher genetic diversities in regions where populations persisted (i.e., refugia). However, it was found that a species' genetic pool is shaped by regions of persistence, adjacent to others experiencing expansions and contractions. Contradicting expectations, refugia seem to play a minor role on the re(colonization) process of previously eroded populations. In addition, the available habitat area for expanding populations and the inherent mechanisms of species dispersal in occupying available habitats were also found to be fundamental in shaping the distributions of genetic diversity. However, results suggest that the high levels of genetic diversity in some populations do not rule out that they may have experienced strong genetic erosion in the past, a process here named shifting genetic baselines. Furthermore, this thesis predicted an ongoing retraction at the rear edges and extinctions of unique genetic lineages, which will impoverish the global gene pool, strongly shifting the genetic baselines in the future.

KEYWORDS » Genetic diversity, genetic structure, climate change, range shifts, kelp forests, fucoids.

RESUMO

O presente estudo revela os principais fatores que controlam a distribuição, a abundância e a diversidade genética de quatro espécies engenheiras do ecossistema. A temperatura do mar, a disponibilidade de nutrientes e o hidrodinamismo demonstraram-se primordiais na regulação da distribuição espacial das populações, atuando em escalas que variam entre as dezenas de metros e as centenas de quilómetros. O uso de Modelos de Distribuição de Espécies (MDE) permitiu prever a distribuição dessas espécies ao longo do tempo e compreender a importância dos períodos glaciares e interglaciares. Esta abordagem, quando associada à análise da variação genética (mtDNA ou microsatélites), permitiu inferir sobre a influência dos padrões de distribuição do passado na diversidade genética contemporânea. Por exemplo, o Último Máximo Glaciar traduziu-se em importantes alterações na distribuição das espécies, deixando assinaturas óbvias de elevada diversidade genética em regiões onde as populações persistiram (i.e., refúgios). Contudo, foi demonstrado que o *pool* genético de uma espécie é moldado por regiões de persistência, adjacentes a outras que experienciaram expansões e contrações das populações. Ao contrário do que se pensava anteriormente, os refúgios possuem um papel menor na (re)colonização de regiões nas quais as populações foram extintas. Para além disso, a área de habitat disponível para as populações que se expandem, bem como os mecanismos de dispersão para ocupar esses habitats revelaram-se fundamentais na regulação da diversidade genética. Porém, os resultados sugerem que o facto de as populações possuírem elevada diversidade genética não inviabiliza a possibilidade de essas terem sofrido processos de erosão genética no passado, um processo aqui denominado *shifting genetic baselines*. O presente trabalho prevê, também, uma regressão das populações dos limites de distribuição e a extinção de linhagens genéticas únicas, o que deverá empobrecer o *pool* genético global das espécies e alterar a informação de base sobre a diversidade genética para o futuro.

PALAVRAS-CHAVE » Diversidade genética, estrutura genética, alterações climáticas, distribuição, florestas de kelp, fucoids.

RESUMO ALARGADO

Compreender os processos que regulam a diversidade genética das populações e prever a sua resposta a futuras alterações climáticas é um tema central da Ecologia, mas também da Conservação e Gestão da Natureza. Em Biogeografia, é comum generalizar-se a relação da diversidade genética com o tamanho das populações, prevendo elevados níveis de diversidade no centro da distribuição das espécies e um declínio em qualquer direção do seu limite de distribuição. Contudo, a variação da diversidade genética incorpora outros processos que atuam ao longo da história evolutiva das espécies. Por exemplo, nos limites de distribuição das espécies, as populações podem ser abundantes com elevada diversidade genética, mas também raras com baixa diversidade e elevada reprodução clonal. Estas divergências fazem da relação entre a distribuição das abundâncias e os padrões de diversidade genética um problema mais complexo do que anteriormente se considerava.

Para responder a estes desafios, tem-se implementado a junção de Modelos de Distribuição de Espécies (MDE) com a análise da variação da diversidade genética (e.g., mtDNA ou microsatélites). Esta é uma abordagem recente que tem possibilitado compreender melhor de que forma os padrões de distribuição das espécies no passado influenciam a diversidade genética contemporânea. Por exemplo, o Último Máximo Glaciar traduziu-se em importantes alterações na distribuição das espécies, deixando assinaturas óbvias de elevada diversidade genética em regiões onde as populações persistiram (i.e., refúgios). Contudo, nesta linha de trabalho, as consequências da fragmentação, da área disponível e do nível de isolamento dos habitats são raramente consideradas. Por exemplo, a área onde as populações persistiram no Último Máximo Glaciar e o seu potencial de dispersão poderão ter desempenhado um papel fundamental na estruturação da diversidade genética contemporânea. A dispersão contemporânea interpopulacional é particularmente importante porque a vulnerabilidade das populações a alterações do ambiente (e.g., alterações climáticas) é em grande parte determinada pela habilidade dessas migrarem para locais onde os habitats são favoráveis. Neste sentido, a incorporação destes mecanismos mais complexos na análise da diversidade genética pode acabar com modelos teóricos baseados em pressupostos estáticos e simplistas. A presente tese, centrada em cinco estudos inéditos, revela os principais fatores que controlam a distribuição, a abundância e a diversidade genética de quatro espécies

engenheiras do ecossistema.

O primeiro estudo (capítulo II) examinou quais os fatores responsáveis pela sincronia das populações da espécie de kelp *Macrocystis pyrifera* ao longo da costa sul da Califórnia. Estudou-se a relação existente entre a sincronia e a distância das populações de kelps adultas, em fase de recrutamento, das abundância de ouriços-do-mar (os principais consumidores de kelp) e de variáveis ambientais. Os resultados demonstraram que a variabilidade regional dos fatores ambientais (i.e., o efeito de Moran) é o principal processo de controlo do sincronismo interpopulacional a escalas espaciais maiores que 1.3km. A menores escalas, foi demonstrado que o sincronismo das populações é controlado pela abundância de ouriços-do-mar e pelo sucesso no recrutamento de kelp. Verificou-se, também, o potencial de sintetizar abordagens de ecologia da paisagem com dinâmica das populações, de modo a identificar os fatores envolvidos nos processos de sincronismo.

O segundo estudo (capítulo III) examinou quais os fatores ambientais que regulam a distribuição da kelp *Saccorhiza polyschides* no seu limite de distribuição (Ibéria-Marrocos), e previu o resultado das alterações climáticas no futuro próximo. Foram utilizados *Generalized Linear Mixed Models* relacionando ocorrências da espécie com dados oceanográficos de elevada resolução provenientes de satélite, considerando o ciclo de vida da espécie (com alternância de gerações) e simulações de dispersão. Os resultados evidenciaram a importância das temperaturas máximas de inverno, bem como o efeito do afloramento costeiro sazonal no controlo da distribuição da espécie. A fraca capacidade de dispersão desta espécie foi também corroborado com a literatura conhecida. Para além disso, foi efetuada a projeção da distribuição para o período compreendido entre 1986 e 2100. Estas previsões demonstraram que a extensão de kelp ao longo da costa decresceu cerca de 50% de 1986 até 2012, deixando a distribuição confinada a regiões de forte afloramento costeiro. As previsões para o futuro tiveram em conta dois cenários de emissão de gases com efeito de estufa. No cenário mais otimista, a distribuição da espécie deverá retrair até 2075, recuperando gradualmente após esse período. No cenário que considera o aumento contínuo de emissão de gases com efeito de estufa, as populações deverão decrescer até 2071, período em que se prevê a extinção desta espécie da região Ibéria-Marrocos. A regressão desta espécie deverá ter severas consequências para a distribuição de habitats essenciais assim como para o balanço das interações tróficas.

O terceiro estudo (capítulo IV) centrou-se no efeito da redução da abundância das populações, nos padrões da diversidade genética da espécie de kelp *Saccorhiza polyschides*. Foram comparados os padrões de diversidade e de diferenciação genética com os de abundância, ao longo de um gradiente caracterizado por populações abundantes e marginais. As assinaturas genéticas de efeitos de *bottleneck* foram também investigadas de modo a determinar se a recente regressão desta espécie se traduziu num efeito negativo no tamanho efetivo das populações. Os resultados demonstraram uma redução da densidade, um aumento da heterogeneidade e um conjunto de extinções locais, desde a região de elevadas abundâncias em direção ao limite de distribuição. Como esperado, foram verificados níveis de diferenciação mais elevados, bem como assinaturas de *bottleneck* na região mais periférica. No entanto, não se verificou uma diminuição na diversidade genética associada a este padrão. A diversidade genética aumentou em direção ao limite de distribuição, apesar dos *bottlenecks* e densidades inferiores, sugerindo que as extinções e recolonizações não reduziram a diversidade genética, ou que essa poderá ter sido muito superior no passado, um processo aqui denominado *shifting genetic baselines*.

Os dois últimos estudos (capítulos V e VI) centraram-se no potencial efeito das alterações de distribuição na diversidade e estrutura genética de duas espécies fucóides (*Fucus vesiculosus* e *Pelvetia canaliculata*). Analisou-se a variação genética das populações (mtDNA ou microsatélites) e modelou-se a distribuição potencial dessas espécies no Último Máximo Glaciar, a meio do período Holoceno e no presente, através da utilização de Modelos de Distribuição de Espécies (MDE). Esta abordagem permitiu verificar o potencial de integrar estudos de filogeografia com MDEs de modo a melhorar as inferências sobre os padrões de distribuição, bem como as implicações evolutivas da alteração das distribuições provocadas pelas alterações climáticas. Demonstrou-se, também, o efeito do Último Máximo Glaciar que se traduziu em importantes alterações nas distribuições das espécies, deixando assinaturas óbvias de elevada diversidade genética em regiões onde as populações persistiram (i.e., refúgios). Contudo, foi demonstrado que o *pool* genético de uma espécie é moldado por regiões de persistência, adjacentes a outras que experienciaram expansões e contrações das populações. Ao contrário do que se pensava anteriormente, os refúgios possuem um papel menor na (re)colonização das regiões nas quais as populações foram extintas. Para além disso, a área de habitat disponível para as populações que se expandem e os mecanismos de dispersão para ocupar esses habitats revelaram-se fundamentais na regulação da diversidade genética. Foi também efetuada a previsão da distribuição dessas espécies para os períodos

2050 e 2100. Essas projeções permitiram inferir sobre uma possível regressão das populações dos limites de distribuição, bem como a extinção de linhagens genéticas únicas, o que deverá empobrecer o gene *pool* global das espécies e alterar a informação de base sobre a diversidade genética para o futuro.

PALAVRAS-CHAVE » Diversidade genética, estrutura genética, alterações climáticas, distribuição, florestas de kelp, fucoids.

STRUCTURE OF THE THESIS

This thesis is organized in seven distinct chapters. The first chapter provides an introduction to the subject and presents the general aims of the thesis. Chapters II to VI constitute independent studies that seek to address the proposed aims. These were written in a style appropriate to be published in scientific journals and can be read separately:

> Chapter II. Synchrony in dynamics of giant kelp forests is driven by both local recruitment and regional environmental controls.
>
> Chapter III. The range-edge of European kelp forests under climate change.
>
> Chapter IV. High and distinct range-edge genetic diversity despite local bottlenecks.
>
> Chapter V. MtDNA phylogeography and Species Distribution Models reveal an extensive biogeographic shift in the high-intertidal seaweed Pelvetia canaliculata.
>
> Chapter VI. Climate changes drive range dynamics and shifting genetic baselines.

In the front page of Chapters II to VI there is important information concerning the co-authors involved in the publication and about the status of publication. Chapter VII provides a general discussion of the main findings of this thesis while chapter VIII synthesizes the overall contribution and consider some future remarks. All figures and tables are shown in the text within each chapter, although the acknowledgements were compiled at the beginning of the thesis.

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LIST OF ABBREVIATIONS

A » Allelic Richness

AIC » Akaike Information Criterion

AGCM » Atmospheric General Circulation Model

AMOVA » Hierarchical analysis of molecular variance

AUC » Area Under the receiver-operated characteristic Curve

BRT » Boosted Regression trees

CCSM4 » Community Climate System Model

CDIP » Coastal Data Information Project

Chla » Chlorophyll a

DNA » Deoxyribonucleic Acid

FCA » Factorial Correspondence Analysis

GAM » General Additive Model

GLMM » General Linear Mixed Model

HE » Expected Heterozygosity (Nei's gene diversity)

IBD » Isolation By Distance

Kd » In-water diffuse attenuation coefficient

KYBP » Thousands of years before present

LGM » Last glacial Maximum (20 KYBP)

MARS » Multivariate Adaptative Regression Splines

MAXENT » Maximum entropy

MH » Mid-Holocene (6 KYBP)

MIROC5 » Model for Interdisciplinary Research on Climate

MODIS » Moderate Resolution Imaging Spectroradiometer

mtDNA » mitochondrial DNA

MYA » millions of years

NCF » Nonparametric Correlation Function

NJ » Neighbour-joining

PCR » Polymerase Chain Reaction

RCP » Representative Concentration Pathways

TBA » Trend Break Analysis

TSS » True Skill Statistics

SDM » Species Distribution Model

SST » Sea surface temperature

SWH » Significant Wave Height

VIF » Variance Inflation Factor

CHAPTER I » GENERAL INTRODUCTION

The genetic diversity of natural populations is the raw evolutionary material that allows adapting to the changing environment, whether this takes the form of new diseases, parasites, competitors, predators, pollution or climate variability (Barrett & Kohn 1991; Frankham, 1996; Frankham et al., 2010). It is a recognized feature determining the long-term survival of populations (Bouzat, 2010) and, therefore, the World Conservation Union has included it within three priority levels of biological conservation (McNeely et al., 1990). The most obvious loss of biodiversity is the extinction of an entire species, however, long before species completely vanish, their genetic diversity is already largely affected (Hughes et al., 1997). Therefore, understanding the processes shaping the genetic variability of populations and predicting its response to novel environment forces is not only a central subject in ecology, but also for sound conservation management (Norberg et al., 2012; Pauls et al., 2013).

A common generalization in biogeography is how the genetic diversity mirrors the effective size of populations (Eckert et al., 2008). This predicts higher levels of genetic diversity at the centre of species distribution, where the environmental conditions are optimal and the success of individuals is higher (Hutchinson's niche concept; Hutchinson, 1957; (reviewed in Sagarin & Gaines, 2002), and a decline towards any direction of the edge of distributions, coupled with an increase of population isolation and differentiation (reviewed in Vucetich & Waite, 2003).

However, the variation of genetic diversity incorporates other processes acting on the evolutionary course of populations (Godt et al., 1996) and empirical data from different distributional ranges do not all support the same general patterns (reviewed by Sagarin et al., 2006). For instance, at edge of specie's distribution, populations may vary from highly abundant and genetically diverse (Neiva et al., 2012), to scarce distributed, where low genetic diversities and clonal reproduction may prevail (Billingham et al., 2003; Arnaud-Haond et al., 2006). Such divergent outcomes make the relationship between the distribution of abundances and the patterns of genetic diversity more complex and interesting than previously assumed (Williams et al., 2003; Helmuth et al., 2005).

RANGE SHIFTS SHAPING THE GENETIC DIVERSITY OF POPULATIONS

When local environmental conditions fall outside the tolerance of individuals, species either experience extinction or shift to extant suitable habitats (Parmesan et al., 1999; Barnosky et al., 2003; Wiens & Graham, 2005; Parmesan, 2006). Such shifts in range may produce significant consequences to the genetic and evolutionary traits of populations. For instance, in areas where persistence occurred for long time, high levels of genetic diversity and unique gene pools are expected (Hewitt, 1999; Hewitt, 2000; Provan & Bennett, 2008), while where local extinctions occurred or limiting niche conditions dominate, populations may lose their genetic diversity due to drift (Frankham et al., 2010), or on more shorter temporal scales, as a result of genetic bottlenecks and inbreeding (Keller & Waller, 2002). In these cases, if inbreeding depression takes place, the overall survival and reproduction of individuals may decease owing to the decrease in heterozygosity and consequently the expression of unfavourable recessive alleles (Husband & Schemske, 1996; Charlesworth & Charlesworth, 1999; O'Grady et al., 2006). The reduction of genetic diversity may also occur due to founder effects, when species expand their ranges and colonize new available habitats. This process will result in colonized areas holding fewer genotypes and lower levels of differentiation when compared to the founding populations (Bernatchez & Wilson, 1998; Hewitt, 1999).

Evidence shows that the glacial and interglacial cycles of the Quaternary (~2.6 MYA to present-time) were particular important in shaping the contemporary distribution of species (Provan & Bennett, 2008; Maggs et al., 2008, Ilves et al., 2010). The compression of isotherms during glacial periods forced cold-temperate species to experience severe contractions, restricting their ranges to small regions of persistence (i.e. glacial refugia; reviewed by Maggs et al., 2008), although broad distributions could have existed if species expanded to southern suitable habitats. On the other way, during interglacial periods, climate conditions would allow persisting populations to shift and colonize northwards, as suitable habitats become available (Provan & Bennett, 2008). Currently we are experiencing the Holocene, an interglacial period that settled cold-temperate species on northern territories as climate warmed ever since the Last Glacial Maximum (LGM; 20 KYBP). But due to the high concentrations of human induced atmospheric carbon dioxide, there is further potential for climate warming and range shifts in the immediate future (Sala et al., 2000; Oechel et al. 2000), and theory predicts that this will be one of the most important drivers for biodiversity loss (Sala et al., 2000; Thomas et al., 2004; Fischlin et al., 2007). This may be particular severe at the edge of distributions, where small variations on the limiting niche of species may originate the extinction of local populations (Habel et al., 2011). The extinction of these threatened populations may critically reduce the overall genetic diversity of species, and consequently their ability to evolve (Pujol & Pannell, 2008; Pearson et al., 2009). Edge populations typically contain high diversity due to historical persistence in climatic refugia, although gene flow from different populations can also be a source of high diversity (Garcia-Ramos & Kirkpatrick, 1997; Vucetich & Waite, 2003; Neiva et al., 2012). In these particular cases, the rapid variations of abundance due to climate variability may overwhelm past history in determining the structure of genetic diversity, because once lost, unique alleles cannot reappear no matter how favourable the habitat becomes latter on.

INFERRING THE PAST DISTRIBUTION OF SPECIES

The aforementioned genetic signatures left by range shifts are frequently used to investigate the phylogeography of species (e.g., Beatty & Provan, 2011), although this procedure may not always be straightforward. For instance, high levels of contemporary gene flow may deeply confound past demographic signatures (Pelc et al., 2009). In addition, inferring for past range dynamics using genetic variation is limited to the contemporary ranges because genes may only be sampled from extant populations.

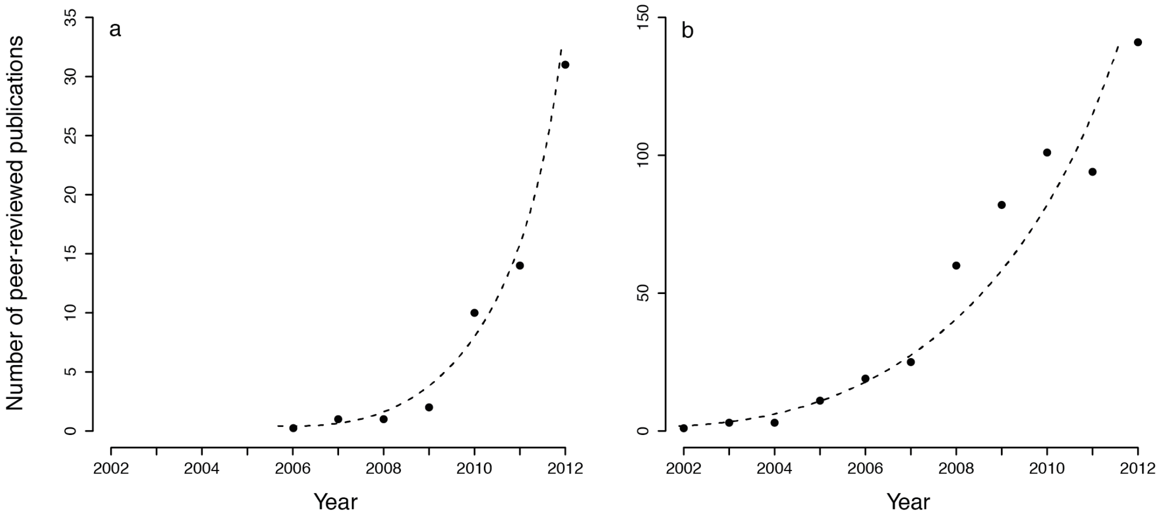

Fig 1. Number of articles published between 2002 and 2012 referring (a) “Species Distribution Model*” and “Phylogeograph*”, and (b) “landscape genetics”. Data obtained from the “Web of Science” (at http://www.isiknowledge.com accessed in August 2013).

To assess distinct hypotheses, Species Distribution Models (SDMs; see Peterson et al., 2011 for a review) have been recently implemented as an independent perspective about past distributions (Fig. 1a; e.g., Bigg et al., 2008, Provan & Maggs, 2012; Rebelo et al., 2012).

These models are rooted in the niche theory as defined by Hutchinson (1957) and relate species presences and absences with environmental conditions. By assuming that species are niche conservationist (Peterson, 1999), SDMs may be transferred into different estimates of climate to predict the whole temporal spectrum of distributions (Guisan & Zimmermann, 2000; Guisan & Thuiller 2005).

The combination of genetic analysis with transferable distribution models may be of further interest. Despite corroborating past range shifts and predicting distributions at global scales, this approach can be used to identify unique genetic lineages that may be currently endangered (D'Amen et al., 2013). In addition, if both methods retrieve consistent outcomes, then niche conservationism is confirmed and model's transferability to different spaces and times is better supported (Araújo & Guisan, 2006). This is particularly important for conservation biology because species that maintained their niche and shifted ranges in the past due to climate change will certainly do so on future climate warming (Araújo et al., 2006).

BRINGING LANDSCAPE REALISM TO THE STUDY OF GENETIC DIVERSITY

The consequences of habitat fragmentation, available area and degree of isolation should also be considered in the present framework. For instance, the size of glacial refugia and their potential rate of dispersal may have played a fundamental role to structure the contemporary genetic variation of populations (Dechaine & Martin, 2004). The incorporation of such environmental realism into the analysis of genetic diversity (e.g., landscape genetics) may lead to the end of models based on static theories and retrieve important insights on the distributions of genetic diversity (Siegel et al., 2008).

Landscape genetics is a growing field of research (Fig. 1b) that combines landscape ecology and population genetics in order to explain the relations between landscape features and the evolutionary processes within species (Manel et al., 2003). The key steps of landscape genetics are to identify the discontinuities in the spatial distribution of genetic diversity (i.e., genetic structure) and to correlate then with landscape environmental features, such as barriers to dispersal (Guillot et al., 2009). In fact, the incorporation of dispersal into landscape analysis (e.g., Velo-Antón et al., 2013) is particularly important because the vulnerability of populations to changes in the local environmental (e.g., warming climate) can be highly determined by their ability to shift distribution to extant suitable habitats (Arribas et al., 2012). However, when reconstructing species distributions (e.g., SDMs), most studies rely on unlikely extreme scenarios such as no dispersal, where populations are unable to track change and experience extinction whenever the habitat becomes unfavourable (Guisan & Thuiller, 2005; Elith & Leathwick, 2009) or unlimited dispersal, with populations using all suitable environmental space (e.g., Thomas et al., 2004; Thuiller, 2004; Araújo & Luoto 2007). Such approaches may lead to the wrong estimates of the distribution and, therefore, of the potential evolutionary distribution of genetic diversity. Furthermore, the fluctuations in the abundance of populations may display some degree of synchrony, i.e., the tendency to vary together through time (Buonaccorsi et al., 2001) even when isolated from each other (Mantel, 1953). Processes influencing recruitment (e.g., dispersal), climate variability or trophic interactions are well known to control the synchrony of populations at different spatial scales. These processes may produce important outcomes, specially in range edge populations dealing with limiting niche conditions, where an increased probability of extinction may arise if they show high levels of synchrony (Heino et al. 1997, Liebhold et al. 2004). In contrast, asynchronous populations may rescue (i.e., recolonize) neighbouring populations through the dispersal of propagules.

SEASCAPE GENETICS OF MARINE FOUNDATION SPECIES

Given the specificities of the marine realm, an independent branch of research emerged from landscape genetics called seascape genetics (Selkoe et al., 2008; Galindo et al., 2010). This challenging approach has however been poorly implemented in marine populations due to precluded direct observations (Storfer et al., 2010; Manel & Holderegger, 2013).

Naturally fragmented habitats populated by seaweeds offer a unique opportunity to investigate and model the dominant factors shaping the distribution and the genetic diversity of populations. Kelp and Fucoid species are one such case, persisting in regional networks of discrete habitat patches in a balance between the extinction of local populations and (re)colonization of empty habitats (e.g., Reed et al. 2006).

Predicting distributions for these taxa is expected to retrieve accurate outcomes because they have strong climatic affinities and are distributed in landscapes with sharp environmental gradients of nutrients, light, seawater temperature and wave action (Hiscock et al., 2004; Cavanaugh et al., 2011, 2013). Moreover, compared to other habitat structuring species, kelps and fucoid are exceptionally dynamic with reduced life span, allowing to better model and track the influence of environmental variability on the synchrony and abundance of populations. However, some of these species possess a complex heteromorphic life cycle alternating from diploid to haploid stages, raising novel and challenging hypothesis and modelling tasks, owing to how the environment might act differently on each life stage (Kain, 1969; Norton, 1978; Schiel & Foster, 2006).

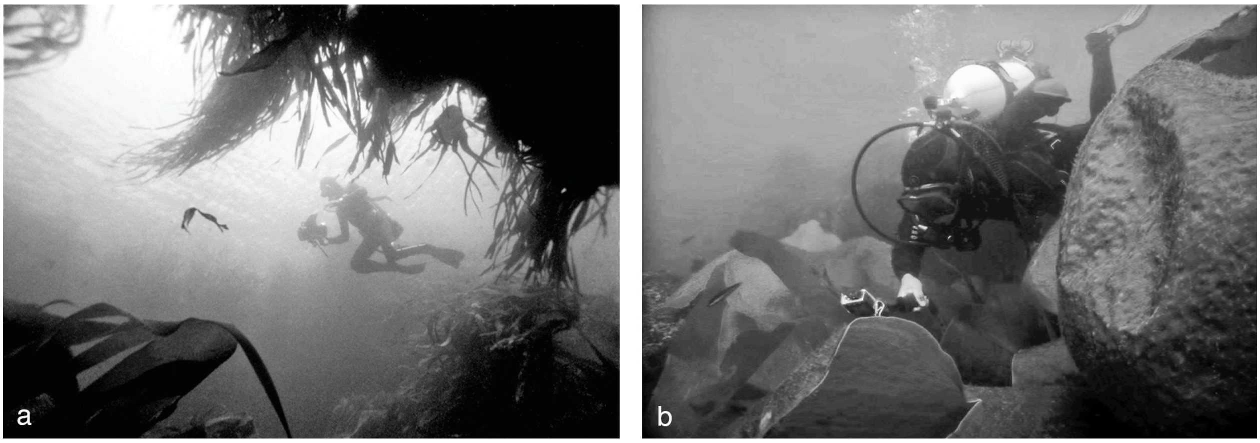

Fig 2. Pictures taken in Arrábida (Setubal, Portugal) during field surveys performed on (a) the 1970s when abundant forests where distributed throughout this coast (credits: Carlos Franco & Ester Serrão) and (b) on 2012 over the last known kelp forest of this coast (credits: Diogo Paulo)

Furthermore, gathering knowledge about the factors shaping the distribution and the genetic diversity of kelps and fucoids is particularly important in the scope of climate change because the future maintenance of ecosystem function will depend on the persistence and maintenance of such foundation species (Bruno et al., 2003; Halpern & Kappel, 2012). These create complex habitats where numerous species find essential resources, shelter and nursery grounds (Steneck et al., 2003; Graham, 2004; Norderhaug et al., 2005). Their extirpation in recent times (Fig. 2) and in the immediate future will certainly have serious economical and ecological consequences.

THESIS AIMS

The main objective of this thesis is to bring insight on the factors shaping the distribution and the genetic diversity of marine foundation species. Specifically, this thesis aimed to:

1. Identify the factors that best explain the occurrence and spatial synchrony of marine foundation species (Chapters II, III);

2. Predict the past, present and future distributions of marine foundation species (Chapter III);

3. Identify the genetic consequences of a sharp decline in abundance and recent contraction of ranges (Chapter IV);

4. Discuss the consistency of using both SDMs and patterns of genetic diversity to investigate historical biogeographic ranges (Chapters V, VI);

5. Test if the distributions of genetic diversity are determined by past climatic range shifts (Chapters V, VI);

6. Predict the implications of future range shifts on the global gene pool of species (Chapter VI).

REFERENCES

Araújo, M.B. & Guisan, A. (2006) Five (or so) challenges for species distribution modelling. Journal of Biogeography, 33, 1677–1688.

Araújo, M.B. & Luoto, M. (2007) The importance of biotic interactions for modelling species distributions under climate change. Global Ecology and Biogeography, 16, 743–753.

Araújo, M.B., Thuiller, W. & Pearson, R.G. (2006) Climate warming and the decline of amphibians and reptiles in Europe. Journal of Biogeography, 33, 1712–1728.

Barnosky, A.D., Hadly, E.A. & Bell, C.J. (2003) Mammalian response to global warming on varied temporal scales. Journal of Mammalogy, 84, 354–368.

Barrett, S.C.H & Kohn, J. (1991) The genetic and evolutionary conse- quences of small population size in plant: implications for conservation. in: Genetics and Conservation of Rare Plants (eds Falk D, Holsinger KE), pp. 3–30. Oxford University Press, New York.

Beatty, G.E. & Provan, J. (2011) Comparative phylogeography of two related plant species with overlapping ranges in Europe, and the potential effects of climate change on their intraspecific genetic diversity. BMC Evolutionary Biology, 11, 29.

Bernatchez, L. & Wilson, C.C. (1998) Comparative phylogeography of Nearctic and Palearctic fishes. Molecular Ecology, 7, 431–452.

Bigg, G.R., Cunningham, C.W., Ottersen, G., Pogson, G.H., Wadley, M.R. & Williamson, P. (2008) Ice-age survival of Atlantic cod: agreement between palaeoecology models and genetics. Proceedings. Biological sciences / The Royal Society, 275, 163–72.

Bouzat, J.L. (2010) Conservation genetics of population bottlenecks: the role of chance, selection, and history. Conservation Genetics, 11, 463–478.

Bruno, J.F., Stachowicz, J.J. & Bertness, M.D. (2003) Inclusion of facilitation into ecological theory. Trends in Ecology & Evolution, 18, 119–125.

Buonaccorsi, J.P., Elkinton, J.S., Evans, S.R. & Liebhold, A.M. (2001) Measuring and testing for spatial synchrony. Ecology, 82, 1668–1679.

Cavanaugh, K.C., Kendall, B.E., Siegel, D., Reed, D.C., Alberto, F. & Assis, J. (2013) Synchrony in dynamics of giant kelp forests is driven by both local recruitment and regional environmental controls. Ecology, 94, 499–509.

Charlesworth, B. & Charlesworth, D. (1999) The genetic basis of inbreeding depression. Genetical Research, 74, 329–340.

D'Amen, M., Zimmermann, N.E. & Pearman, P.B. (2013) Conservation of phylogeographic lineages under climate change. Global Ecology and Biogeography, 22, 93–104.

DeChaine, E.G., & Martini, A.P. (2004) Historic cycles of fragmentation and expansion in Parnassius smintheus (papilionidae) inferred using mitochondrial DNA. Evolution: International Journal of Organic Evolution, 58, 113–27.

Eckert, C.G., Samis, K.E. & Lougheed, S.C. (2008) Genetic variation across species' geographical ranges: the central-marginal hypothesis and beyond. Molecular ecology, 17, 1170–88.

Elith, J. & Leathwick, J.R. (2009) Species Distribution Models: Ecological Explanation and Prediction Across Space and Time. Annual Review of Ecology, Evolution, and Systematics, 40, 677–697.

Fischlin, A., Midgley, G.F., Price, J.T., Leemans, R., Gopal, B., Turley, C., Rounsevell, M.D.A., Dube, O.P., Tarazona, J. & Velichko, A.A. (2007) Ecosystems, their properties, goods and services. Climate Change 2007 Impacts Adaptation and Vulnerability Contribution of Working Group II to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change, pp. 211–272.

Frankham, R. (1996) Relationship of genetic variation to population size in wildlife. Conservation Biology, 10, 1500–1508.

Frankham, R., Ballou, J.D. & Briscoe, D.A. (2010) Introduction to conservation genetics, (ed. by C.U. Press) Cambridge, UK.

Galindo, H.M., Pfeiffer-Herbert, A.S., McManus, M. a, Chao, Y., Chai, F. & Palumbi, S.R. (2010) Seascape genetics along a steep cline: using genetic patterns to test predictions of marine larval dispersal. Molecular ecology, 19, 3692–707.

Garcia-Ramos, G. & Kirkpatrick, M. (1997) Genetic models of adaptation and gene flow in peripheral populations. Evolution, 51, 21–28.

Godt, M.J.W., Johnson, B.R. & Hamrick, J.L. (1996) Genetic diversity and population size in four rare southern Appalachian plant species. Conservation Biology, 10, 796–805.

Graham, M.H. (2004) Effects of Local Deforestation on the Diversity and Structure of Southern California Giant Kelp Forest Food Webs. Ecosystems, 7, 341–357.

Guillot, G., Leblois, R., Coulon, A. & Frantz, A.C. (2009) Statistical methods in spatial genetics. Molecular ecology, 18, 4734–56.

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

Guisan, A. & Zimmermann, N.E. (2000) Predictive habitat distribution models in ecology. Ecological Modelling, 135, 147–186.

Habel, J.C., Rödder, D., Schmitt, T. & Nève, G. (2011) Global warming will affect the genetic diversity and uniqueness of Lycaena helle populations. Global Change Biology, 17, 194–205.

Halpern, B. & Kappel, C. (2012) Extinction Risk in a Changing Ocean, (ed. by L. Hannah) Island Press/Center for Resource Economics, Washington, DC.

Heino, M., Kaitala, V., Ranta, E. & Lindström, J. (1997) Synchronous dynamics and rates of extinction in spatially structured populations. Proceedings of the Royal Society B Biological Sciences, 264, 481–486.

Helmuth, B., Kingsolver, J.G. & Carrington, E. (2005) Biophysics, physiological ecology, and climate change: does mechanism matter? Annual review of physiology, 67, 177–201.

Hewitt, G. (2000) The genetic legacy of the Quaternary ice ages. Nature, 405, 907–913.

Hewitt, G.M. (1999) Post-glacial re-colonization of European biota. Biological Journal of the Linnean Society, 68, 87–112.

Hiscock, K., Southward, A., Tittley, I. & Hawkins, S. (2004) Effects of changing temperature on benthic marine life in Britain and Ireland. Aquatic Conservation Marine and Freshwater Ecosystems, 14, 333–362.

Hughes, J.B., Daily, G.C. & Ehrlich, P.R. (1997) Population diversity: its extent and extinction. Science, 278, 689–692.

Husband, B.C. & Schemske, D.W. (1996) Evolution of the magnitude and timing of inbreeding depression in plants. Evolution, 50, 54–70.

Hutchinson, G.E. (1957) Concluding Remarks. Cold Spring Harbour Symposium on Quantitative Biology.

Ilves, K.L., Huang, W., Wares, J.P. & Hickerson, M.J. (2010) Colonization and/or mitochondrial selective sweeps across the North Atlantic intertidal assemblage revealed by multi-taxa approximate Bayesian computation. Molecular Ecology, 19, 4505–4519.

Kain, J.M. (1969) The biology of Laminaria hyperborea V. Comparison with early stages of competitors. Journal of the Marine Biological Association of the United Kingdom, 49, 455–473.

Keller, L. & Waller, D. (2002) Inbreeding effects in wild populations. Trends in Ecology & Evolution, 17, 19–23.

Liebhold, A., Koenig, W.D. & Bjornstad, O.N. (2004) Spatial Synchrony in Population Dynamics. Annual Review of Ecology Evolution and Systematics, 35, 467–490.

Maggs, C. a, Castilho, R., Foltz, D., Henzler, C., Jolly, M.T., Kelly, J., Olsen, J., Perez, K.E., Stam, W., Väinölä, R., Viard, F. & Wares, J. (2008) Evaluating signatures of glacial refugia for North Atlantic benthic marine taxa. Ecology, 89, S108–22.

Manel, S. & Holderegger, R. (2013) Ten years of landscape genetics. Trends in ecology & evolution, 1–8.

Manel, S., Schwartz, M.K., Luikart, G. & Taberlet, P. (2003) Landscape genetics: combining landscape ecology and population genetics. Trends in Ecology & Evolution, 18, 189–197.

McNeely, J.A., Miller, K.R., Reid, W. V, Mittermeier, R.A. & Werner, T.B. (1990) Conserving the World's Biological Diversity. Gland and Washington, D.C., The World Bank, World Resources Institute, International Union for the Conservancy of Nature, and World Wildlife Fund, 193 pp.

Neiva, J., Pearson, G.A., Valero, M. & Serrão, E.A. (2012) Drifting fronds and drifting alleles: range dynamics, local dispersal and habitat isolation shape the population structure of the estuarine seaweed Fucus ceranoides. Journal of Biogeography, 39, 1167–1178.

Norberg, J., Urban, M.C., Vellend, M., Klausmeier, C.A. & Loeuille, N. (2012) Eco-evolutionary responses of biodiversity to climate change. Nature Climate Change, 2, 1–5.

Norderhaug, K.M., Christie, H., Fossô, J.H.O. & Fredriksen, S.P. (2005) Fish-macrofauna interactions in a kelp (Laminaria hyperborea) forest. Journal of the Marine Biological Association of the United Kingdom, 85, 1279–1286.

Norton, T.A. (1978) The factors influencing the distribution of Saccorhiza polyschides in the region of Lough Ine. Journal of the Marine Biological Association of the United Kingdom, 58, 527–536.

Oechel, W.C., Vourlitis, G.L., Hastings, S.J., Zulueta, R.C., Hinzman, L. & Kane, D. (2000) Acclimation of ecosystem CO2 exchange in the Alaskan Arctic in response to decadal climate warming. Nature, 406, 978–981.

Ogrady, J., Brook, B., Reed, D., Ballou, J., Tonkyn, D. & Frankham, R. (2006) Realistic levels of inbreeding depression strongly affect extinction risk in wild populations. Biological Conservation, 133, 42–51.

Parmesan, C., Ryrholm, N., Stefansecu, C., Hill, J.K., Thomas, C.D., Descimon, H., Huntley, B., Kaila, L., Kullberg, J., Tammaru, T., Tennent, W.J., Thomas, J.A. & Warren, M. (1999) Poleward shifts in geographical ranges of butterfly species associated with regional warming. Nature, 399, 579–583.

Parmesan, C. (2006) Ecological and Evolutionary Responses to Recent Climate Change. Annual Review of Ecology, Evolution, and Systematics, 37, 637–669.

Pearson, G.A., 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. Journal of Ecology, 97, 450–462.

Pelc, R.A., Baskett, M.L., Tanci, T., Gaines, S.D. & Warner, R.R. (2009) Quantifying larval export from South African marine reserves. Marine Ecology Progress Series, 394, 65–78.

Peterson, A. T. (2011) Ecological niche conservatism: a time-structured review of evidence. Journal of Biogeography, 38, 817–827.

Peterson, A.T. (1999) Conservatism of Ecological Niches in Evolutionary Time. Science, 285, 1265–1267.

Provan, J. & Bennett, K.D. (2008) Phylogeographic insights into cryptic glacial refugia. Trends in ecology & evolution, 23, 564–71.

Provan, J. & Maggs, C. (2012) Unique genetic variation at a species' rear edge is under threat from global climate change. Proceedings. Biological sciences / The Royal Society, 279, 39–47.

Pujol, B. & Pannell, J.R. (2008) Reduced responses to selection after species range expansion. Science, 321, 96.

Rebelo, H., Froufe, E., Brito, J.C., Russo, D., Cistrone, L., Ferrand, N. & Jones, G. (2012) Postglacial colonization of Europe by the barbastelle bat: agreement between molecular data and past predictive modelling. Molecular ecology, 21, 2761–74.

Reed, D.C., Kinlan, B.P., Raimondi, P.T., Washburn, L., Gaylord, B., Drake, P.T., Jacob, P.K. & Peter, F.S. (2006) A metapopulation perspective on patch dynamics and connectivity of giant kelp. Marine Metapopulations (ed. by J.P. Kritzer Sale Pf), pp. 353–386. Academic Press, San Diego.

Reed, D.C., Rassweiler, A., Carr, M.H., Cavanaugh, K.C., Malone, D.P. & Siegel, D. (2011) Wave disturbance overwhelms top-down and bottom-up control of primary production in California kelp forests. Ecology, 92, 2108–16.

Sagarin, R. & Gaines, S. (2002) Geographical abundance distributions of coastal invertebrates: using one-dimensional ranges to test biogeographic hypotheses. Journal of Biogeography, 8, 985–997.

Sagarin, R.D., Gaines, S.D. & Gaylord, B. (2006) Moving beyond assumptions to understand abundance distributions across the ranges of species. Trends in ecology evolution, 21, 524–30.

Sala, O.E., Chapin, F.S., Armesto, J.J., Berlow, E., Bloomfield, J., Dirzo, R., Huber-Sanwald, E., Huenneke, L.F., Jackson, R.B., Kinzig, A., Leemans, R., Lodge, D.M., Mooney, H.A., Oesterheld, M., Poff, N.L., Sykes, M.T., Walker, B.H., Walker, M. & Wall, D.H. (2000) Biodiversity - Global biodiversity scenarios for the year 2100. Science, 287, 1770–1774.

Schiel, D.R. & Foster, M.S. (2006) The Population Biology of Large Brown Seaweeds: Ecological Consequences of Multiphase Life Histories in Dynamic Coastal Environments. Annual Review of Ecology, Evolution, and Systematics, 37, 343–372.

Selkoe, K. a, Henzler, C.M. & Gaines, S.D. (2008) Seascape genetics and the spatial ecology of marine populations. Fish and Fisheries, 9, 363–377.

Siegel, D.A., Mitarai, S., Costello, C.J., Gaines, S.D., Kendall, B.E., Warner, R.R. & Winters, K.B. (2008) The stochastic nature of larval connectivity among nearshore marine populations. Proceedings of the National Academy of Sciences of the United States of America, 105, 8974–8979.

Steneck, R.S., Graham, M.H., Bourque, B.J., Corbett, D., Erlandson, J.M., Estes, J. a. & Tegner, M.J. (2003) Kelp forest ecosystems: biodiversity, stability, resilience and future. Environmental Conservation, 29, 436–459.

Storfer, A., Murphy, M. a, Spear, S.F., Holderegger, R. & Waits, L.P. (2010) Landscape genetics: where are we now? Molecular ecology, 19, 3496–514.

Thomas, C.D., Cameron, A., Green, R.E., Bakkenes, M., Beaumont, L.J., Collingham, Y.C., Erasmus, B.F.N., De Siqueira, M.F., Grainger, A., Hannah, L., Hughes, L., Huntley, B., Van Jaarsveld, A.S., Midgley, G.F., Miles, L., Ortega-Huerta, M.A., Peterson, A.T., Phillips, O.L. & Williams, S.E. (2004) Extinction risk from climate change. Nature, 427, 145–8.

Vucetich, J.A.J. & Waite, T.A.T. (2003) Spatial patterns of demography and genetic processes across the species' range: Null hypotheses for landscape conservation genetics. Conservation Genetics, 4, 639 – 645.

Wiens, J.J. & Graham, C.H. (2005) Niche conservatism: Integrating Evolution, Ecology, and Conservation Biology. Annual Review of Ecology Evolution and Systematics, 36, 519–539.

Williams, C.K., Ives, A.R. & Applegate, R.D. (2003) Population dynamics across geographical ranges: Time-series analyses of three small game species. Ecology, 84, 2654–2667.

CHAPTER II » SYNCHRONY IN DYNAMICS OF GIANT KELP FORESTS IS DRIVEN BY BOTH LOCAL RECRUITMENT AND REGIONAL ENVIRONMENTAL CONTROLS

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KEYWORDS » Giant kelp; Landsat; Macrocystis pyrifera; Moran effect; population dynamics; remote sensing; southern California; spatial autocorrelation; synchrony; time series; wave disturbance.

ABSTRACT

Populations of many species display spatially synchronous fluctuations in abundance. Synchrony is most commonly attributed to three processes: factors that influence recruitment (e.g., dispersal, early survival), large-scale environmental variability, and spatially autocorrelated trophic interactions. However it is often difficult to link population synchrony to a specific dominant process, particularly when multiple synchronizing forces are operating. We utilized a new satellite-based dataset of giant kelp (*Macrocystis pyrifera*) canopy biomass to examine population synchrony in southern California kelp forests on spatial scales ranging from 50 m to 300 km and temporal scales ranging from 1 to 11 years. We examined the relationship between synchrony and distance for adult kelp populations, kelp recruits, sea urchin abundance (a major grazer of kelp), and environmental variables known to influence kelp population dynamics. Population synchrony in giant kelp decreased with distance between populations: an initial rapid exponential decrease between 50 m and 1.3 km was followed by a second, large-scale decrease between distances of 1.3 km and 172 km. The 50 m to 1.3 km spatial scale corresponded to the scales of synchrony in the abundance of sea urchins and young kelp recruits, suggesting that local drivers of predation and recruitment influence small-scale synchrony in kelp populations. The spatial correlation patterns of environmental variables, particularly wave height, were similar to the synchrony-distance relationship of kelp populations from 1.3 km to 172 km, suggesting that regional environmental variability, i.e., the Moran effect, was the dominant process affecting synchrony at larger spatial scales. This two-step pattern in the relationship between kelp biomass synchrony and distance was apparent in each of the 11 years of our study. Our results highlight the potential for synthesizing approaches from both landscape and population ecology in order to identify the multiple processes that generate synchrony in population dynamics.

INTRODUCTION

Understanding how and why populations vary in space and time is a central challenge in ecology. A great deal of theoretical work has addressed how various processes interact to create spatial and temporal patterns in population abundance (Kareiva & Wennergren, 1995; Bascompte & Solé, 1998). Testing this theory with empirical data has been challenging because there are few species for which long-term abundance data across large spatial scales are available.

One commonly observed spatiotemporal pattern in ecology is synchrony, the tendency of populations to fluctuate together through time (Buonaccorsi et al., 2001). Synchrony is most commonly calculated as the correlation between two populations through time (Bjørnstad, 1999b). Such trends have been observed in a variety of animal (Hanski & Woiwod, 1993; de Valpine et al., 2010) and plant (Koenig & Knopes, 2000) populations. Covariance in population dynamics is generally attributed to three types of mechanisms: regional stochasticity (often in the form of environmental variability), recruitment processes (such as dispersal) and trophic interactions. In his classic study of the Canadian lynx, P. A. P. Moran hypothesized that spatially separated populations are synchronized by regional, density independent variability in temperature, a mechanism later termed the Moran effect (Moran, 1953). If local dynamics among populations are similar and not highly nonlinear, the Moran effect predicts that population synchrony will mirror environmental synchrony (e.g., Bjørnstad, 2000). Dispersal can also synchronize populations through the movement of individuals or reproductive stages (Ranta et al., 1995). Finally, trophic interactions such as predation and parasitoidism have been invoked as a mechanism to synchronize populations at spatial scales corresponding to the scale of synchrony of the predator population (Ims & Andreassen, 2000).

Theoretical studies have shown that associating synchrony with a particular forcing process can be difficult. For example, dispersal can generate synchrony over distances longer than the scale of dispersal (Lande et al., 1999; Gouhier et al., 2010) and interactions between dispersal and environmental effects can reduce each factor's synchronizing effect (Kendall et al., 2000). However, the degree to which synchronizing processes can be differentiated will depend on the particular system in question. If one factor is substantially more influential than others or if the factors operate on very different spatial scales, then population dynamics may display “characteristic spatial scales of regulation” (Bjørnstad et al., 1999a), making it easier to link pattern with process (de Roos et al., 1991). Also, in many species, autocorrelation in population dynamics declines with increasing distance. The rate of this decline and the distance at which spatial autocorrelation falls to zero can serve as tools for identifying synchronizing mechanisms.

However, analyzing patterns of population synchrony in isolation is typically not sufficient to draw conclusions about the processes producing these patterns (Abbott, 2007). One must also evaluate the spatial autocorrelation of environmental controls, dispersal, and trophic interactions. If populations are autocorrelated over long distances relative to dispersal and exhibit a decline in synchrony with distance comparable to that of large-scale environmental controls, then environmental fluctuations are potentially the cause of the large-scale correlation (Peltonen et al., 2002). On the other hand, rapid decreases in synchrony over relatively short distances may be driven by dispersal or local trophic interactions (de Roos et al., 1991). For sessile organisms, rapid decreases in synchrony can also reflect small-scale variability in environmental processes that control recruitment success (e.g., topography, soil type, elevation, light). In most cases the relationship between synchrony and distance in populations will likely be controlled by a combination of processes, and very few empirical studies have simultaneously examined the roles of multiple processes in causing spatial autocorrelation in population dynamics. Still, caution is warranted when inferring causality by matching patterns of synchrony among populations with the patterns of their potential regulating factors. For example, Lande et al. (1999) demonstrated that small-scale dispersal could induce synchrony at large scales in the presence of environmental correlation when the dispersal rate is much larger than the strength of density regulation.

During the past decade the significance of synchrony-distance relationships has been examined in several species using novel statistical techniques (Bjørnstad et al., 1999a; Bjørnstad & Falck, 2001; de Valpine et al., 2010). Still, the spatial resolution and / or extent of these studies have been limited. Either the spatial resolution of observations was equal to or coarser than the dispersal distance of the species under investigation (Bjørnstad et al., 1999a; Peltonen et al., 2002) or the extent was too small to observe spatial variability in environmental factors (de Valpine et al., 2010). As a result, most past studies of synchrony have not been able to fully evaluate how the roles of different synchronizing processes vary across spatial scales (but see Gouhier et al., 2010).

We utilized a new long-term, large-scale, high-resolution remotely sensed dataset of giant kelp (*Macrocystis pyrifera*) canopy biomass in the coastal waters of southern California (Cavanaugh et al., 2011) as a case study to examine patterns of spatial synchrony across scales ranging from tens of meters to hundreds of kilometers. Compared to other habitat structuring primary producers, giant kelp forests are exceptionally dynamic. Short lifespans of both kelp fronds (4-6 months) and entire kelp plants (2-3 years) combine with rapid growth (~2% of total biomass per day) to produce a standing biomass that turns over 6 to 7 times per year (e.g., Reed et al., 2008, 2011). Growth and mortality of giant kelp is strongly influenced by environmental factors such as light, wave height, and nutrient levels (reviewed in Graham et al., 2007). Therefore, we expected to observe at least some synchrony in kelp dynamics due to seasonal cycles in these controls. Hence, our analyses focused on how patterns of synchrony in giant kelp populations declined with distance and how these patterns varied over time. In order to identify the most important synchronizing processes, we compared the synchrony distance curve of giant kelp to patterns of autocorrelation in environmental variables, predator abundance, and giant kelp recruitment. We examined synchrony in changes of kelp biomass rather than raw biomass in order to emphasize autocorrelation patterns in the growth and mortality of giant kelp populations. Using changes in biomass also has the benefit of removing long-term trends that can induce spurious correlation (Bjørnstad et al., 1999b; Koenig, 1999).

Sea surface temperature (used as a proxy for nutrient levels in this region) and storm-driven wave disturbance, two important environmental controls of kelp biomass, are correlated on scales much larger than the scale of kelp dispersal (Reed et al., 2006b; Cavanaugh et al., 2011; see also results to follow). Therefore any decreases in synchrony observed over large distances would likely reflect a large scale Moran effect, while decreases over very short distances could be due to dispersal or other local processes that influence giant kelp recruitment (e.g., bottom irradiance, local currents, competition). Grazers could induce synchrony in kelp populations on scales corresponding to the scales of synchrony in grazer abundances. Unlike regional scale environmental factors such as waves and nutrients, we did not have much a priori knowledge of the spatial scales of synchrony in patterns of kelp recruitment or grazer abundance.

The strength and timing of the seasonal cycle in kelp abundance varies a great deal among years (Cavanaugh et al., 2011), and so we might expect that the patterns of synchrony in kelp populations also vary substantially among years. To explore this inter-annual variability we examined the relationship between kelp biomass synchrony and distance separately for each year from 2000-2011. We show that by combining large-scale, high-spatial resolution data of giant kelp with data characterizing environmental variables and grazer abundance, it may be possible to identify the effects of multiple synchronizing processes on the relationship between kelp synchrony and distance. The availability of long-term time series data from satellite sensors such as Landsat ™ has increased dramatically in recent years, and so these methods can be used to characterize synchrony across multiple space and time scales in a variety of habitats where changes in abundance can be tracked from satellite imagery.

METHODS

GIANT KELP DATA

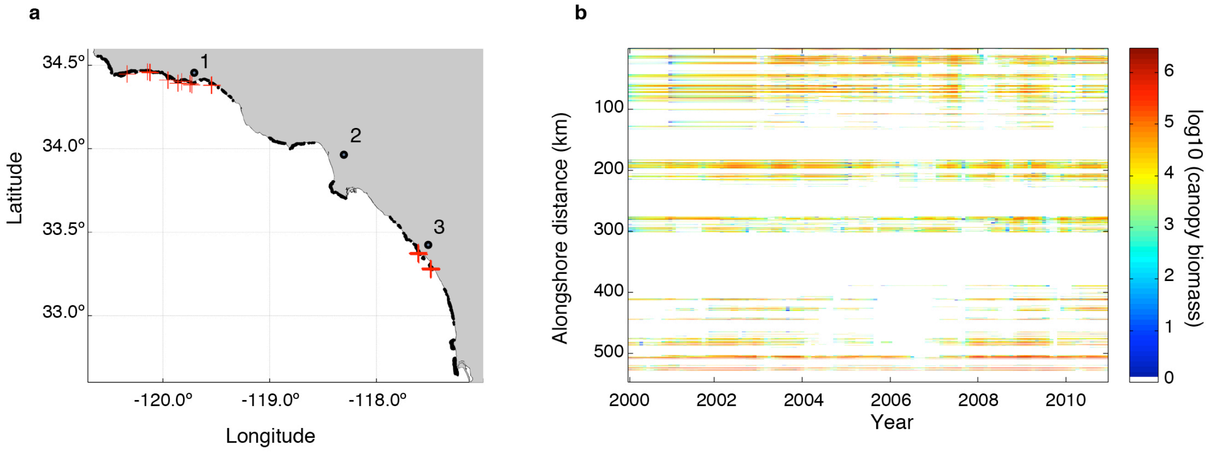

Fig 1. (a) Map of study area. The black points represent the areas where kelp appeared at least once during 2000-2010 and the red crosses represent the locations of the urchin and kelp recruit transects. Offshore islands are not shown. (b) Time series of along-coast canopy biomass binned into 50 m coastline segments between 2000-2010. The y-axis gives the alongshore distance starting from the northwest corner of the study area.

We tracked giant kelp canopy biomass along the mainland California coast from Pt. Sal to the US / Mexico border (approx. 550 km, Fig. 1) from January 2000 to January 2011 using 30m resolution multispectral Landsat 5 ™ satellite imagery. Methods used to process and calibrate the Landsat 5 ™ imagery into kelp canopy biomass (kg) are detailed in Cavanaugh et al. (2011). All of the following statistical analysis and spatial modeling activities were performed using the MATLAB (2011) and R (2011) software packages. We estimated canopy biomass from Landsat images taken approximately once every 1-2 months and interpolated the canopy biomass time series onto a regular 1-month time scale using a cubic spline (MATLAB function ‘spline’). To facilitate the calculation of alongshore synchrony we binned the kelp data into 50 m alongshore coastline segments by assigning each pixel of kelp canopy to the closest coastline segment. Each 50 m coastline segment was considered a site for later statistical analysis. In order to confirm that changes in giant kelp canopy biomass accurately reflected the population dynamics of giant kelp throughout the entire region, we compared canopy biomass to the density of adult plants determined from diver surveys collected as part of a 5-year study of kelp forests near San Clemente, CA (Reed et al., 2006a). Each summer from 2000 to 2004 divers measured the density of adult kelp plants in six 40 m x 40 m modules at 7 sites (n = 210). Each year we selected the Landsat image closest in time to the diver survey and compared the satellite estimates of canopy biomass at each site to the diver measured adult plant density. There was a very strong linear relationship between canopy biomass and adult plant density ($R^2 = 0.85$, $p < 0.001$, slope = $2.24 * 10^{-4}$ plants•m^{-2}•kg^{-1}, y-intercept = 0.06 plants/m^2, $F_{1,35} = 183$), indicating that our Landsat time series of canopy biomass accurately represented the population dynamics of adult giant kelp.

ENVIRONMENTAL DATA

Nutrients, specifically nitrogen, have been shown to limit kelp growth in southern California (Jackson, 1977; Gerard, 1982). Although kelp growth appears not to be influenced by water temperature per se (North & Zimmerman, 1984), local sea surface temperature (SST) and nutrients (specifically nitrate + nitrite) show a strong negative linear relationship in southern California (Fram et al., 2008, Lucas et al., 2011). Therefore, we used satellite observations of local SST as a proxy for nitrate/nitrite levels. Monthly mean SST was assessed using merged MODIS Terra and MODIS Aqua daytime 1 km resolution satellite observations (Kahru et al., 2009). This SST dataset covered the entire region for which we had kelp data (Fig. 1a). To place the SST data on the same grid as the kelp canopy biomass data we found the MODIS pixel that was closest to the center of each 50 m coastline segment. Because the SST data was coarser than the kelp canopy data (1 km vs. 50 m), the resolution of the synchrony-distance analysis for SST was limited to 1 km.

Large waves associated with storm events are a major source of disturbance in kelp populations in southern California (Dayton & Tegner 1984; Reed et al., 2008). Wave events can also induce synchrony in the recovery of kelp populations by removing existing canopy, thereby reducing shading and promoting juvenile growth (Graham et al., 1997). We calculated local wave disturbance using significant wave height measurements from the Coastal Data Information Project's (CDIP) swell model (http://cdip.ucsd.edu). This swell model used a linear refraction-diffraction wave propagation model to transform offshore deep-water buoy measurements of the wave field to locations along the coast at a 10m depth (O'Reilly & Guza, 1993). The model provided hourly data at 10 m depth for points spaced 1 km apart across our entire study area. We calculated the maximum significant wave height in each month at each model analysis location. Maximum significant wave height was used rather than mean significant wave height because extreme wave events have the greatest effect on kelp populations (Denny, 1988). As we did with the SST data, we matched each model analysis location with the nearest 50 m coastline segment.

URCHIN DATA

Sea urchins are responsible for the vast majority of kelp biomass lost to herbivory (Harrold & Pearse, 1987); grazing rates of other fish and invertebrates in California kelp forests are generally low (Foster & Schiel, 1985). Red and purple sea urchins (*Strongylocentrotus franciscanus*, *S. purpuratus*) are by far the most abundant species of urchin in southern California and account for most of the kelp grazing in this region (Foster & Schiel, 1985). Spatial autocorrelation in sea urchin abundance, and by extension rates of kelp grazing, could cause synchrony in kelp populations at scales corresponding to the scales of autocorrelation in urchin abundance. However, causality could also operate in the opposite direction as consumer synchrony could be driven by producer abundance. In either case we would expect correspondence between the scales of synchrony in changes in kelp and urchin abundances. We used data from annual surveys of the combined density of red and purple sea urchins at 32 transects along the Santa Barbara coastline and 18 transects along the San Clemente coastline (red crosses in Fig. 1a) to examine synchrony in herbivore dynamics (Reed, 2010). The 50 transects were located between 20 m and 300 km apart and the median pairwise distance between transects was 60 km. Red and purple urchins were counted by divers in six 1-m2 quadrats uniformly spaced along fixed 40 x 2 m transects. Surveys were conducted at each transect once per year during the summer; 11 years of data (2000-2010) were collected at the Santa Barbara sites and 8 years of data (2000-2007) were collected at the San Clemente sites. Sea urchins are long-lived and so annual sampling is sufficient to characterize their population dynamics (Ebert & Southon, 2003). Kelp forests that are heavily impacted by urchin grazing often display relatively low and stable levels of kelp abundance (i.e., dampened seasonal cycles in abundance) for multiple years (Lawrence, 1975). Therefore, long-term changes in urchin dynamics have the potential to influence synchrony measured on monthly to seasonal time scales.

GIANT KELP RECRUITMENT DATA

While the macroscopic stage of giant kelp is sedentary and firmly anchored to the bottom, its microscopic spores disperse freely in the water column and typically travel distances on the order of meters to kilometers before settling to the seafloor (Reed et al., 2006b). Once spores settle to the bottom, they require firm substrate and sufficient light and nutrients for successful recruitment (Graham et al., 2007). The amount of light and nutrients available to recently settled spores can vary greatly in space and time (Deysher & Dean, 1986). Therefore spatial autocorrelation in these variables could create spatial patterns in kelp recruitment, which could in turn impact synchrony in adult populations (Nisbet & Bence, 1989). If this is the case, then patterns of synchrony in kelp recruitment should resemble those of adult density as determined by Landsat imagery. We used annual surveys of the density of giant kelp juveniles < 1 year old (defined as all individuals with fewer than 3 fronds) from 32 transects along the Santa Barbara coastline and 18 transects along the San Clemente coastline (red crosses in Fig. 1a) to examine synchrony in recruitment at scales of 50 m to 300 km. Surveys were conducted along the same transects used for the urchin surveys described above.

SYNCHRONY ANALYSIS

Synchrony between sites is usually measured as the pairwise correlation between time series of abundances or changes in abundances (Bjørnstad et al., 1999b). In this study we used first-differenced time series of log(canopy biomass + 1) in order to examine synchrony in growth and mortality of giant kelp populations. Log transformations were used to normalize the abundance data. Sites (50 m coastline segments) that did not have any kelp during the study period were not included in the analysis. SST, maximum wave height, urchins, and kelp recruit abundance are all likely to affect kelp growth rates directly, so for these explanatory variables we examined pairwise correlations in abundance / magnitude rather than changes in abundance / magnitude. We used spatial autocorrelation techniques and the nonparametric correlation function (NCF, ‘Sncf’ function in R, Bjørnstad et al., 1999a) to examine and model the relationship between synchrony and distance for the giant kelp canopy biomass, SST, wave height, urchin, and kelp recruit datasets (Sokal & Oden, 1978). While the largest along-coast distance between two sites of giant kelp in our study area was 547 km, sample sizes were much larger for distances < 300 km, and so we used 300 km as the maximum distance for all analyses.

The NCF uses a smoothing spline to estimate a continuous function describing synchrony as a function of distance (Bjørnstad et al., 1999b). We used √n, where n is the number of sampling locations for each variable, as the degrees of freedom for each NCF (this is the default value in the 'Sncf' package). Conventional parametric approaches for estimating statistical significance and confidence intervals for pairwise correlations could not be used because of spatial autocorrelation in the data. Therefore we calculated confidence intervals using bootstrap resampling with 1000 iterations. For the kelp biomass synchrony analysis we used the temporal bootstrapping method described in de Valpine et al. (2010) in order to account for variability in the temporal process as well as spatial sampling variability. This method recreates the dataset by resampling contiguous 3-month blocks of data with replacement. We quantified the spatial scale of synchrony in our variables using three different methods. First, we calculated the distance at which synchrony was no longer significantly greater than zero. However, many of our variables displayed significant positive synchrony across the entire study area. In these instances we calculated the distance at which synchrony was equal to the regional mean of the NCF. Where possible, we also modeled each NCF as an exponential or double exponential decay function using least squares fits (Chiles & Delfiner, 1999),

$$a + b\,(1 - e^{\frac{-3x}{c}}) \qquad \text{(Eq. 1)}$$

for the exponential function and,

$$a + b\,(1 - e^{\frac{-3x}{c}}) + d\,(1 - e^{\frac{-3x}{f}}) \qquad \text{(Eq. 2)}$$

for the double exponential function, where x is the distance between pixels and a, b, c, d, and f are the fit parameters. a represents the modeled y-intercept value. The c and f parameters provide a measure of the length scale of synchrony.

We modeled the synchrony-distance correlation function of the giant kelp canopy biomass data first using the entire 11-year time series and then again separately for each year in order to examine how the correlation function changed through time. Giant kelp populations often experience annual cycles driven by seasonal changes in wave energy, nutrients, and light availability; however, the timing and strength of these cycles vary a great deal from year to year (Cavanaugh et al., 2011). Therefore, annual correlation functions (i.e., correlation functions created from monthly data from a single year) should capture the spatial scale of similarity in these annual cycles. We also calculated the annual correlation functions for SST and wave height and compared these to the kelp annual correlation functions. The urchin and kelp recruit data were collected annually so we were not able to calculate annual correlation functions for these variables.

RESULTS

SPATIAL SYNCHRONY IN GIANT KELP, ENVIRONMENTAL, AND URCHIN DATA

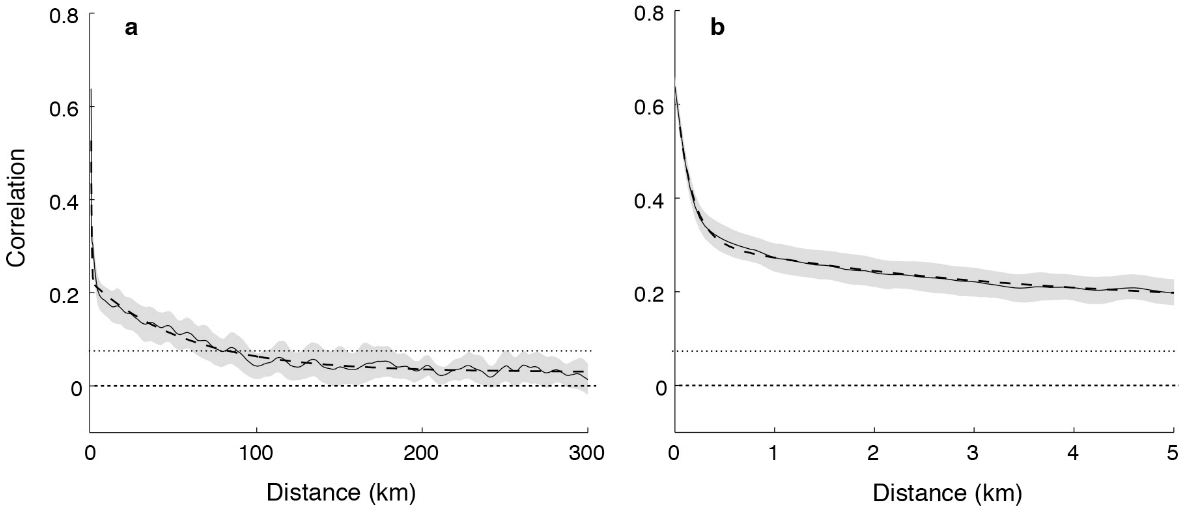

Fig 2. Nonparametric spatial correlation functions (NCF) and modeled double exponential fit for changes in log(kelp biomass + 1). (b) shows the same data from (a) but with a different x-axis scale. In each plot, the solid black line represents the NCF and the grey shaded areas give the 95% bootstrap confidence intervals. The dashed curve represents the modeled double exponential fit for the NCF. The dotted horizontal line gives the regional mean correlation and the dashed horizontal line represents 0 synchrony.

Synchrony in giant kelp canopy biomass changes decreased with increasing distance following a double exponential decay function with steps at two very different spatial scales: c = 1.3 ± 0.15 km and f = 172 ± 10 km (Fig. 2, Appendix S1 in Supporting Information). The double exponential function provided a substantially better fit than the single exponential (R^2 = 0.99 vs. 0.88, S1). An F-test demonstrated that the improved fit provided by the double exponential model was statistically significant ($F_{2,59}$ = 216, p < 0.01). Mean synchrony among adjacent sites was high (0.53 ± 0.01), but the spatial correlation function decayed exponentially out to a distance of 1.3 km, where the mean pairwise correlation was 0.22 ± 0.03 (Fig. 2b). The second exponential decrease occurred on a much larger scale, flattening at 172 km with a pairwise correlation of 0.04 ± 0.03 (Fig. 2a). Between distances of 172 km and 300 km synchrony was low, but significantly greater than 0. The regional mean synchrony in kelp biomass between 0 and 300 km was 0.08 ± 0.03, and the synchrony-distance curve fell below this regional mean level at a distance of 74 ± 15 km (Fig 2a).

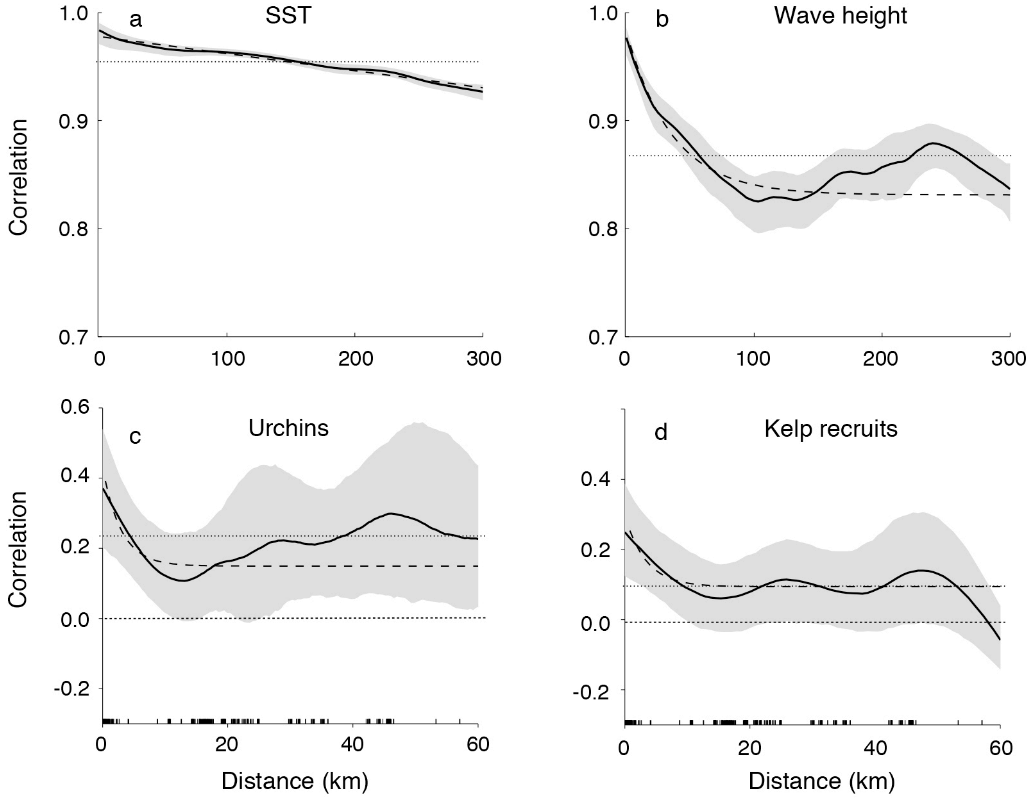

Figure. 3. Nonparametric spatial correlation functions for changes in (a) SST, (b) wave height, (c) log(urchin abundance + 1), and (d) log(kelp recruit abundance + 1). Note difference in scale of (c) and (d). The grey shaded areas in each plot represent the 95% bootstrap confidence intervals. The dashed line in (a) represents the modeled linear fit for the SST NCF curve and the dashed curves in (b), (c), and (d) represent the modeled exponential decay fits for the wave height, urchin, and kelp recruit NCFs. The dotted horizontal lines give the regional mean correlation and the dashed horizontal lines represent 0 synchrony. Rug plots (dashes on x-axis) on (c) and (d) show the pairwise distances between sample sites.

SST and significant wave height exhibited high levels of autocorrelation across the study area, but the magnitude of synchrony for both variables generally declined with increasing distance (Fig. 3a & 3b). The SST NCF decreased linearly between 0 and 300 km with a y-intercept of 0.98 and slope of -2 * 10^8 (Fig. 3a). The initial decrease in the wave height NCF between 0 and 120 km was well modeled by the exponential decay function (Fig. 3b; see Appendix S2 in

Supporting Information for exponential model parameters). Over this range the wave height NCF decreased from 0.98 ± 0.02 to 0.83 ± 0.03. The wave height NCF then increased slightly between 120 and 240 km.

We observed moderate positive synchrony in sea urchin abundance at distances < 60 km (Fig. 3c). Synchrony declined from 0.37 ± 0.16 to 0.12 ± 0.12 between 0 and 11 km, and this initial decrease followed the exponential decay function (S2). Between 11 and 70 km synchrony appeared to increase slightly, however the confidence intervals at these distances were large (because of limited sample size) and so we cannot reject the hypothesis that the synchrony-distance relationship is flat across these distances. Synchrony in the annual abundance of kelp recruits decreased exponentially between 0 and 10 km, falling from 0.25 ± 0.12 to 0.08 ± 0.09 (Fig. 3d). Kelp recruit synchrony was not significantly different from 0 at distances greater than 10 km. The spatial coverage of both the urchin and kelp recruit datasets was limited and so it was difficult to determine the significance of changes in synchrony in these variables at scales larger than 25 km (as shown by the rug plots and large confidence intervals in Figs. 3c & 3d).

TEMPORAL VARIABILITY IN GIANT KELP SPATIAL SYNCHRONY

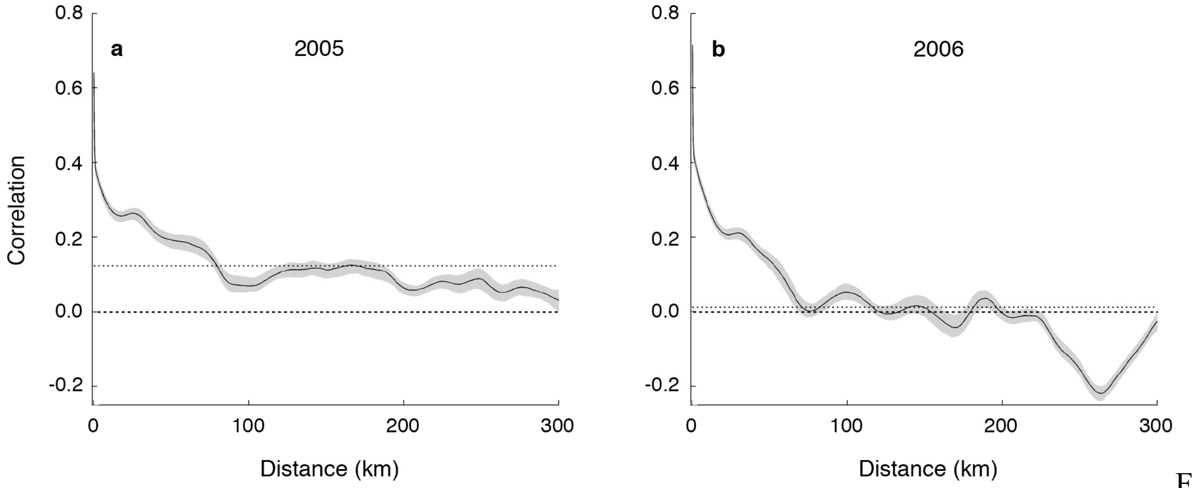

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Fig. 4. Annual nonparametric spatial correlation functions for changes in log(biomass + 1) of kelp in 50 m alongshore coastline using monthly data from (a) January 1, 2005 to December 31, 2005 and (b) January 1, 2006 to December 31, 2006. The grey shaded areas in each plot represent the 95% bootstrap confidence intervals. The dotted horizontal lines give the regional mean correlation and the dashed horizontal lines represent 0 synchrony. Annual NCFs for other years are given in Appendix S3 in Supporting Information.

Table I. Magnitude of spatial synchrony in kelp biomass data at different distances and the length scale of kelp synchrony. The length scale was calculated as the distance at which the nonparametric correlation function reached the regional mean synchrony level. $\rho(0)$ represents the y-intercept of the nonparametric correlation function. Numbers in brackets are the 95% confidence intervals.

	2000	**2001**	**2002**	**2003**	**2004**	**2005**	**2006**	**2007**	**2008**	**2009**	**2010**
$\rho(0)$	0.70 [0.67 0.73]	0.64 [0.62 0.68]	0.72 [0.70 0.75]	0.67 [0.65 0.69]	0.65 [0.63 0.67]	0.64 [0.62 0.66]	0.71 [0.69 0.74]	0.74 [0.72 0.76]	0.67 [0.65 0.69]	0.65 [0.63 0.67]	0.63 [0.61 0.65]
$\rho(5)$	0.37 [0.33 0.41]	0.39 [0.34 0.42]	0.41 [0.37 0.46]	0.35 [0.32 0.37]	0.29 [0.26 0.32]	0.29 [0.26 0.33]	0.30 [0.28 0.32]	0.48 [0.46 0.49]	0.31 [0.29 0.33]	0.34 [0.32 0.37]	0.21 [0.19 0.23]
$\rho(70)$	0.26 [0.23 0.30]	0.08 [0.05 0.10]	0.33 [0.29 0.36]	0.10 [0.08 0.11]	0.02 [0.00 0.04]	0.17 [0.15 0.19]	0.01 [-0.01 0.04]	0.37 [0.36 0.39]	0.14 [0.13 0.16]	0.14 [0.13 0.15]	0.10 [0.08 0.12]
Scale (km)	102 [101 104]	85 [61 107]	85 [81 90]	37 [34 39]	65 [62 68]	74 [67 77]	62 [57 65]	95 [85 115]	85 [71 88]	80 [76 83]	28 [25 62]

In each of the 11 years of our study, giant kelp synchrony displayed a 2-step decrease with distance: an initial rapid decline at small scales (0-5 km) was followed by a more gradual decline at large scales (5-200 km; Fig. 4 & S3). Table I lists the NCF pairwise correlations at 0, 5, and 70 km for each year; in all years synchrony decreased significantly between these distance classes. While all years displayed this stepwise decrease in synchrony, the magnitude of correlation at each distance class and the distance at which the NCF reached the regional mean synchrony level varied across years (Table I). Local correlation, $\rho(0)$, and correlation at 5 km were relatively consistent, ranging from 0.63 to 0.74 and 0.21 to 0.48 respectively (coefficients of variation = 0.06 and 0.21). The correlation at 70 km was more variable: it ranged from 0.01 to 0.37 and had a coefficient of variation of 0.76. The length scale of kelp synchrony, defined here as the distance at which the NCF reached the regional synchrony level, also ranged widely from 28 to 102 km. This pattern indicates that much of the temporal variability in the annual spatial correlation functions occurs at larger, regional scales. We compared the annual length scales of kelp synchrony to the annual length scales of SST and wave height (Appendix S4 in Supporting Information) but did not find a significant relationship with either variable ($p = 0.40$ and 0.48 respectively). Defining the length scales of kelp, SST, and wave height as the distance at which kelp synchrony reached 0 or as the flattening parameters of the modeled exponential functions (c and f from Eq. 1 & 2) did not change these results.

DISCUSSION

Researchers have long called for more interaction between the fields of population and landscape ecology (Levin, 1992; Wiens, 1997). This study demonstrates how remote sensing and geospatial analysis techniques, widely used by landscape ecologists, can be combined with time series analysis of population dynamics to analyze spatial autocorrelation in populations. This approach can help address the well-recognized problem that many conclusions regarding spatial population dynamics are limited by the scale of the study design (Wiens, 1989; Bjørnstad et al., 1999a). Landsat ™ provides relatively uninterrupted coverage from 1984-2011, and so these methods can be applied to examine long-term synchrony patterns in other habitats where changes in species abundance can be quantified from satellite imagery (e.g., seagrasses, coral reefs, wetlands, grasslands). However, the ability to observe synchrony over multiple generations will depend on the lifespan of the species in question, and so these techniques may not be applicable for habitats made up of long-lived species (e.g., pine forests). In these cases it may be more informative to examine synchrony in phenology or recruitment.

The spatial resolution (50 m) and extent (550 km) of our study spanned over 5 orders of magnitude. The spatial resolution was fine enough to cover the spatial scales of dispersal for this species (meters to kilometers, Reed et al., 2006b; Alberto et al., 2010), while the extent was large enough to examine the spatial structure of large-scale environmental controls that are known to influence giant kelp populations (Graham et al., 2007). The temporal resolution and extent was sufficient to capture intra-annual as well as inter-annual variation in kelp biomass. Between 2000-2011 we identified a two-step decrease in synchrony with distance: an initial exponential decrease between 50 m and 1.3 km followed by a large-scale exponential decrease between 1.3 and 172 km. The large difference in the spatial scales of these 2 patterns suggests that multiple processes are responsible for synchronizing giant kelp populations. Lande et al. (1999) demonstrated that small-scale dispersal could induce synchrony on much larger scales if the dispersal rate (roughly speaking, the fraction of the local population that disperses per unit time) is large relative to the strength of density dependence. However, only the spores of giant kelp disperse, so that, as a fraction of biomass, the dispersal rate (sensu Lande et al., 1999) is quite small. Since giant kelp dispersal is limited to relatively short distances (meters to kilometers, Reed et al., 2006b; Alberto et al., 2010) and there are a variety of density-dependent processes acting at the local scale that impact the growth and mortality of giant kelp (reviewed in Schiel & Foster, 2006), we do not think that dispersal is playing a major role in long-range synchrony.

Grazing by sea urchins and local processes that influence recruitment of giant kelp likely explain some of the initial exponential decrease in kelp canopy biomass synchrony between 50 m and 1.3 km. Synchrony in both urchin abundance and kelp recruitment was positive and significant at small scales, but declined rapidly on spatial scales similar to the initial exponential decrease in kelp synchrony (Fig. 3c & Fig. 3d). Grazing may induce synchrony in kelp populations by causing mortality that is spatially autocorrelated at local scales. The processes controlling recruitment include dispersal limitation of planktonic spores, bottom irradiance, sedimentation, competition, and grazing. Fertilization in giant kelps occurs after dispersal and requires dense spore settlement (> 1 spore per mm^2), thereby limiting the effective dispersal distance in giant kelp (Reed et al., 1991). Reed et al. (2006b) performed a series of empirical and modeling studies of spore dispersal and estimated that the scale of dispersal in giant kelp is on the order of meters to kilometers. This result agrees with theoretical diffusive models of dispersal that show exponential decreases in spatial autocorrelation with distance on spatial scales similar to the scale of average dispersal (Bjørnstad et al., 1999a; chapter 5 in Okubo & Levin, 2002). While we were not able to quantify the spatial autocorrelation of local environmental factors such as bottom irradiance, sedimentation, and the effects of competition, many of these features vary on small scales and are important determinants of recruitment success for giant kelp (reviewed in Graham, 2007). It was not possible for us to separate the roles of dispersal, local environmental variability, and grazing in synchronizing kelp populations at small scales using these observational data; manipulative studies are needed to address this issue.

We hypothesize that the large-scale decrease in giant kelp synchrony is primarily due to large-scale environmental controls (i.e., the Moran effect), particularly wave disturbance. The Moran effect predicts that the synchrony of populations controlled by large-scale environmental perturbations should decline in an identical or parallel manner to the synchrony of the environmental variables (Moran, 1953). The length scale of this large-scale decrease (74 km when calculated as the distance where the NCF reaches its regional mean synchrony level) corresponded to the length scale of the wave height NCF (61 km, compare Fig. 2 to Fig. 3b). In addition, the double exponential and exponential models of the kelp and wave height NCFs flattened at similar length scales, 172 km and 120 km respectively. The most probable mechanism by which wave disturbance influences kelp synchrony is by causing spatially correlated mortality on scales corresponding to the scales of wave height autocorrelation. However, large wave events may also induce spatially correlated recruitment and growth of kelp populations. Wave disturbance can clear space and create light conditions that promote the recruitment and juvenile growth of a new cohort of giant kelp (Graham et al., 1997). Synchrony in changes in SST, a proxy for nutrients, also declined with distance over large scales and so may be contributing to the large-scale decline in kelp synchrony. Nutrient levels can strongly influence giant kelp growth rates (Jackson, 1977; Gerard, 1982), and prolonged low nutrient conditions, such as those associated with El Niño events, can cause regional scale mortality events (Dayton & Tegner, 1984). However, SST synchrony did not demonstrate an exponential decline and SST was highly autocorrelated over the entire study area, therefore we hypothesize that wave driven disturbance plays a larger role than nutrients in setting the spatial scale of regional kelp synchrony. These results are consistent with those of other studies that have found nutrient availability and wave disturbance to be important in accounting for regional differences in the dynamics of giant kelp (Dayton et al., 1999; Edwards, 2004; Reed et al., 2011). Sea urchins, the major grazer of kelp, did show some positive synchrony in population dynamics at scales of up to 60 km (Fig. 3c), and so urchins could also play a role in large-scale kelp synchrony.

The stepwise pattern in the kelp biomass NCF was significant in each of the 11 years of the study (Table I & S3), demonstrating that this pattern is evident on annual as well as inter-annual time scales. It is important to note that the NCF created from the entire time series (2000-2011, Fig. 2) represents the long-term pattern in synchrony, and that this decadal scale pattern in unlikely to be observed in a given year. The relatively high variability in both the magnitude of synchrony at large spatial scales and the length scale of synchrony for the annual kelp correlation functions (Table I & S3) indicates that much of the temporal variability in patterns of giant kelp synchrony occurs on the larger spatial scales that appear to be regulated by environmental factors. However, we were unable to explain the variability in the length scale of giant kelp using the length scale of SST or wave height. The lack of a significant relationship between these variables may be partly due to the complexity of the annual kelp correlation functions. This complexity makes it difficult to quantify the length scale of kelp synchrony. The annual kelp correlation functions do not all follow a double exponential decline and the point where the NCF reaches the mean level of synchrony did not fully capture the shape of the NCF (S3). Also, the relationship between the length scale of kelp synchrony and its driving factors is probably complex and nonlinear on short time scales. For instance, a single large storm event can induce large-scale synchrony in kelp populations by removing all the kelp in a very large region (Edwards, 2004). The relationship between annual maximum wave height and kelp mortality saturates at high wave heights (Cavanaugh et al., 2011) and so as long as the wave heights across a given region are all above a certain threshold, mortality will be high and consistent across that entire region, even if there is spatial variability in wave height across the region. Over longer time periods the effect of these short-term discrepancies in scale are likely averaged out by repeated cycles of disturbance and recovery.

It is especially important to understand how multiple processes synchronize populations for systems that function as metapopulations (see Reed et al., 2006b for a discussion of giant kelp as a metapopulation). The metapopulation concept refers to a collection of local populations linked by limited dispersal and has been used to describe a wide variety of terrestrial (Hanski & Gilpin, 1997) and marine (Kritzer & Sale, 2006) ecosystems. Synchrony is especially important in these systems because metapopulation theory predicts that higher levels of synchrony in local population dynamics will lead to a higher probability of extinction of the metapopulation (Heino et al., 1997, Liebhold et al., 2004). If local subpopulations fluctuate together, then they will tend to go extinct at the same time. On the other hand, if spatial synchrony is low then abundant subpopulations can contribute propagules that recolonize neighboring extinct patches, thereby increasing the persistence of the metapopulation. For example, in an analysis of wintering North American birds, Koenig (2001) found a significant positive relationship between spatial autocorrelation at short distances and the length of extinctions of resident species. However, theoretical studies have also shown that the degree to which spatial synchrony impacts metapopulation persistence is highly dependent on the spatial distribution of the subpopulations (Adler & Nuemberger, 1994). Johst & Drechsler (2003) modeled metapopulations of various spatial configurations and found that increased habitat clustering increased metapopulation persistence in both static and dynamic landscapes. More empirical work is needed to understand how the spatial distribution of subpopulations, the length scale of dispersal, and the length scale of synchrony interact to control extinction risk in real-world of metapopulations.

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REFERENCES

Abbott, K.C. (2007) Does the pattern of population synchrony through space reveal if the Moran effect is acting? Oikos, 116, 903–912.

Adler, F.R. & Nuernberger, B. (1994) Persistence in patchy irregular landscapes. Theoretical Population Biology, 45, 41–75.

Alberto, F., Raimondi, P.P.T., Reed, D.D.C., Coelho, N.C., Leblois, R., Whitmer, A. & Serrão, E.A. (2010) Habitat continuity and geographic distance predict population genetic differentiation in giant kelp. Ecology, 91, 49–56.

Bascompte, J. & Solé, R.V. (1988) Spatiotemporal patterns in nature. Trends in Ecology & Evolution, 13, 173–174.

Bjornstad, O.N. (2000) Cycles and synchrony: two historical “experiments” and one experience. Journal of Animal Ecology, 69, 869–873.

Bjørnstad, O.N. & Falck, W. (2001) Nonparametric spatial covariance functions: Estimation and testing. Environmental and Ecological Statistics, 8, 53–70.

Bjørnstad, O.N., Ims, R.A. & Lambin, X. (1999) Spatial population dynamics: analyzing patterns and processes of population synchrony. Trends in Ecology & Evolution, 14, 427–432.

Bjørnstad, O.N., Stenseth, N.C. & Saitoh, T. (1999) Synchrony and Scaling in Dynamics of Voles and Mice in Northern Japan. Ecology, 80, 622–637.

Buonaccorsi, J.P., Elkinton, J.S., Evans, S.R. & Liebhold, A.M. (2001) Measuring and testing for spatial synchrony. Ecology, 82, 1668–1679.

Cavanaugh, K., Siegel, D., Reed, D. & Dennison, P. (2011) Environmental controls of giant kelp biomass in the Santa Barbara Channel, California. Marine Ecology Progress Series, 429, 1–17.

Chiles, J.P. & P., D. (1999) Geostatistics, modelling spatial uncertainty. (ed. by Wiley-Interscience) New York.

Dayton, P., Tegner, M.J., Edwards, P.B. & Riser, K.L. (1999) Temporal and spatial scales of kelp demography: the role of oceanographic climate. Ecological Monographs, 69, 219–250.

Dayton, P.K. & Tegner, M.J. (1984) Catastrophic storms, el nino, and patch stability in a southern california kelp community. Science, 224, 283–285.

Denny, M.W. (1988) Biology and the Mechanics of the Wave-Swept Environment, (ed. by P.U. Press) Princeton.

Deysher, L.E. & Dean, T.A. (1986) Interactive effects of light and temperature on sporophyte production in the giant kelp Macrocystis pyrifera. Marine Biology, 93, 17–20.

Ebert, T.A. & Southon, J.R. (2003) Red sea urchins (Strongylocentrotus franciscanus) can live over 100 years: confirmation with A-bomb 14carbon. Fishery Bulletin, 101, 915–922.

Edwards, M.S. (2004) Estimating scale-dependency in disturbance impacts: El Ninos and giant kelp forests in the northeast Pacific. Oecologia, 138, 436–447.

Foster, M. & Schiel, D. (1985) The ecology of giant kelp forests in California: A community profile. Biological report: United States Fish and WIldlife Service, 85.

Fram, J.P., Stewart, H.L., Brzezinski, M.A., Gaylord, B., Reed, D.C., Williams, S.L. & MacIntyre, S. (2008) Physical pathways and utilization of nitrate supply to the giant kelp, Macrocystis pyrifera. Limonology And Oceanography, 53, 1589–1603.

Gerard, V.A. (1982) Growth and utilization of internal nitrogen reserves by the giant kelp Macrocystis pyrifera in a low-nitrogen environment. Marine Biology, 27–35.

Gouhier, T.C., Guichard, F. & Menge, B.A. (2010) Ecological processes can synchronize marine population dynamics over continental scales. Proceedings of the National Academy of Sciences of the United States of America, 107, 8281–8286.

Graham, M., Harrold, C., Lisin, S., Light, K., Watanabe, J. & Foster (1997) Population dynamics of giant kelp Macrocystis pyrifera along a wave exposure gradient. Marine Ecology Progress Series, 148, 269–279.

Graham, M.H., Vasquez, J.A. & Buschmann, A.H. (2007) Global ecology of the giant kelp Macrocystis: from ecotypes to ecosystems. Oceanography and Marine Biology: an Annual Review, 45, 39–88.

Hanski, I. & Woiwod, I.P. (1993) Spatial synchrony in the dynamics of moth and aphid populations. Journal of Animal Ecology, 62, 656–668.

Hanski, I.A. & Gilpin, M.E. (1997) Metapopulation Biology: Ecology, Genetics, and Evolution, (ed. by I. Hanski and Michael E Gilpin) Academic Press.

Harrold, C. & Pearse, J.S. (1987) Echinoderm studies. (ed. by E. M. Jangoux and J. M. Lawrence), pp. 137–233. Rotterdam, the Netherlands.

Heino, M., Kaitala, V., Ranta, E. & Lindström, J. (1997) Synchronous dynamics and rates of extinction in spatially structured populations. Proceedings of the Royal Society B Biological Sciences, 264, 481–486.

Ims, R.A. & Andreassen, H.P. (2000) Spatial synchronization of vole population dynamics by predatory birds. Nature, 408, 194–196.

Inc., T.M. ed. (2011) MATLAB version 7.12, Natick, Massachusetts.

Jackson, G.A. (1977) Nutrients and production of giant kelp, Macrocystis pryifera, off southern California. Limnology and Oceanography, 22, 979–995.

Johst, K. & Drechsler, M. (2003) Are spatially correlated or uncorrelated disturbance regimes better for the survival of species? Oikos, 103, 449–456.

Kahru, M., Kudela, R., Manzano-Sarabia, M. & Mitchell, B.G. (2009) Trends in primary production in the California Current detected with satellite data. Journal of Geophysical Research, 114, 1–7.

Kareiva, P. & Wennergren, U. (1995) Connecting landscape patterns to ecosystem and population processes. Nature, 373, 299–302.

Kendall, B.E., Bjrnstad, O.N., Bascompte, J., Keitt, T.H. & Fagan, W.F. (2000) Dispersal, environmental correlation, and spatial synchrony. The American Naturalist, 155, 628–636.
Koenig, W. (1999) Spatial autocorrelation of ecological phenomena. Trends in Ecology & Evolution, 14, 22–26.

Koenig, W. & Knops, J. (2000) Patterns of Annual Seed Production by Northern Hemisphere Trees: A Global Perspective. The American naturalist, 155, 59–69.

Koenig, W.D. (2001) Spatial Autocorrelation And Local Disappearances In Wintering North American Birds. Ecology, 82, 2636–2644.

Kritzer, J.P. & Sale, P.F. (2006) Marine metapopulations, Academic Press, San Diego.

Lande, Engen & Sæther (1999) Spatial scale of population synchrony: Environmental correlation versus dispersal and density regulation. The American Naturalist, 154, 271–281.

Lawrence, J.M. (1975) On the relationships between marine plants and sea urchins. Oceanography and Marine Biology - An Annual Review, 213–286.

Levin, S.A. (1992) The Problem of Pattern and Scale in Ecology: The Robert H. MacArthur Award Lecture. Ecology, 73, 1943–1967.

Liebhold, A., Koenig, W.D. & Bjornstad, O.N. (2004) Spatial Synchrony in Population Dynamics. Annual Review of Ecology Evolution and Systematics, 35, 467–490.

Lucas, A.J., Dupont, C.L., Tai, V., Largier, J.L., Palenik, B. & Franks, P.J.S. (2011) The green ribbon: Multiscale physical control of phytoplankton productivity and community structure over a narrow continental shelf. Limonology And Oceanography, 56, 611–626.

Moran, P. (1953) The statistical analysis of the Canadian Lynx cycle. Australian Journal of Zoology, 1, 291.

Nisbet, R.M. & Bence, J.R. (1989) Alternative dynamic regimes for canopy-forming kelp: a variant on density-vague population regulation. American Naturalist, 377–408.

North, W.J. & Zimmerman, R.C. (1984) Influences of macronutrients and water temperatures on summertime survival of Macrocystis canopies. Hydrobiologia, 419–424.

O'Reilly, W.C. & Guza, R.T. (1993) A comparison of two spectral wave models in the Southern California Bight. Coastal Engng, 19, 263–282.

Okubo, A. & Levin, S.A. (2002) Diffusion and Ecological Problems, (ed. by Springer) New York.

Peltonen, M., Liebhold, A.M., Bjørnstad, O.N. & Williams, D.W. (2002) Spatial Synchrony In Forest Insect Outbreaks : Roles Of Regional Stochasticity And Dispersal. Ecology, 83, 3120–3129.

R Development Core Team (2013) R: A Language and Environment for Statistical Computing.

Ranta, E., Kaitala, V., Lindstrom, J. & Linden, H. (1995) Synchrony in population dynamics. Proceedings of the Royal Society B Biological Sciences, 262, 113–118.

Reed, D. (2010) SBCLTER: Reef: Kelp Forest Community Dynamics: Invertebrate and algal density. Santa Barbara Coastal Long Term Ecological Research Project.

Reed, D.C., Neushul, M. & Ebeling, A.W. (1991) Role of Settlement Density on Gametophyte Growth and Reproduction in the Kelps Pterygophora-Californica and Macrocystis-Pyrifera (Phaeophyceae). Journal of Phycology, 27, 361–366.

Reed, D.C., Schroeter, S.C. & Huang, D. (2006) An experimental investigation of the use of artificial reefs to mitigate the loss of giant kelp forest habitat. A case study of the San Onofre Nuclear Generating Station's artificial reef project, (ed. by California Sea Grant College Program) San Diego.

Rnstad, O.B., Ims, R. & Lambin, X. (1999) Spatial population dynamics: analyzing patterns and processes of population synchrony. Trends in ecology evolution, 14, 427–432.

De Roos, A.M., McCauley, E. & Wilson, W.G. (1991) Mobility versus density-limited predator-prey dynamics on different spatial scales. Proceedings of the Royal Society B Biological Sciences, 246, 117–122.

Sokal, R.R. & Oden, N.L. (1978) Spatial autocorrelation in biology 2. Some biological implications and four applications of evolutionary and ecological interest. Biological Journal of the Linnean Society, 10, 229–249.

De Valpine, P., Scranton, K. & Ohmart, C.P. (2010) Synchrony of population dynamics of two vineyard arthropods occurs at multiple spatial and temporal scales. Ecological Applications, 20, 1926–1935.

Wiens, J. (1997) Metapopulation biology: ecology, genetics, and evolution. (ed. by E. I. A. Hanski and M. E. Gilpin), Academic Press, San Diego.

Wiens, J.A. (1989) Spatial Scaling in Ecology. Functional Ecology. British Ecological Association, 385–397.

SUPPLEMENTAL INFORMATION

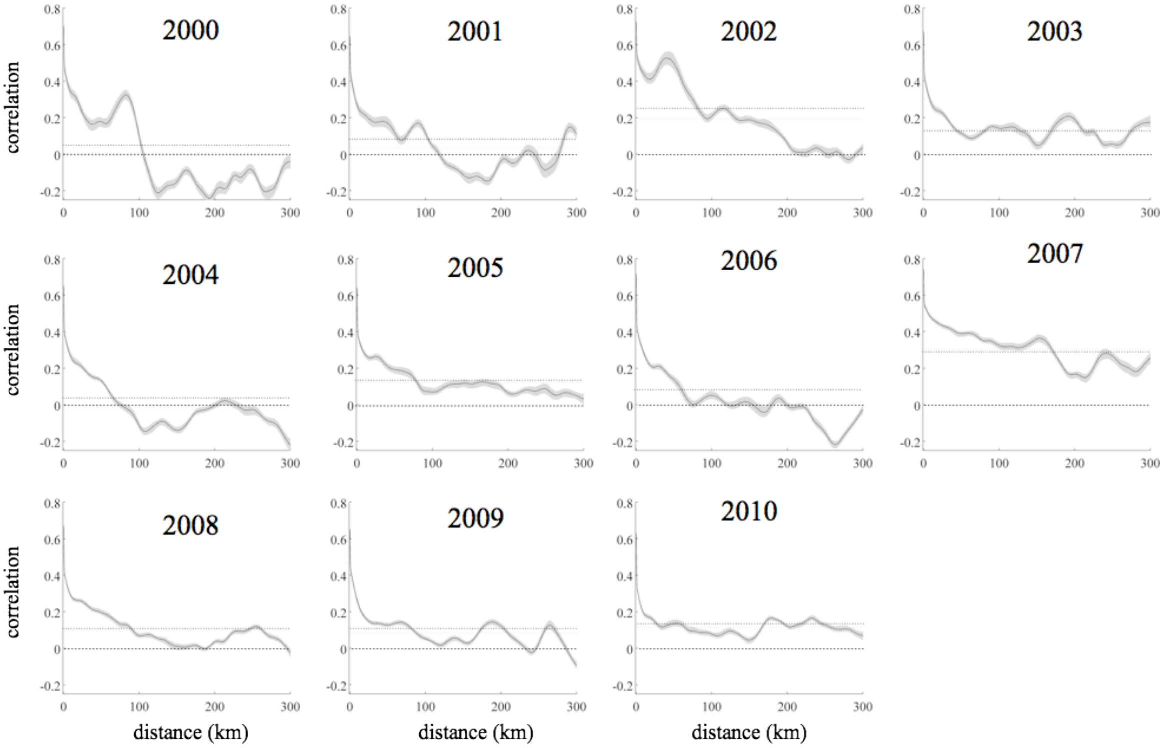
Appendix S1. Least squares estimates of exponential and double exponential decay function parameters (from Eqs. 1 & 2) for giant kelp biomass nonparametric spatial correlation functions. Numbers in brackets are the 95% confidence intervals. The last column gives the R^2 for the comparison between the nonparametric spatial covariance function and the modeled curve.

	a	**b**	**c**	**d**	**f**	**R^2**
Exponential	0.32 [0.31 0.33]	-0.28 [-0.29 -0.26]	92 [83 100]	NA	NA	0.88
Double exponential	0.52 [0.51 0.54]	-0.31 [-0.33 -0.30]	1.3 [1.18 1.45]	-0.18 -0.19 -0.17]	172 [163 182]	0.99

Appendix S2. Least squares estimates of exponential decay function parameters (from Eq. 1) for wave height, urchin abundance, and kelp recruit abundance nonparametric spatial correlation functions. Numbers in brackets are the 95% confidence intervals.

	a	**b**	**c**
Wave Height	0.97 [0.96 0.98]	-0.15 [-0.16 -0.14]	120 [100 140]
Urchin	0.42 [0.38 0.47]	-0.29 [-0.33 -0.25]	11 [8 13]
Kelp Recruit	0.30 [0.24 0.36]	-0.20 [-0.26 -0.14]	10 [6 14]

Appendix S3. Annual nonparametric spatial correlation functions for changes in log(biomass + 1) of kelp in 50 m alongshore coastline using monthly data for each year from 2000 to 2010. The grey shaded areas in each plot represent the 95% bootstrap confidence intervals. The dotted horizontal lines give the regional mean correlation and the dashed horizontal lines represent 0 synchrony.



Appendix S4. The length scale of Sea Surface Temperature (SST) and wave height synchrony for each year from 2000 to 2011. The length scale was calculated as the distance at which the nonparametric correlation function reached the regional mean synchrony level. Numbers in brackets are the 95% confidence intervals.

	2000	**2001**	**2002**	**2003**	**2004**	**2005**	**2006**	**2007**	**2008**	**2009**	**2010**
SST	115	152	130	138	162	161	123	135	147	158	108
length scale (km)	[82 193]	[97 180]	[78 174]	[105 190]	[138 177]	[126 175]	[84 171]	[65 190]	[82 179]	[41 191]	[82 185]
Wave height	65	61	71	62	61	61	58	54	60	60	70
length scale (km)	[48 89]	[33 86]	[43 96]	[40 82]	[46 74]	[39 93]	[39 88]	[35 74]	[45 77]	[52 68]	[51 92]

CHAPTER III » THE RANGE-EDGE OF EUROPEAN KELP FORESTS UNDER CLIMATE CHANGE

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ABSTRACT

Global climate change is affecting the distribution of several species, particularly at the range edge of distributions, where small variations on the peripheral niche of species may produce the extinction of populations. The maintenance of ecosystem function for the future is dependent on the persistence of foundation species such as kelps. In line with a worldwide trend in kelp distribution contraction at low latitude ranges, the southern ranges of the kelp *S. polyschides* have recently shifted, although the main causes and the extent of contraction have not been addressed. Using Generalized Linear Mixed Models relating distribution records with high-resolution remote sensing data, this study inferred the major environmental forces shaping the distribution of this species and predicted range dynamics by hindcasting distributions to 1986-2012 and forecasting to 2013-2100. This was performed by coupling distribution models with simulations of dispersal, on a multiple life cycle approach, a challenging framework that has rarely been implemented. Results showed that the southern ranges of *S. polyschides* are primarily shaped by physiological limitations imposed by extreme winter temperatures and by seasonal upwelling, which delivers essential nutrients for recruitment. The simulations corroborated the expected low dispersal capacity of this species, while the reconstruction of distributions restrained by dispersal inferred a decrease of ~50% in extent of kelp from 1986 to 2012, confining distribution to regions of strong upwelling. Different consequences of future climate were predicted by using contrasting scenarios of greenhouse gas emissions. In the most optimistic scenario, the extent decreased until 2075 with populations restricted to the northwest of the Iberia Peninsula. Increasing emissions produced a constant decline until 2071, when the range edge populations of *S. polyschides* are to be extinct. The demise of most range edge populations due to climate change seems plausible, which will certainly produce severe consequences for the distribution of essential habitats and for the balance of trophic interactions.

INTRODUCTION

Recent climate change has produced several shifts in the distributions and abundances of species (Root et al., 2003, Parmesan & Yohe, 2003; Parmesan, 2006; Moritz et al., 2008; Nicastro et al., 2013). The upcoming climate has further potential for causing range shifts (Sala et al., 2000; Millenium Ecosystem Assessment, 2005), becoming one of the most important drivers for biodiversity change in the immediate future (Sala et al., 2000; Thomas et al., 2004; Fischlin et al., 2007), particularly at the so-called trailing edges, where small variations on the peripheral niche of species may produce the extinction of extant populations (Somero, 2010). Future structuring and maintenance of ecosystem function will depend on the persistence of foundation species such as kelps (Hoegh-Guldberg & Bruno, 2010; Halpern & Kappel, 2012). These create complex habitats that provide essential resources, shelter and nursery grounds for many marine organisms (Steneck et al., 2002; Graham, 2004; Norderhaug et al., 2005), mostly when present in dense stands (i.e., kelp forests). While kelp forests are naturally resilient systems, the ongoing warming of the oceans is progressively shifting their distribution worldwide (Hoegh-Guldberg & Bruno, 2010; Wernberg et al., 2010; Raybaud et al., 2013), which may produce severe consequences for the distribution of essential habitats and for the balance of trophic interactions of numerous species (Halpern & Kappel, 2012).

Understanding the processes driving the spatial distribution of foundation species and predicting their biological responses to climate variability is therefore not only a central subject in ecology, but also for conservation management (Van der Putten et al., 2010). To address such issues, many studies have successfully implemented Species Distribution Modelling (SDMs, see Peterson et al., 2011 for a review) for several species (e.g., Thomas et al., 2004; Guisan & Thuiller 2005; Raybaud et al., 2013). These models are deeply rooted in the climatic niche theory as defined by Hutchinson (1957), benefiting from a straightforward translation into a wide range of statistical methods, linking species presence and absence data with environmental conditions, that may be transferred into past and future estimates of climate to infer the whole temporal spectrum of distributions (Guisan & Zimmermann, 2000; Guisan & Thuiller, 2005).

Environmental factors like nutrients and light availability, seawater temperature and wave action are well known to shape the distribution and productivity of kelps at multiple spatial and temporal scales (Hiscock et al., 2004; Reed at al., 2011; Cavanaugh et al., 2011, 2013).

Kelps display a complex heteromorphic life cycle that includes a diploid macroscopic sporophyte and a haploid microscopic gametophyte (Matson & Edwards, 2007). Hence, understanding the responses of kelps to climate variability can be a challenging task because the environment may act differently on each life stage (Kain, 1969; Norton, 1978; Schiel & Foster, 2006) and the responses by one stage can affect the abundance of the other stage (e.g., Ladah & Zertuche-González, 2007).

The vulnerability of a species to climate change is determined in large part by its ability to alter its range (i.e., via dispersal) to extant suitable habitats (Arribas et al., 2012). However, most reconstructions on species ranges consider unlikely extreme scenarios of unlimited dispersal or no dispersal at all (e.g., Thomas et al., 2004; Thuiller, 2004; Araújo & Luoto, 2007). This may lead to wrong estimations of the potential use of available habitat because species either use all suitable climatic space or are unable to track climate change and experience local extinctions whenever conditions fall outside tolerance limits (Guisan & Thuiller, 2005; Elith & Leathwick, 2009). In the same way, the ability of species to persist during periods of unfavorable conditions is not usually considered, resulting in the underestimation of persistence at local scales (Arribas et al., 2012). The incorporation of these processes in the accurate reconstruction of kelp distributions is a crucial step because kelps are known to have relatively limited dispersal (Billot et al., 2003; Gaylord et al., 2006; Reed et al., 2006) and some of their microscopic life stages may be able to persist during environmental conditions that are unfavorable to the macroscopic phase (Carney & Edwards, 2006; Barradas et al., 2011; Carney et al., 2013).

Here we use regression techniques relating distribution records with high-resolution remote sensing data to: (1) investigate the environmental predictors that best explain the distribution of the annual kelp *Saccorhiza polyschides*, (2) examine the relationship between interannual climate variability on the extent of *S. polyschides*, by predicting its distribution in the period 1986-2100, and (3) estimate persistence and population turnover. These questions were addressed by coupling SDMs with measures of dispersal and arrested development on a multiple life cycle approach, a challenging framework that has rarely been implemented (Guisan & Thuiller, 2005).

We focused our study along the Atlantic coast between the Iberian Peninsula and northern Africa. This region, hereafter designated as Iberia-Morocco, is an interesting model to address our questions because it is an important temperate biogeographic transition zone (Boaventura et al., 2002; Diekmann et al., 2005; Lima & Queiroz, 2006; Henriques et al., 2007) where a considerable number of species reach their distributional limits (e.g., Pereira et al., 2006; Lima et al., 2007). One such species is *Saccorhiza polyschides*, which is an important foundation species that forms kelp forests in European waters (Birkett et al., 1998), and is the main canopy building species in Iberia-Morocco (Izquierdo et al., 1995; Assis et al., 2009, 2013).

Furthermore, the Iberia-Morocco region is disproportionately affected by climate change (review by Belkin, 2009) and empirical evidence shows that range shifts for *S. polyschides* already took place there (Fernández et al., 2011; Assis et al., 2013), yet the main causes and the extent of contractions have not been addressed, despite the fact that local extinctions will certainty have substantial ecological and economic consequences.

METHODS

FOCAL SPECIES AND STUDY REGION

The present study was conducted with the annual kelp *S. polyschides*, along the coastlines of the Iberian Peninsula and Northern Africa, from the Bay of Biscay to southern Morocco, and throughout the Spanish and Moroccan Mediterranean coasts (~4050 Km; Fig. 1). This region is the southern range edge for coastal *S. polyschides*. Beyond it, this kelp only occurs on the offshore banks of Gorringe, Alboran and Messina, particular deep habitats (to about 80 m depth) not affected by climate variability in the same ways as shallow coastal waters, thus not useful to address our questions.

In the Iberia-Morocco shores, *S. polyschides* recruits in spring and the adult sporophytes reach their highest abundance throughout summer. These adults release spores in late summer and die in the autumn. Settled spores produce gametophytes that after fertilization wait for spring conditions to resume recruitment (Pereira et al., 2011).

DATA ON SPECIES OCCURRENCES AND CLIMATE

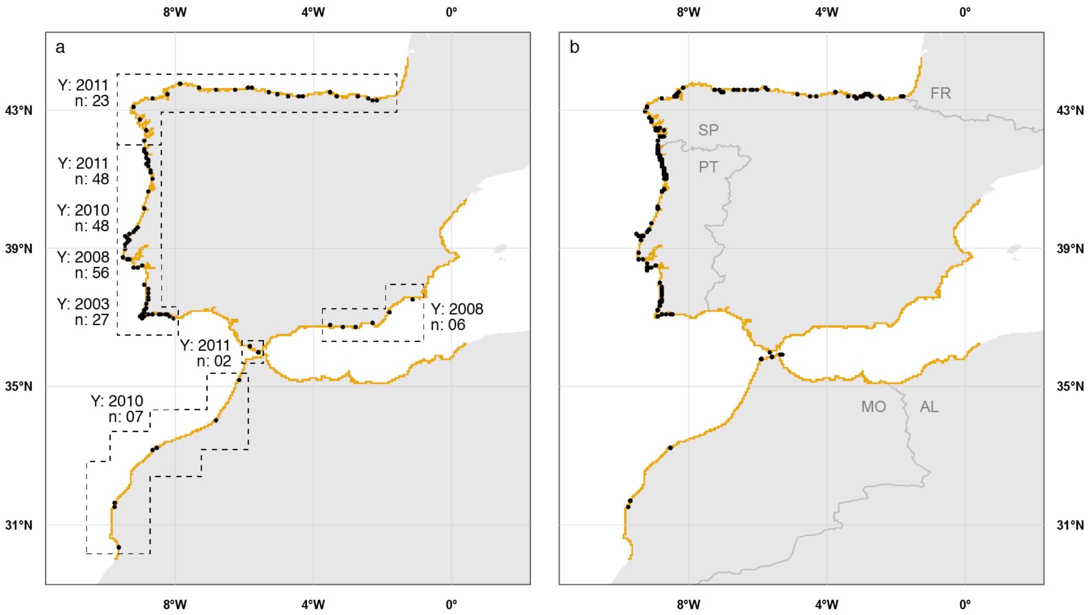

Fig 1. Study region (~4050 km; FR: France, SP: Spain, PT: Portugal, MO: Morocco, Al: Algeria). Orange contour along the coast represent the modeling cells on a 5 km resolution. (a) Sampling effort for *S. polyschides* (number of sites per region and year; black dots represent sampling sites). (b) Data compiled from references (black dots represent sites where information for *S. polyschides* was available)

Presence / absence records of *S. polyschides* were gathered throughout Iberia-Morocco by means of SCUBA diving and snorkelling in the summers of 2003, 2008, 2010 and 2011 (Fig. 1a). These surveys were performed on rocky reef sites by swimming randomly for periods up to 60 minutes. To avoid false absences, if no kelp was found within a site, at least one other survey was performed within 1km from the initial one. Historical georeferenced records (since 1986) were also compiled from literature (Fig. 1b; references can be obtain upon request). Newly collected and historical data were merged and gridded into 5 km cells to match the resolution of the environmental predictor variables (see below).

Seasonal environmental predictors were generated per year from daily remote sensing data (Appendix S1 in Supporting Information provides all details regarding satellite data acquisition, temporal range, original resolution and derived metrics). These predictors were selected to reflect the limiting factors acting on kelp physiology (Sea Surface Temperature – SST), disturbances that may impact their habitat and structure (Significant Wave Height – SWH) and essential resources (In-water diffuse attenuation coefficient at 490 nm m^{-1} – Kd; Chlorophyll a – Chla, as a proxy for nutrients). Seasons were defined as “previous summer”, "winter" and "spring" because each record of kelp (performed on macroscopic adults) was the result of (1) the reproductive success of a previous generation of adults, (2) the development, fertility and survival of gametophytes in the following winter and (3) the recruitment of juveniles throughout spring. All predictors were gridded using bilinear interpolation to 5 km resolution cells (Fig. 1a,b). Since satellite data are available for different time intervals, the statistical models were conduced for 1986-2012 using SST only, for 1994-2012 using SST and SWH and for 1998-2012 using SST, SWH, Kd and Chla (S1).

STATISTICAL MODELING

Given our sampling design (replicated blocks across space and time) we adopted the Generalized Linear Mixed Models (GLMM; see Bolker et al., 2009) framework. This is a suitable method for modeling complex spatial and temporal correlation structures since it accounts for dependencies within hierarchical groups by introducing random effects (Dormann et al., 2007; Bolker et al., 2009; Fieberg et al., 2010). The presence / absence records of kelp were the model's response, while the environmental predictors considering the year and location of each record were the explanatory variables. Models were run with a logit-link function and binomial error distribution, and the "year of record" and "cell of record" were included as random effect terms (e.g., Zuur, 2009; Ludwig et al., 2012). By doing so, we were able to better generalize our conclusions / predictions to new sites and periods of time (i.e., to improve model's transferability; Wenger & Olden, 2012).

All predictors were normalized to have a mean of zero and standard deviation of one in order to put the estimated coefficients on the same scale and to improve the convergence of models (Zuur, 2009). Moreover, since collinearity between predictors can result in estimates that are difficult to interpret (Kivinen et al., 2008), Spearman rank correlations were computed for all pairs of predictors and the Variance Inflation Factor (VIF) was determined (with values greater than ten suggesting collinearity).

ENVIRONMENT SHAPING THE DISTRIBUTION OF *S. POLYSCHIDES*

To find which predictors best explain the distribution of *S. polyschides* (i.e., hypothesis testing; Dormann et al., 2008), GLMMs were fitted for the three periods of time with all possible combinations of non-correlated predictors (Spearman $R \leq | 0.5 |$), an approach known for reduced bias (e.g., Whittingham et al., 2006). From all possible outcomes, the best-fit selection followed the relative Akaike Information Criterion (AIC), and the goodness-of-fit was inferred by $R2_{GLMM}$ algorithm (Nakagawa & Schielzeth, 2013). Homogeneity of variances and normality of the errors were assessed by graphical inspection of the residuals versus fitted values and by the fitted model against the quantiles of the model residuals (Q-Q plot). The degree of auto-correlation in the models' residuals was measured by computing a smooth correlogram measuring Moran's I at discrete distance classes (Zuur, 2009).

S. POLYSCHIDES DISTRIBUTION THROUGH TIME

The distribution of *S. polyschides* throughout the Iberia-Morocco was predicted by developing a transferable model, trained with the presence / absence records and the environmental predictors, and projected into the climate conditions of different years. To do so, our dataset was divided in two. The first set, for model training, was generated by randomly selecting 70% of all presence / absence records throughout space and time. The second, for testing the model results, was generated with the remaining 30%, hence producing an independent dataset for cross-validation.

Multiple GLMMs were fitted iteratively with the training data and all possible combinations of non-correlated predictors. For each fitted model, a predictive map was developed and reclassified into a binary presence-absence surface based on a threshold maximizing the sum of sensitivity and specificity (e.g., Manel et al., 2001; Thuiller et al., 2009). The combination of predictors retrieving the most accurate prediction of distribution was identified as the one with the highest Area Under the receiver-operated characteristic Curve (AUC) when cross-validated against the testing data. AUC measures the capacity of the model to discriminate between presences and absences. Values range from 0 to 1, with 0.5 indicating a null or poor predictive model and values above 0.9 generally classified as an outstanding prediction (Thuiller et al., 2009).

The iterations of model fitting were repeated 100 times, and at each time, the randomization of training and testing data was performed. This resulted in 100 sets of predictors with very high discriminatory potential (AUCs of iterations ranged from 0.961 to 0.991). The final projections on distribution were performed by merging with a median function (i.e., ensemble modeling; Araújo & Whittaker, 2005; Araújo & New, 2007; Marmion et al., 2009; Buisson et al., 2010) the predicted responses of 100 models generated with the most discriminatory sets of predictors and the climate data on a yearly basis. To hindcast the distribution, the ensembles were fed with remote sensing data for the longest period 1986-2012 with SST only. This was possible because the ensembles performed with data from 1986-2012 (SST), 1994-2012 (SST and SWH) and 1999-2012 (SST, SWH, Kd and Chla), for the matching period 1999-2012, retrieved similar projections. This was found by testing differences in the mean AUC values with a Mann–Whitney nonparametric test (e.g., Tarkhnishvili et al., 2012) for the matching period of the ensembles (AUC 1996-2012: 0.972 ± 0.05; AUC 1994-2012: 0.976 ± 0.05; AUC 1999-2012: 0.974 ± 0.06; Mann–Whitney p: < 0.001). To forecast the distribution, SST data were used from two Atmospheric General Circulation Models (AGCM): the Community Climate System Model (CCSM4) and the Model for Interdisciplinary Research on Climate (MIROC5) (e.g., Rebelo et al., 2012). This was achieved by compiling daily data from 2013 to 2100, under the Representative Concentration Pathway (RCP) 2.6 scenario, where greenhouse gas emissions are reduced substantially over time, and the RCP8.5 scenario, characterized by increasing gas emissions over time (Moss et al., 2010; Rogelj et al., 2012). Since ensemble modeling is also useful for uncertain datasets (Araújo & New, 2007), when using the AGCMs, in addition to multiple subset of predictors, the projections were made by merging the resulting surfaces of both CCSM4 and MIROC5.

Persistence maps were generated for the periods 1986-2012, 2013-2050 and 2051-2100 by assigning to each cell the frequency of annual occurrence during each time period. These occurrences were inferred using 3 different reconstructions: (1) no dispersal, with cells experiencing permanent extinction whenever the habitat becomes unsuitable (2) unlimited dispersal, with presences as a direct function of habitat suitability and (3) by implementing dispersal distance per year and arrested development period (latency) of microscopic stages. Since there is no robust information about these metrics, we simulated their effect on the marginal AUC. Multiple matrices of distribution were generated (coastal cells x years) with increasing dispersal distances (D; 1 to 100km; step 1km) and latency periods (L; 1 to 5 years; step 1 year), starting from a state of no dispersal and no latency. Because we had no reference from the past distribution, the simulations started with the earliest predicted distribution (year 1986). From this state, for every i cell predicted with suitable habitat at a given t year, a presence in i at t was introduced if one of the following conditions were met: (1) there was a previous presence in i cell at any t - L year; (2) there was a rescue effect from cells with presence records at t - 1 year, distancing equal or less D km from i. The simulations retrieved 10,000 matrices, and the best combination of D and L was found as the one retrieving the highest marginal value over the AUC.

The extent of coastline was determined for those regions where kelp occurred at any time, and independently for those cells where recent range shifts were detected. Inter-annual variability in the extent of kelp was assessed by Trend Break Analysis (TBA; Verbesselt et al., 2012; Jong et al., 2012). All analysis described were conducted in R (R Development Core Team, 2012) using package lme4, Bfast, raster, rgdal, geoR, SDMTools.

RESULTS

Along the Iberia-Morocco region, presences and absences of *S. polyschides* were recorded on 217 coastal surveys (94 unique sites during 4 years). This dataset was enhanced with 535 historical records (117 unique sites since 1986) compiled from the available literature (Fig. 1a,b).

EXPLANATORY PREDICTORS AND MODELING ACCURACY

Table I. Summary of the best-fit Generalized Linear Mixed Models (GLMMs) developed independently for 3 periods (1986-2012, 1994-2012 and 1999-2012) to test which predictors best explained the distribution of S. polyschides. Selection made by the Akaike Information Criterion (AIC) and goodness-of-fit inferred using R2GLMM. Estimates, standard errors and Pr(>|z|) reported for each model.

	1986-2012				1994-2012				1999-2012			
AIC	320.4				306.7				289.3			
$R2_{GLMM}$	0.688				0.702				0.712			
Predictor	Estimate	Error	Pr(>|z|)	VIF	Estimate	Error	Pr(>|z|)	VIF	Estimate	Error	Pr(>|z|)	VIF
SST6	-19.349	3.551	< 0.001	1.020	-10.373	1.530	< 0.001	1.024	-9.821	1.454	< 0.001	1.052
SST18	3.708	1.249	0.002	1.020	1.654	0.621	0.007	1.054	1.913	0. 634	0.002	1.022
SWH17	-	-	-		-0.1733	0.073	0.018	1.036	-	-	-	
Kd17	-	-	-		-	-	-		-0.257	0.118	0.030	1.034

The best-fitted models explained most of the variation in *S. polyschides* presence / absence data and showed no evidence of collinearity between predictors (Model's $R2_{GLMM}$: 0.688 to 0.712; VIFs < 10; Table I). Furthermore, the best-fitted models complied with homogeneity of variances and normality of the residuals and their degree of auto-correlation was minimum and not significant, indicating a random spatial pattern of residuals.

The most important environmental predictor for kelp distribution was the maximum winter SST (SST6; Table I) followed by the number of consecutive spring days with cold SST

(SST18; Table I). These had opposite effects on the model's responses: the lower the SST6 and the higher the SST18, the greater the probability of kelp occurrence. The number of consecutive spring days with high waves (SWH17) and the number of consecutive spring days with attenuated light (Kd17) were also identified as explanatory variables on the models developed for 1994-2012 and 1999-2012, respectively (Table I). Both SWH17 and Kd17 explained relatively little variation in the model's compared to SST6 and SST18.

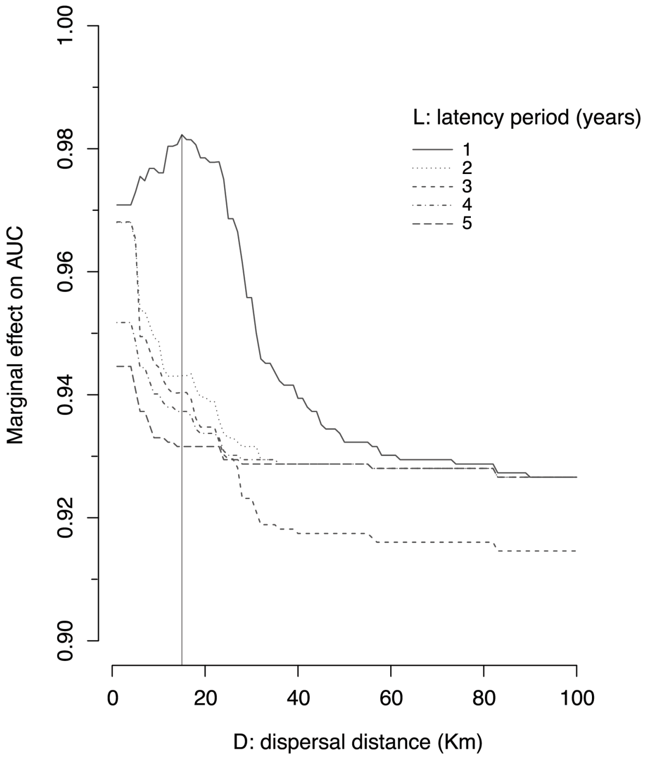

Fig 2. Simulation of the effect of maximum dispersal distance (D, step 1 km) and latency period (L, step 1 year) on the marginal value of AUC, starting from a state of no dispersal and no latency capacity.

Simulations showed that a maximum dispersal distance of 17 km per year and a latency period of 1 year produced the highest marginal value of AUC (Fig. 2). Using these measures, the accuracy of our predictions increased ~0.012 AUC units, from a reference point of no dispersal with AUC: 0.970 (Appendix S2 in Supporting Information). The reconstruction made with unlimited dispersal caused AUC to decrease from 0.982 to 0.918 (S2); thus, further analysis and discussion will focus on the most accurate reconstruction of distribution.

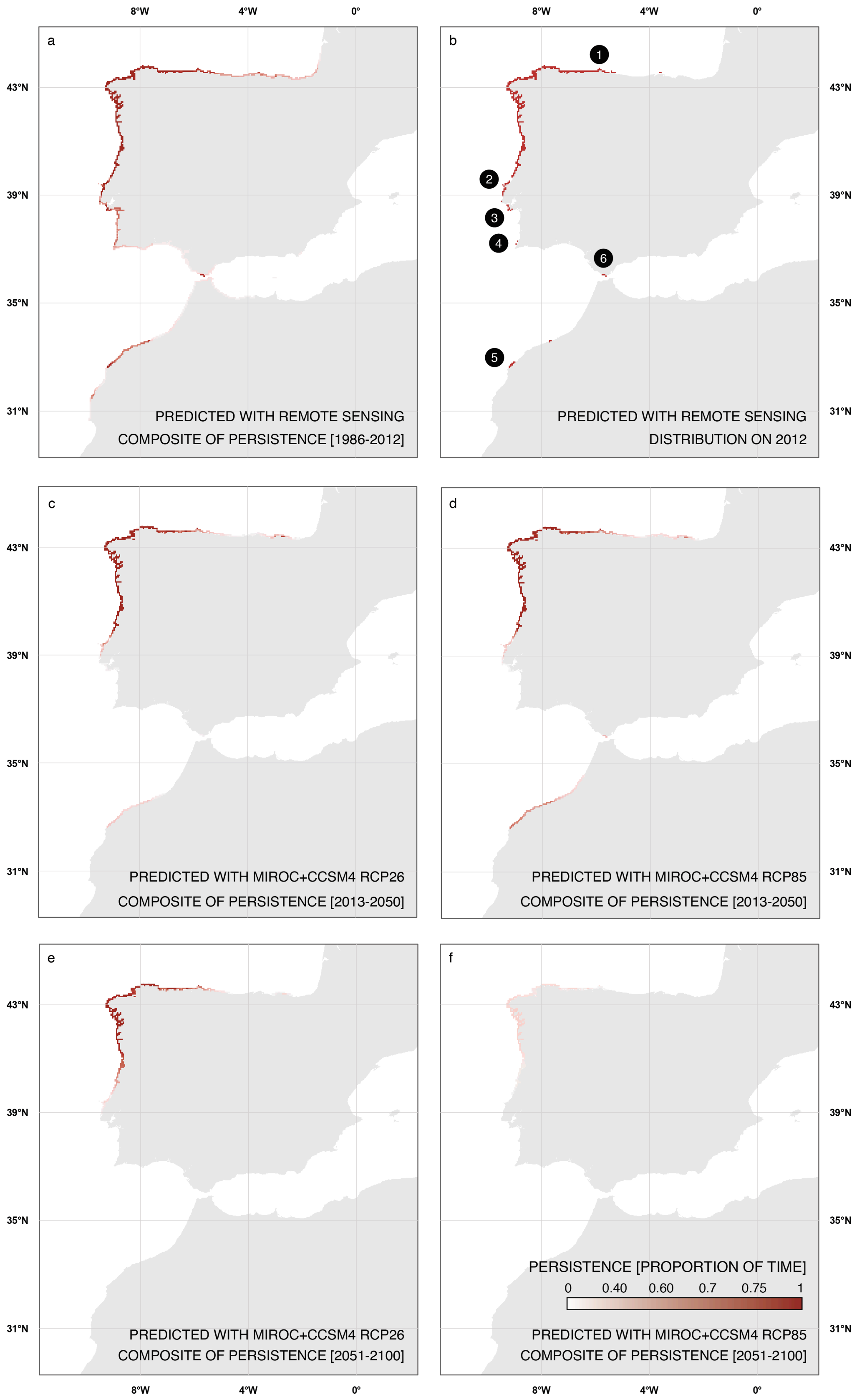

Fig 3. (a) Composite of modelled persistence for the period 1986-2012. (b) Modelled distribution for the year 2012 (Numbers represent Regions Of Interest: ROI 1: Cabo de Peñas; ROI 2: Peniche; ROI 3: Arrábida; ROI 4: Sagres; ROI 5: western Morocco; ROI 6: Gibraltar). Composite of modelled persistence for (c,d) the period 2013-2050 and (e,f) 2051-2100 using AGCMs (MIROC5 and CCSM4) with the scenarios RCP2.6 and RCP8.5.

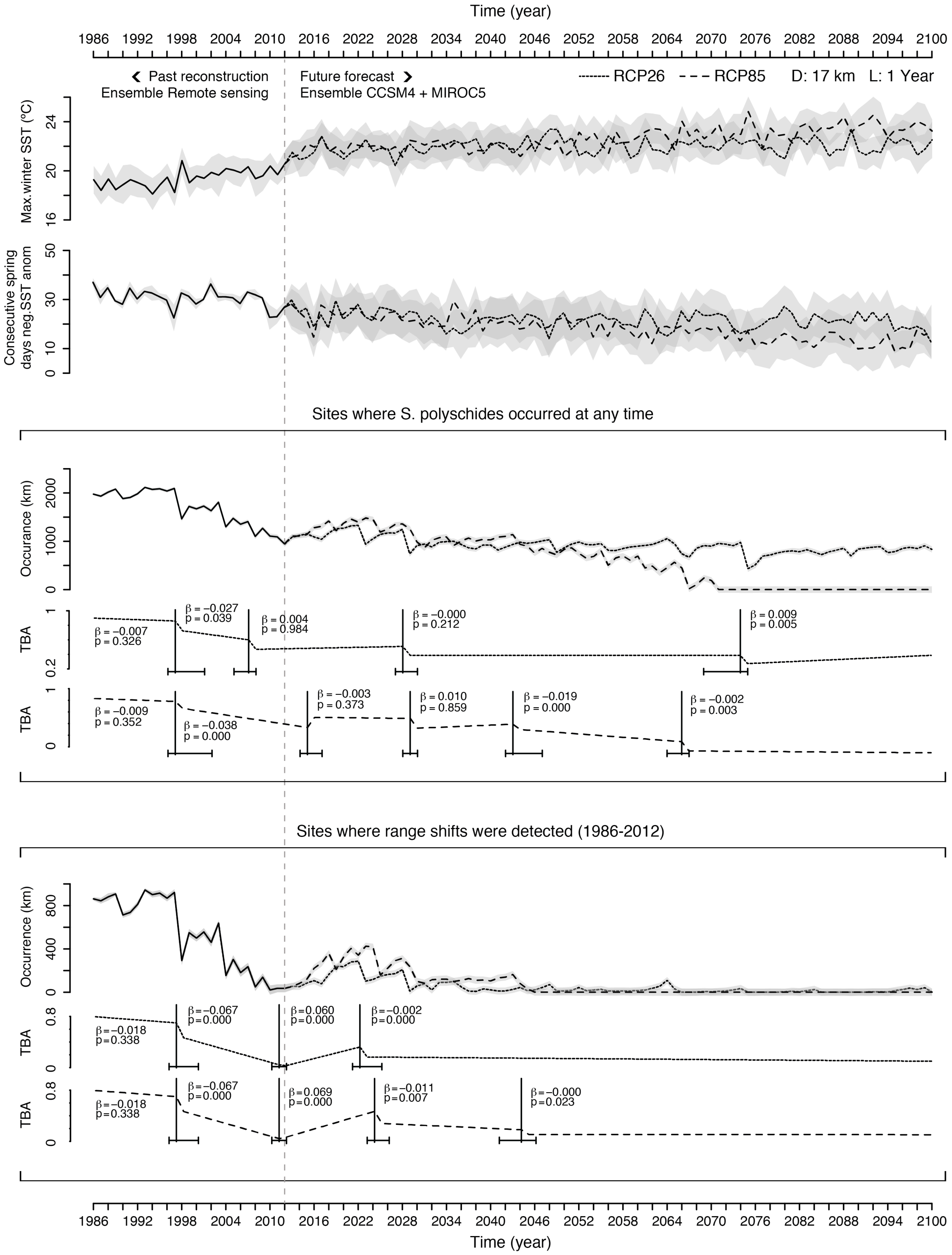

Fig 4. Maximum winter Sea Surface Temperature (SST, ºC) and number of consecutive days with negative anomaly of SST (reference period 1986-2012). Ensemble distribution models of S. polyschides with specific measures of dispersal (D) and latency (L), generated with remote sensing data (period 1986-2012) and AGCMs (MIROC5 and CCSM4) under two scenarios of greenhouse gas emissions (RCP26 and RCP8.5) for those sites where *S. polyschides* occurred at any time and where range shifts were detected, as mean probability of occurrence and kms of coastline with kelp. Shaded polygons represent the standard error of the ensembles. Trend break analysis (TBA) by emission scenario. Vertical bars display the time of observed changes (break points with slope and p-value). Confidence intervals are also exhibited for each break point.

S. POLYSCHIDES DISTRIBUTION AT THE RANGE-EDGE

The hindcast models integrating dispersal and latency (D = 17 km; L = 1 year) retrieved an excellent description of distribution (AUC: 0.982), showing that in the last 26 years, *S. polyschides* occurred from the Bay of Biscay to southern Morocco, in southern Portugal and in the Gibraltar region (Fig. 3a).

This distribution was relatively stable from 1986 to 1997 (mean extent: 2015.81 ± 78.44 km; TBA p: 0.326; Fig. 4), however a significant decline in the extent was predicted onwards until 2007 with RCP2.6 (TBA p: 0.039) and until 2015 with RCP8.5 (TBA p: < 0.001). This led the extent to drop to 944.11 ± 51.96 km by 2012, with shifts in range primarily in the north of Spain, the southwest and southern coasts of Portugal, in Gibraltar and along western Morocco (Fig. 3a). The current distribution (year 2012) restricted the populations to the northwest of the Iberia Peninsula, from Cabo de Peñas to Peniche, Arrábida and to some isolated sites near Sagres, western Morocco and Gibraltar (Fig. 3b).

Our models predicted a further reduction in the range in the future. With RCP2.6, there were two significant breaks in the trend analysis, one in 2029 (to 742.62 ± 40.12 km) and another in 2075 (to 434.64 ± 51.32 km), followed by an increasing period (TBA p: 0.005 Fig. 3c, 3e, 4) to 851.08 km by 2100. With the RCP8.5, breaks were detected in 2044 (to 1164.12 km ± 64.11 km) and in 2066 (to 73.47 km ± 62.78 km). The predicted extent continued to decline (TBA p: 0.003) reaching a state of extinction by 2071 (Fig. 3d, 3f, 4). Particularly for those regions where range shifts occurred in the past (1986-2012), the extent of coastline increased from 21.14 ± 4.35 km to 285.85 ± 29.87 by 2022 with RCP2.6 and to 416.32 ± 30.27 by 2024 with RCP8.5. This positive variation was the result of a higher probability of occurrence in the north of Spain until 2024 and in the Moroccan region until 2029 (Appendix S3 in Supporting Information). However, both scenarios forecasted a major decrease onwards (TBAs p: < 0.001). The extent of these regions using RCP2.6 was predicted to be 32.22 ± 8.15 km in 2100 while RCP8.5 predicted extinction in these regions by 2061 (Fig. 3f, 4).

DISCUSSION

This study inferred the major environmental forces shaping the distribution of an important foundation species and predicted significant range shifts on the recent past and future scenarios of climate change. It also demonstrated the feasibility of using a multiple life cycle approach for the reconstruction of species distribution, along with the inference and integration of dispersal and latency periods. Furthermore, while most SDMs are performed using presence-only methods due to opportunistic data collections (Elith & Leathwick, 2009), our models benefited from the availability of field absence records. An enhanced dataset, coupled with the use of ensemble modeling and biologically meaningful predictors such as cumulative heat stress (as used by Carilli et al., 2012) proved to be a robust approach (as shown by Araújo & New, 2007), with the inferred past distribution in very good agreement with the observed records.

FACTORS SHAPING THE DISTRIBUTION OF *S. POLYSCHIDES*

The explanatory models showed that the demography of this kelp is mainly determined at the gametophyte and young sporophyte levels (during winter and spring), a result already demonstrated by other studies (e.g., Norton, 1978; van den Hoeck, 1982). The maximum winter SST had the largest effect size on the models' response. During this season, the fertilization of the female gametophyte is perhaps the most vulnerable phase, with reduced fertility if exposed to temperatures higher than ~18º C (reviewed by Fernández, 2011). The survival of the gametophytes also seems affected (as shown for genus *Laminaria*; Lüning, 1980), yet with a higher critical threshold of ~20º C. Such temperatures are not uncommon in winter throughout Iberia-Morocco (mean winter SST: 15.75 ± 1.41º C), with some sites experiencing up to 24.85º C. However, since high temperature waters are typically nutrient depleted (Kamykowski & Zentara, 1986), our models' negative response to winter temperatures could be related to nutrient deprivation (as shown for the southern Californian populations of *Macrocystis pyrifera*; Reed et al., 1996; Dayton et al., 1999).

The consecutive number of spring days with cold SST was a good predictor of the distribution of *S. polyschides*. Given the cumulative nature of this predictor, its positive effect on the model's response may be related to the availability of nutrients resulting from seasonal upwelling (Relvas et al., 2007). Throughout the southern ranges of kelps, where nutrient-depleted waters prevail (Matson & Edwards 2007), the upwelling of deep, cold and nutrient rich-waters into shallow coastal regions (Relvas et al., 2007) seems to be essential for the recruitment and growth of juvenile kelps, a phase with long lasting effects on the cohorts' structure (Tegner et al., 1997, Dayton et al., 1999). Such events are common in the Iberia-Morocco during spring and summer (Botas et al., 1990; Sarhan et al., 2000; Pastor et al., 2008; Alvarez et al., 2009; Cravo et al., 2010; Miranda et al., 2012), and they can be easily tracked by the number of days when favorable conditions persist (Alvarez et al., 2005; Alvarez-Salgado et al., 2006), a state that leaves a clear sign on the negative anomaly of SST (Relvas & Barton, 2005; Oliveira et al., 2009). Given the lack of significance of Chlorophyll a in our models, one could question the relationship between cold spring SST and nutrient availability for recruitment. Chlorophyll a is commonly used as a proxy for nutrients but its relation with the upwelling is not immediate due to complex phytoplankton dynamics (Pelegrí et al., 2005; Cravo et al., 2010). Our models may respond better to the variability of nutrient triggering during the recruitment phase, than to its effect on remotely sensed Chlorophyll a, which may only be detected months after the initial enrichment of the surface waters (Garcia-Muñoz et al., 2005). This highlights the use of environmental predictors based on high-resolution data, which allows capturing coastal processes on a daily basis (as emphasized by Lima & Wethey, 2012), such as the triggering of seasonal upwelling events enriching coastal waters.

DISPERSAL AND ARRESTED DEVELOPMENT OF *S. POLYSCHIDES*

Our simulations incorporating dispersal distances improved the accuracy of the predicted distribution and supports the belief that *S. polyschides* has a limited degree of dispersal. Our estimate of a maximum dispersal ability of 17 Km per year is in line with studies of *Macrocystis pyrifera* and *Laminaria digitata* that showed dispersal in scales of a couple to tens of kilometers (Billot et al., 2003; Gaylord et al., 2006; Reed et al., 2006; Alberto et al., 2010). In addition, this distance seems reasonable considering that most spores of the kelps *Macrocystis pyrifera* and *Pterygophora californica* stopped swimming after ~24 h (Reed et al., 1992) and that the coastal currents of Iberia-Morocco are frequently up to ~15 cm s-1 (Martins, 2002), suggesting ~13 km of potential dispersal distance. However, large-scale dispersal is expected by occasional floating rafts of kelp. These may be particular important for population restoration of denuded habitats (Hernández-Carmona et al., 2006) because they remain functionally reproductive for long periods (Macaya et al., 2005). Although our simulation only considered local to regional dispersal distances from a parental to contiguous cells, one can't discard such large-scale events since they must have occurred when distant available habitats such as offshore seamounts were colonized by *S. polyschides* (Assis et al., 2013). Yet, these events are likely uncommon since the spores released by rafts have a very low probability of reaching suitable rocky habitat in adequate densities to allow an effective colonization (Reed et al., 2006), as fertilization is dependent upon the proximity of male and female gametophytes (Reed, 1990).

The inferred latency period of the microscopic stages was no longer than the natural cycle between two consecutive generations of sporophytes. Most of what is known about the longevity of these stages is derived from laboratory experiments, with some studies demonstrating that they may last for several years (e.g., Neushul, 1983). Field evidence for the Iberian Peninsula corroborate our results, identifying delayed stages only on the order of months and not years (Barradas et al., 2011). If these cryptic stages are able to persist longer, then this would allow the co-existence of multiple cohorts of this annual species.

THE CONTRACTION OF THE SOUTHERN RANGE-EDGE OF *S. POLYSCHIDES*

Our models suggest a decrease of 53.95 ± 1.51 % in the extent of kelp forests in Iberia-Morocco from 1986 to 2012. In this region, the recent warming of superficial waters is a well-documented trend (Fig. 4; Lima & Wethey, 2012), however the predicted breaks were coincident with the heat waves of 1997-1998 and 2004-2005. In fact, climate change is paced by extreme warming episodes (Parker et al., 1992) and range shifts generally occur abruptly, as physiological thresholds are exceeded (Harley & Paine, 2009; Stuart-Smith et al., 2010). Particularly the former and most severe event (1997-1998), also documented by other studies (Lemos & Pires, 2004; Peliz et al., 2005), was further coupled with unfavorable upwelling conditions and strong river runoffs (Dong et al., 2000), factors that seem to reduce the probability of kelp occurrence.

Range shifts of *S. polyschides* in Iberia-Morocco are not unique. Other species of macroalgae have shifted their range along this coast (Lima et al., 2007; Nicastro et al., 2013). Our predicted shifts confined the current distribution to regions that benefit from intense upwelling. These are the northwest of the Iberian Peninsula (Miranda et al., 2012) and some isolated sites in the southwest of Portugal (Relvas, 2007), Gibraltar (Sarhan et al., 2000) and western Morocco (Pastor et al., 2008). It is suggested that the upwelling regions of the world have recently changed, with upwelling becoming more persistent, longer and stronger (McGregor et al., 2007). This may well be the case for western Morocco and southwest

Portugal (see McGregor et al., 2007 and Relvas et al., 2009), where kelps prevailed despite local extinctions and reduced abundances (Assis et al., 2013; Appendix S4 in Supporting Information). Such reduction in abundance is particularly evident in the southwest Portugal, where genetic bottlenecks were recently detected and a shift in genetic baselines was proposed (Assis et al., 2013). On the other hand, a decrease in the seasonality and intensity of the northwest Iberian upwelling system has been proposed (Alvarez et al., 2010). This decrease didn’t cause extinctions in our study, nor in the study by Fernández (2011), but throughout the extant populations of this region, individuals live fewer months and a smaller proportion became reproductive when compared to the populations studied there before the 2000s (Fernández, 2011).

FUTURE TRENDS IN THE DISTRIBUTION OF *S. POLYSCHIDES*

The rapid predicted range shifts for *S. polyschides*, corroborated by our field evidence and other studies, opens the possibility that this species has niche conservatism, which is not uncommon for marine species (e.g., Peterson, 2011). This is particularly interesting for conservation because species with niche conservatism that experienced range shifts during the past are most likely to do so in future warming scenarios (Araújo & Whittaker, 2005). In fact, many species are predicted to shift ranges throughout the Atlantic and Mediterranean coasts during the 21st century (Lima et al., 2007; Lasram et al., 2010). Our future projections are in agreement with these expectations, however the use of different greenhouse gas emissions led to different predicted consequences (Fig. 4). In the most optimistic scenario (RCP2.6), *S. polyschides* is predicted to decrease in extent until 2075 before recovering to 57.83 ± 1.52 % of the past-predicted extent of the Iberia-Morocco, with extant populations confined to the northwest of the Iberia Peninsula. The predictions made with increasing emissions over time (RCP8.5) are more severe as the extent is predicted to decline constantly until 2071, when kelp forests are to be extinct from Iberia-Morocco.

Some degree of recovery was predicted in the first years of future predictions until 2022-2024, particularly with RCP8.5 along western Morocco and northeast of Spain (S3). This is explained by the AGCMs data variability for the period 2013-2050. Despite the general warming trend of such simulations, they predicted a minor anomaly in the maximum winter SST and an actual increase in the number of spring days with cold SST for both northern Iberia and western Morocco (Appendix S5 and S6 in Supporting Information). It is possible that these simulations for future climate take into account the future trend of upwelling conditions, that are predicted to be more intense as global warming increases (Bakun, 1990; McGregor et al., 2007), halting the negative effects of climate change at local scales (Lima & Queiroz, 2006; Miranda et al., 2012). Although, another hypothesis that can't be discarded, has to do with a possible underestimation of the warming by the AGCMs, as it is documented for the drying and cooling of the Iberia-Morocco on such simulations performed for 20.000 years before present (Ramstein et al., 2007). If such estimates are wrong, then the decrease in extent of kelp could happen earlier than predicted because these populations of northern Iberia and western Morocco wouldn't recover in the near future as predicted.

The loss of most range edge kelp forests seems plausible under future climate scenarios, particularly for the long term, and the negative consequences that will arise should be considered. Both scenarios used in this study suggest that this will occur for populations in the northeast and southwest portions of the Iberian Peninsula, in Gibraltar and throughout western Morocco. The demise of these populations as foundation species may cause changes in the whole ecosystem, particularly in the overall biomass and diversity of the numerous associated species (Ellison et al., 2005). Furthermore, even if dispersal occurs, it may not be a suitable escape mechanism for unique populations to persist, since along these coastlines there are important barriers that may halt migration. This may be the case of the continental edges of the Iberian Peninsula and Morocco, where the limited dispersal of *S. polyschides* will result in extinctions, as species may be unable to migrate across the large Atlantic water mass that separates them. Such extinctions would erode entire unique genetic lineages (see Assis et al., 2013) thereby reducing the overall genetic diversity of this species and compromising its evolutionary and adaptive potential to face further disturbances (Pujol & Pannell, 2008).

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REFERENCES

Alberto, F., Raimondi, P.P.T., Reed, D.D.C., Coelho, N.C., Leblois, R., Whitmer, A. & Serrão, E.A. (2010) Habitat continuity and geographic distance predict population genetic differentiation in giant kelp. Ecology, 91, 49–56.

Alvarez, I., DeCastro, M., Gomez-Gesteira, M. & Prego, R. (2005) Inter- and intra-annual analysis of the salinity and temperature evolution in the Galician Rías Baixas–ocean boundary (northwest Spain). Journal of Geophysical Research: Oceans, 110, 1978–2012.

Alvarez, I., Gomez-Gesteira, M., deCastro, M., Gomez-Gesteira, J.L. & Dias, J.M. (2010) Summer upwelling frequency along the western Cantabrian coast from 1967 to 2007. Journal of Marine Systems, 79, 218–226.

Alvarez, I., Ospina-Alvarez, N., Pazos, Y., deCastro, M., Bernardez, P., Campos, M.J., Gomez-Gesteira, J.L., Alvarez-Ossorio, M.T., Varela, M., Gomez-Gesteira, M. & Prego, R. (2009) A winter upwelling event in the Northern Galician Rias: Frequency and oceanographic implications. Estuarine, Coastal and Shelf Science, 82, 573–582.

Alvarez-Salgado, A., Nieto-Cid, M., Gago, J., Brea, S., Castro, C.G., Doval, M.D. & Perez, F.F. (2006) Stoichiometry of the degradation of dissolved and particulate biogenic organic matter in the NW Iberian upwelling. Journal of Geophysical ResearchOceans, 111.

Araújo, M. & Whittaker, R. (2005) Reducing uncertainty in projections of extinction risk from climate change. Global Ecology and Biogeography, 14, 529–538.

Araújo, M.B. & Luoto, M. (2007) The importance of biotic interactions for modeling species distributions under climate change. Global Ecology and Biogeography, 16, 743–753.

Araújo, M.B. & New, M. (2007) Ensemble forecasting of species distributions. Trends in ecology & evolution, 22, 42–7.

Arribas, P., Abellán, P., Velasco, J., Bilton, D.T., Millán, A. & Sánchez-Fernández, D. (2012) Evaluating drivers of vulnerability to climate change: a guide for insect conservation strategies. Global Change Biology, 18, 2135–2146.

Assis, J., Castilho Coelho, N., Alberto, F., Valero, M., Raimondi, P., Reed, D. & Alvares Serrão, E. (2013) High and Distinct Range-Edge Genetic Diversity despite Local Bottlenecks. PLoS ONE, 8, e68646.

Assis, J., Tavares, D., Tavares, J., Cunha, A., Alberto, F., Serrão, E.A. & Ea (2009) Findkelp, a GIS-based community participation project to assess Portuguese kelp conservation status. Journal of Coastal Research, 3, 1469–1473.

Bakun, A. (1990) Global climate change and intensification of coastal ocean upwelling. Science, 247, 198–201.

Barradas, A. & Alberto, F. (2011) Fast sporophyte replacement after removal suggests banks of latent microscopic stages of Laminaria ochroleuca (Phaeophyceae) in tide pools in northern Portugal. CBM-Cahiers de Biologie, 52, 435–439.

Belkin, I.M. (2009) Rapid warming of Large Marine Ecosystems. Progress in Oceanography, 81, 207–213.

Billot, C., Engel, C., Rousvoal, S., Kloareg, B. & Valero, M. (2003) Current patterns, habitat discontinuities and population genetic structure: the case of the kelp Laminaria digitata in the English Channel. Marine Ecology Progress Series, 253, 111–121.

Birkett, D., Maggs, C., Dring, M.J. & Boaden, P.J.S. (1998) Infralittoral reef biotopes with kelp species. Infralittoral reef biotopes with kelp species (ed. by S.A. of M.S. (UK M.Sac. Project)), p. 174.

Boaventura, D., Re, P., Cancela Da Fonseca, L., Hawkins, S.J., Ré, P. & Fonseca, L.C. Da (2002) Intertidal Rocky Shore Communities of the Continental Portuguese Coast: Analysis of Distribution. Marine Ecology, 23, 69–90.

Bolker, B.M., Brooks, M.E., Clark, C.J., Geange, S.W., Poulsen, J.R., Stevens, M.H.H. & White, J.-S.S. (2009) Generalized linear mixed models: a practical guide for ecology and evolution. Trends in ecology & evolution, 24, 127–35.

Botas, J.A., Fernandez, E., Bode, A. & Anadon, R. (1990) A persistent upwelling off the Central Cantabrian Coast (Bay of Biscay). Estuarine, Coastal and Shelf Science, 30, 185–199.

Buisson, L., Thuiller, W., Casajus, N., Lek, S. & Grenouillet, G. (2010) Uncertainty in ensemble forecasting of species distribution. Global Change Biology, 16, 1145–1157.

Carilli, J., Donner, S.D. & Hartmann, A.C. (2012) Historical temperature variability affects coral response to heat stress. PloS one, 7, e34418.

Carney, L., Bohonak, A., Edwards, M. & Alberto, F. (2013) Genetic and experimental evidence for a mixed age and mixed origin bank of microscopic stages in a southern California kelp forest. . 94 (9): . Ecology, 94, 1955–1965.

Carney, L. & Edwards, M. (2006) Cryptic processes in the sea: a review of delayed development in the microscopic life stages of marine macroalgae. Algae, 21, 161–168.

Cavanaugh, K., Siegel, D., Reed, D. & Dennison, P. (2011) Environmental controls of giant-kelp biomass in the Santa Barbara Channel, California. Marine Ecology Progress Series, 429, 1–17.

Cavanaugh, K.C., Kendall, B.E., Siegel, D. a, Reed, D.C., Alberto, F. & Assis, J. (2013) Synchrony in dynamics of giant kelp forests is driven by both local recruitment and regional environmental controls. Ecology, 94, 499–509.

Cravo, A., Relvas, P., Cardeira, S., Rita, F., Madureira, M. & Sánchez, R. (2010) An upwelling filament off southwest Iberia: Effect on the chlorophyll a and nutrient export. Continental Shelf Research, 30, 1601–1613.

Dayton, P.K., Tegner, M.J., Edwards, P.B. & Riser, K.L. (1999) Temporal and spatial scales of kelp demography: The role of oceanographic climate. Ecological Monographs, 69, 219–250.

Diekmann, O.E., Coyer, J.A., Ferreira, J., Olsen, J.L., Stam, W.T., Pearson, G.A. & Serrão, E.A. (2005) Population genetics of Zostera noltii along the west Iberian coast: consequences of small population size, habitat discontinuity and near-shore currents. Marine Ecology Progress Series, 290, 89–96.

Dong, B.W., Sutton, R.T., Jewson, S.P., O'Neill, A. & Slingo, J.T. (2000) Predictable winter climate in the North Atlantic sector during the 1997-1999 ENSO cycle. Geophysical Research Letters, 27, 985–988.

Dormann, C.F., Purschke, O., García Márquez, J.R., Lautenbach, S. & Schröder, B. (2008) Components of uncertainty in species distribution analysis: a case study of the Great Grey Shrike. Ecology, 89, 3371–86.

Dormann, F.C., M. McPherson, J., B. Araújo, M., Bivand, R., Bolliger, J., Carl, G., G. Davies, R., Hirzel, A., Jetz, W., Daniel Kissling, W., Kühn, I., Ohlemüller, R., R. Peres-Neto, P., Reineking, B., Schröder, B., M. Schurr, F. & Wilson, R. (2007) Methods to account for spatial autocorrelation in the analysis of species distributional data: a review. Ecography, 30, 609–628.

Elith, J. & Leathwick, J.R. (2009) Species Distribution Models: Ecological Explanation and Prediction Across Space and Time. Annual Review of Ecology, Evolution, and Systematics, 40, 677–697.

Ellison, A.M., Bank, M.S., Clinton, B.D., Colburn, E.A., Elliott, K., Ford, C.R., Foster, D.R., Kloeppel, B.D., Knoepp, J.D., Lovett, G.M., Mohan, J., Orwig, D.A., Rodenhouse, N.L., Sobczak, W. V, Stinson, K.A., Stone, J.K., Swan, C.M., Thompson, J., Holle, B. Von & Webster, J.R. (2005) Loss of foundation species: consequences for the structure and dynamics of forested ecosystems. Frontiers in Ecology and the Environment, 3, 479–486.

Fernández, C. (2011) The retreat of large brown seaweeds on the north coast of Spain : the case of Saccorhiza polyschides. European Journal of Phycology, 46, 37–41.

Fieberg, J., Matthiopoulos, J., Hebblewhite, M., Boyce, M.S. & Frair, J.L. (2010) Correlation and studies of habitat selection: problem, red herring or opportunity? Philosophical Transactions of the Royal Society of London - Series B: Biological Sciences, 365, 2233–2244.

Fischlin, A., Midgley, G.F., Price, J.T., Leemans, R., Gopal, B., Turley, C., Rounsevell, M.D.A., Dube, O.P., Tarazona, J. & Velichko, A.A. (2007) Ecosystems, their properties, goods and services. Climate Change 2007 Impacts Adaptation and Vulnerability Contribution of Working Group II to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change, pp. 211–272.

García-Muñoz, M., Arístegui, J., Pelegrí, J.L., Antoranz, A., Ojeda, A. & Torres, M. (2005) Exchange of carbon by an upwelling filament off Cape Ghir (NW Africa). Journal of Marine Systems, 54, 83–95.

Gaylord, B., Reed, D.C., Raimondi, P.T. & Washburn, L. (2006) Macroalgal spore dispersal in coastal environments: mechanistic insights revealed by theory and experiment. Ecological Monographs, 76, 481–502.

Graham, M.H. (2004) Effects of Local Deforestation on the Diversity and Structure of Southern California Giant Kelp Forest Food Webs. Ecosystems, 7, 341–357.

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

Guisan, A. & Zimmermann, N.E. (2000) Predictive habitat distribution models in ecology. Ecological Modeling, 135, 147–186.

Halpern, B. & Kappel, C. (2012) Extinction Risk in a Changing Ocean, (ed. by L. Hannah) Island Press/Center for Resource Economics, Washington, DC.

Harley, C.D.G. & Paine, R.T. (2009) Contingencies and compounded rare perturbations dictate sudden distributional shifts during periods of gradual climate change. Proceedings of the National Academy of Sciences of the United States of America, 106, 11172–11176.

Henriques, M., Gonçalves, E.J. & Almada, V.C. (2007) Rapid shifts in a marine fish assemblage follow fluctuations in winter sea conditions. Marine Ecology Progress Series, 340, 259–270.

Hernández-Carmona, G., Hughes, B. & Graham, M.H. (2006) Reproductive Longevity of Drifting Kelp Macrocystis Pyrifera (Phaeophyceae) in Monterey Bay, Usa. Journal of Phycology, 42, 1199–1207.

Hiscock, K., Southward, A., Tittley, I. & Hawkins, S. (2004) Effects of changing temperature on benthic marine life in Britain and Ireland. Aquatic Conservation Marine and Freshwater Ecosystems, 14, 333–362.

Hoegh-Guldberg, O. & Bruno, J.F. (2010) The impact of climate change on the world's marine ecosystems. Science (New York, N.Y.), 328, 1523–8.

Hutchinson, G.E. (1957) Concluding Remarks. Cold Spring Harbour Symposium on Quantitative Biology.

Izquierdo, J., García, T. & Pérez-Ruzafa, I. (1995) Mapas de distribución de algas marinas de la Península Ibérica e Islas Baleares. IX. Saccorhiza polyschides (Lightf) Rau. y Chorda filum (L.) Stackh. (Laminariales, Fucophyceae). Botanica complutensis.

Jong, R., Verbesselt, J., Schaepman, M.E. & Bruin, S. (2012) Trend changes in global greening and browning: contribution of short-term trends to longer-term change. Global Change Biology, 18, 642–655.

Kain, J.M. (1969) The biology of Laminaria hyperborea V. Comparison with early stages of competitors. Journal of the Marine Biological Association of the United Kingdom, 49, 455–473.

Kamykowski, D. & Zentara, S.-J. (1986) Predicting plant nutrient concentrations from temperature and sigma-t in the upper kilometer of the world ocean. Deep Sea Research Part A. Oceanographic Research Papers, 33, 89–105.

Kivinen, S., Luoto, M., Heikkinen, R.K., Saarinen, K. & Ryttäri, T. (2008) Threat spots and environmental determinants of red-listed plant, butterfly and bird species in boreal agricultural environments. Biodiversity & Conservation, 17, 3289–3305.

Ladah, L. & Zertuche-González, J. (2007) Survival of microscopic stages of a perennial kelp (Macrocystis pyrifera) from the center and the southern extreme of its range in the Northern Hemisphere after exposure to simulated El Niño stress. Marine Biology, 152, 677–686.

Lemos, R.T. & Pires, H.O. (2004) The upwelling regime off the West Portuguese Coast, 1941–2000. International Journal of Climatology, 24, 511–524.

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

Lima, F.P., Ribeiro, P.A., Queiroz, N., Hawkins, S.J. & Santos, A.M. (2007) Do distributional shifts of northern and southern species of algae match the warming pattern? Global Change Biology, 13, 2592–2604.

Lima, F.P. & Wethey, D.S. (2012) Three decades of high-resolution coastal sea surface temperatures reveal more than warming. Nature communications, 3, 704.

Lüning, K. (1980) Critical levels of light and temperature regulating the gametogenesis of three Laminaria species (Phaeophyceae). Journal of Phycology, 16, 1–15.

Macaya, E.C., Boltana, S., Hinojosa, I. a., Macchiavello, J.E., Valdivia, N. a., Vasquez, N.R., Buschmann, A.H., Vasquez, J. a., Alonso Vega, J.M. & Thiel, M. (2005) Presence of Sporophylls in Floating Kelp Rafts of Macrocystis Spp. (Phaeophyceae) Along the Chilean Pacific Coast1. Journal of Phycology, 41, 913–922.

Manel, S., Williams, H.C. & Ormerod, S.J. (2001) Evaluating presence – absence models in ecology : the need to account for prevalence. Journal of Applied Ecology, 38, 921–931.

Marmion, M., Parviainen, M., Luoto, M., Heikkinen, R.K. & Thuiller, W. (2009) Evaluation of consensus methods in predictive species distribution modeling. Diversity and Distributions, 15, 59–69.

Martins, C.S. (2002) Surface circulation in the eastern North Atlantic, from drifters and altimetry. Journal of Geophysical Research, 107, 3217.

Matson, P.G. & Edwards, M.S. (2007) Effects of ocean temperature on the southern range limits of two understory kelps, Pterygophora californica and Eisenia arborea, at multiple life-stages. Marine Biology, 151, 1941–1949.

McGregor, H. V, Dima, M., Fischer, H.W. & Mulitza, S. (2007) Rapid 20th-century increase in coastal upwelling off northwest Africa. Science, 315, 637–639.

Millennium Ecosystem Assessment (2005) Ecosystems and Human Well-being: Biodiversity Synthesis, (ed. by W.R. Institute) Washington, DC.

Miranda, P.M. a., Alves, J.M.R. & Serra, N. (2012) Climate change and upwelling: response of Iberian upwelling to atmospheric forcing in a regional climate scenario. Climate Dynamics, 40, 2813–2824.

Moritz, C., Patton, J.L., Conroy, C.J., Parra, J.L., White, G.C. & Beissinger, S.R. (2008) Impact of a century of climate change on small-mammal communities in Yosemite National Park, USA. Science, 322, 261–264.

Moss, R.H., Edmonds, J. a, Hibbard, K. a, Manning, M.R., Rose, S.K., van Vuuren, D.P., Carter, T.R., Emori, S., Kainuma, M., Kram, T., Meehl, G. a, Mitchell, J.F.B., Nakicenovic, N., Riahi, K., Smith, S.J., Stouffer, R.J., Thomson, A.M., Weyant, J.P. & Wilbanks, T.J. (2010) The next generation of scenarios for climate change research and assessment. Nature, 463, 747–56.

Nakagawa, S. & Schielzeth, H. (2013) A general and simple method for obtaining R2 from generalized linear mixed-effects models. Methods in Ecology and Evolution, 4, 133–142.
Neushul, M. (1983) An overview of basic research on kelp and the kelp forest ecosystem. W Bascom. The Effects of Waste Disposal on Kelp Communities (ed. by Univ Calif Inst Mar Res), pp. 282–300. San Diego.

Nicastro, K.R., Zardi, G.I., Teixeira, S., Neiva, J., Serrão, E. a & Pearson, G. a (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.

Norderhaug, K.M., Christie, H., Fosså, J.H.O. & Fredriksen, S.P. (2005) Fish-macrofauna interactions in a kelp (Laminaria hyperborea) forest. Journal of the Marine Biological Association of the United Kingdom, 85, 1279–1286.

Norton, T.A. (1978a) The factors influencing the distribution of Saccorhiza polyschides in the region of Lough Ine. Journal of the Marine Biological Association of the United Kingdom, 58, 527–536.

Norton, T.A. (1978b) The factors influencing the distribution of Saccorhiza polyschides in the region of Lough Ine. Journal of the Marine Biological Association of the United Kingdom, 58, 527–536.

Oliveira, P.B., Nolasco, R., Dubert, J., Moita, T. & Peliz, Á. (2009) Surface temperature, chlorophyll and advection patterns during a summer upwelling event off central Portugal. Continental Shelf Research, 29, 759–774.

Parker, D.E., Legg, T.P. & Folland, C.K. (1992) A new daily Central England Temperature Series, 1772–1991. International Journal of Climatology, 12, 317–342.

Parmesan, C. (2006) Ecological and Evolutionary Responses to Recent Climate Change. Annual Review of Ecology, Evolution, and Systematics, 37, 637–669.

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

Pastor, M. V., Pelegrí, J.L., Hernández-Guerra, A., Font, J., Salat, J. & Emelianov, M. (2008) Water and nutrient fluxes off Northwest Africa. Continental Shelf Research, 28, 915–936.

Peliz, A., Dubert, J., Santos, A., Oliveira, P. & Lecann, B. (2005) Winter upper ocean circulation in the Western Iberian Basin—Fronts, Eddies and Poleward Flows: an overview. Deep Sea Research Part I Oceanographic Research Papers, 52, 621–646.

Pereira, S.G., Lima, F.P., Queiroz, N.C., Ribeiro, P.A. & Santos, A.M. (2006) Biogeographic Patterns of Intertidal Macroinvertebrates and their Association with Macroalgae Distribution along the Portuguese Coast. Hydrobiologia, 555, 185–192.

Pereira, T. & Engelen, A. (2011) Temperature effects on the microscopic haploid stage development of Laminaria ochroleuca and Sacchoriza polyschides, kelps with contrasting life histories. Cahiers de Biologie Marine, 52, 395–403.

Peterson, a. T. (2011) Ecological niche conservatism: a time-structured review of evidence. Journal of Biogeography, 38, 817–827.

Pujol, B. & Pannell, J.R. (2008) Reduced responses to selection after species range expansion. Science, 321, 96.

Van der Putten, W.H., Macel, M. & Visser, M.E. (2010) Predicting species distribution and abundance responses to climate change: why it is essential to include biotic interactions across trophic levels. Philosophical transactions of the Royal Society of London. Series B, Biological sciences, 365, 2025–34.

Ben Rais Lasram, F., Guilhaumon, F., Albouy, C., Somot, S., Thuiller, W. & Mouillot, D. (2010) The Mediterranean Sea as a “cul-de-sac” for endemic fishes facing climate change. Global Change Biology, 16, 3233–3245.

Ramstein, G., Kageyama, M., Guiot, J., Wu, H., Hély, C., Krinner, G. & Brewer, S. (2007) How cold was Europe at the Last Glacial Maximum? A synthesis of the progress achieved since the first PMIP model-data comparison. Climate Of The Past Discussions, 3, 197–220.

Raybaud, V., Beaugrand, G., Goberville, E., Delebecq, G., Destombe, C., Valero, M., Davoult, D., Morin, P. & Gevaert, F. (2013) Decline in Kelp in West Europe and Climate. PloS one, 8, e66044.

Rebelo, H., Froufe, E., Brito, J.C., Russo, D., Cistrone, L., Ferrand, N. & Jones, G. (2012) Postglacial colonization of Europe by the barbastelle bat: agreement between molecular data and past predictive modeling. Molecular ecology, 21, 2761–74.

Reed, D.C. (1990) The effects of variable settlement and early competition on patterns of kelp recruitment. Ecology, 71, 776–787.

Reed, D.C., Amsler, C.D. & Ebeling, A.W. (1992) Dispersal in kelps: factors affecting spore swimming and competency. Ecology, 72, 1577 – 1585.

Reed, D.C., Ebeling, A.W., Anderson, T.W. & Anghera, M. (1996) Differential reproductive responses to fluctuating resources in two seaweeds with different reproductive strategies. Ecology, 77, 300–316.

Reed, D.C., Kinlan, B.P., Raimondi, P.T., Washburn, L., Gaylord, B., Drake, P.T., Jacob, P.K. & Peter, F.S. (2006) A metapopulation perspective on patch dynamics and connectivity of giant kelp. Marine Metapopulations (ed. by J.P. Kritzer Sale Pf), pp. 353–386. Academic Press, San Diego.

Reed, D.C., Rassweiler, A., Carr, M.H., Cavanaugh, K.C., Malone, D.P. & Siegel, D. a (2011) Wave disturbance overwhelms top-down and bottom-up control of primary production in California kelp forests. Ecology, 92, 2108–16.

Relvas, P. & Barton, E. (2005) A separated jet and coastal counterflow during upwelling relaxation off Cape São Vicente (Iberian Peninsula). Continental Shelf Research, 25, 29–49.

Relvas, P., Barton, E.D., Dubert, J., Oliveira, P.B., Peliz, Á., da Silva, J.C.B. & Santos, A. M.P. (2007) Physical oceanography of the western Iberia ecosystem: Latest views and challenges. Progress in Oceanography, 74, 149–173.

Relvas, P., Luís, J. & Santos, a. M.P. (2009) Importance of the mesoscale in the decadal changes observed in the northern Canary upwelling system. Geophysical Research Letters, 36, L22601.

Rogelj, J., Meinshausen, M. & Knutti, R. (2012) Global warming under old and new scenarios using IPCC climate sensitivity range estimates. Nature Climate Change, 1–6.

Root, T.L., Price, J.T., Hall, K.R., Schneider, S.H., Rosenzweig, C. & Pounds, J.A. (2003) Fingerprints of global warming on wild animals and plants. Nature, 421, 57–60.

Sala, O.E., Chapin, F.S., Armesto, J.J., Berlow, E., Bloomfield, J., Dirzo, R., Huber-Sanwald, E., Huenneke, L.F., Jackson, R.B., Kinzig, A., Leemans, R., Lodge, D.M., Mooney, H.A., Oesterheld, M., Poff, N.L., Sykes, M.T., Walker, B.H., Walker, M. & Wall, D.H. (2000) Biodiversity - Global biodiversity scenarios for the year 2100. Science, 287, 1770–1774.

Sarhan, T., Vargas, M. & Vargas, J.M. (2000) Upwelling mechanisms in the northwestern Alboran Sea. Journal of Marine Systems, 23, 317–331.

Schiel, D.R. & Foster, M.S. (2006) The Population Biology of Large Brown Seaweeds: Ecological Consequences of Multiphase Life Histories in Dynamic Coastal Environments. Annual Review of Ecology, Evolution, and Systematics, 37, 343–372.

Steneck, R.S., Graham, M.H., Bourque, B.J., Corbett, D., Erlandson, J.M., Estes, J. a. & Tegner, M.J. (2003) Kelp forest ecosystems: biodiversity, stability, resilience and future. Environmental Conservation, 29, 436–459.

Stillman, J.H. & Somero, G.N. (2000) A comparative analysis of the upper thermal tolerance limits of eastern Pacific porcelain crabs, genus Petrolisthes: influences of latitude, vertical zonation, acclimation. Physiological and Biochemical Zoology, 73, 200–208.

Stuart-Smith, R.D., Barrett, N.S., Stevenson, D.G. & Edgar, G.J. (2010) Stability in temperate reef communities over a decadal time scale despite concurrent ocean warming. Global Change Biology, 16, 122–134.

Tarkhnishvili, D., Gavashelishvili, A. & Mumladze, L. (2012) Palaeoclimatic models help to understand current distribution of Caucasian forest species. Biological Journal of the Linnean Society, 105, 231–248.

Tegner, M.J., Dayton, P.K., Edwards, P.B. & Riser, K.L. (1997) Large-scale, low-frequency oceanographic effects on kelp forest succession:a tale of two cohorts. Marine Ecology Progress Series, 146, 117–134.

Thomas, C.D., Cameron, A., Green, R.E., Bakkenes, M., Beaumont, L.J., Collingham, Y.C., Erasmus, B.F.N., De Siqueira, M.F., Grainger, A., Hannah, L., Hughes, L., Huntley, B., Van Jaarsveld, A.S., Midgley, G.F., Miles, L., Ortega-Huerta, M.A., Peterson, A.T., Phillips, O.L. & Williams, S.E. (2004) Extinction risk from climate change. Nature, 427, 145–8.

Thuiller, W. (2004) Patterns and uncertainties of species’ range shifts under climate change. Global Change Biology, 10, 2020–2027.

Thuiller, W., Lafourcade, B., Engler, R. & Araújo, M.B. (2009) BIOMOD - a platform for ensemble forecasting of species distributions. Ecography, 32, 369–373.

Van den Hoek, C. (1982) The distribution of benthic marine algae in relation to the temperature regulation of their life histories. Biological Journal of the Linnean Society, 18, 81-144

Wenger, S.J. & Olden, J.D. (2012) Assessing transferability of ecological models: an underappreciated aspect of statistical validation. Methods in Ecology and Evolution, 3, 260–267.

Wernberg, T., Thomsen, M.S., Tuya, F., Kendrick, G. a, Staehr, P. a & Toohey, B.D. (2010) Decreasing resilience of kelp beds along a latitudinal temperature gradient: potential implications for a warmer future. Ecology letters, 13, 685–94.

Whittingham, M.J., Stephens, P.A., Bradbury, R.B. & Freckleton, R.P. (2006) Why do we still use stepwise modeling in ecology and behaviour? Journal of Animal Ecology, 75, 1182–1189.

Zuur, A., Elena, N., Walker, N., Saveiliev, A. & Smith, G. (2009) Mixed Effects Models and Extensions in Ecology with R, (ed. by Springer Verlag.) New York.

SUPPLEMENTAL INFORMATION

Appendix S1. Environmental predictors used for modeling purposes. Predictors' name (SST - Sea Surface Temperature; Kd - In-water diffuse attenuation coefficient; SWH - Significant Wave Height; CHLa - Clorophil a), temporal range, original resolution, units and derived metric (Winter: NDJF; Spring: MAM; Summer: JJAS).

Predictor	**Temporal range**	***Resolution***	**Units**	**Derived metric**[1]
SST[2,3]	1992-2011 2013-2100	~5km ~25km/~95km	ºC	1 - Minimum Previous Summer 2 - Mean Previous Summer 3 - Maximum Previous Summer 4 - Minimum Winter 5 - Mean Winter 6 - Maximum Winter 7 - Minimum Spring 8 - Mean Spring 9 - Maximum Spring 10 - Previous Summer deviation from the monthly mean 11 -Winter deviation from the monthly mean 12 - Spring deviation from the monthly mean 13 - Number of Previous Summer days above long term monthly mean 14 - Number of Previous Summer days bellow long term monthly mean 15 - Number of Winter days above long term monthly mean 16 - Number of Winter days bellow long term monthly mean 17 - Number of Spring days above long term monthly mean 18 - Number of Spring days bellow long term monthly mean
Kd[4]	1997-2011	~9km/~4km	m^{-1}	
SWH[5]	1992-2011	~32km	m	
Chla[6]	1997-2011	~9km/~4km	$mg.m^{-3}$	

[1] The mean, minimum and maximum values of each predictor were determined per season (summer: predictors 1 to 3; winter: 4 to 6; spring: 7 to 10). Also, the summer, winter and spring deviations above and below the season mean ± 1 standard deviations (summer: 10; winter: 11; spring: 12) were calculated, as well as the number of consecutive days above and below the season monthly mean ± 1 standard deviation (summer: + 13 and - 14; winter: + 15 and - 16; spring: + 17 and - 18).

[2] Sea Surface Temperature (SST) was derived from the Operational Sea Surface Temperature and Sea Ice Analysis (OSTIA; Stark et al., 2007), which combines infrared and microwave satellite data from the Group for High-Resolution Sea Surface Temperature (GHRSST) with in situ measurements on a resolution of ~5km (Martin et al., 2007).

[3] Sea Surface Temperature for future projections was derived from two Atmospheric General Circulation Models: the Community Climate System Model (CCSM4) and the Model for Interdisciplinary Research on Climate (MIROC5), on a resolution of ~25km and ~95km, respectively, under the scenarios RCP 2.6 and RCP8.5.

[4] In-water diffuse attenuation coefficient (Kd) was derived from SeaWiFS (Sea Wide Field Sensor) satellite radiance (Gohin et al., 2005) and MODIS (Moderate Resolution Imaging Spectroradiometer) satellite spectroradiometer (Huot et al., 2005) on a resolution of ~9km and

~4km, respectively. This metric as a direct relation with the traditional “secchi disk depth” (Chen et al., 2007).

[5] Significant Wave Height (SWH) was derived from AVISO altimeter data (Schaeffer et al., 2012) obtained by analyzing the shape and intensity of the altimeter radar beam reflected from the sea surface (radar echo).

[6] Chlorophyll a (Chla) was used as a proxy for nutrients. This information derived from SeaWiFS (Gohin et al., 2005) and MODIS (Huot et al., 2005) on a resolution of ~9km and ~4km, respectively.

Chen, Z., Muller-Karger, F. & Hu, C. (2007) Remote sensing of water clarity in Tampa Bay. Remote Sensing of Environment, 109, 249–259

Donlon, C.J., Martin, M., Stark, J.D., Roberts-Jones, J., Fiedler, E. & Wimmer, W. (2011) The Operational Sea Surface Temperature and Sea Ice analysis (OSTIA). Remote Sensing of the Environment.

Gohin, F., Loyer, S., Lunven, M., Labry, C., Froidefond, J.M., Delmas, D., Huret, M. & Herbland, A. (2005) Satellite-derived parameters for biological modeling in coastal waters: Illustration over the eastern continental shelf of the Bay of Biscay. Remote Sensing of Environment, 95, 29-46.

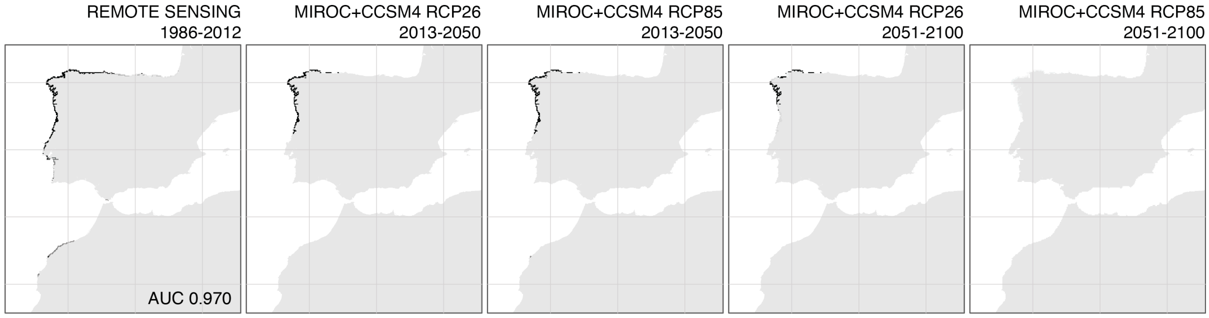
Huot, Y., Brown, C.A. & Cullen, J.J. (2005) New algorithms for MODIS sun-induced chlorophyll fluorescence and a comparison with present data products, Oceanography Methods, 3, 108–130.

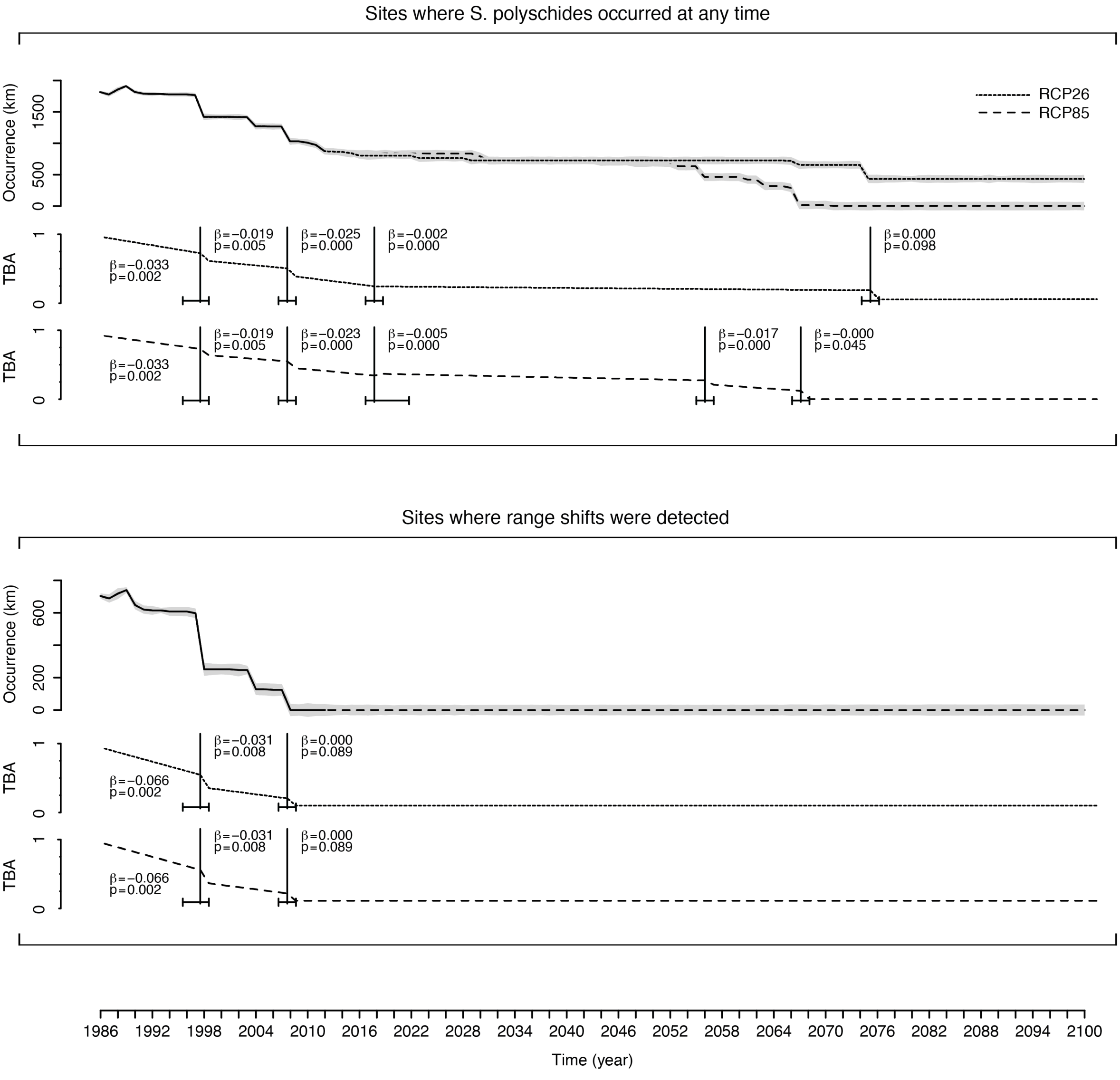
Schaeffer P., Faugere, Y., Legeais, J.F., Ollivier, A., Guinle, T., & Picot N. (2012) The CNES CLS11 Global Mean Sea Surface Computed from 16 Years of Satellite Altimeter Data. Marine Geodesy, 2012, Special Issue, Jason-2, Vol.35.

Zhang, H.M., Reynolds, R.W. & Bates, J.J. (2006) Blended and Gridded High Resolution Global Sea Surface Wind Speed and Climatology from Multiple Satellites: 1987 - Present. American Meteorological Society 2006 Annual Meeting, Atlanta, GA, January 29 - February 2, 2006.

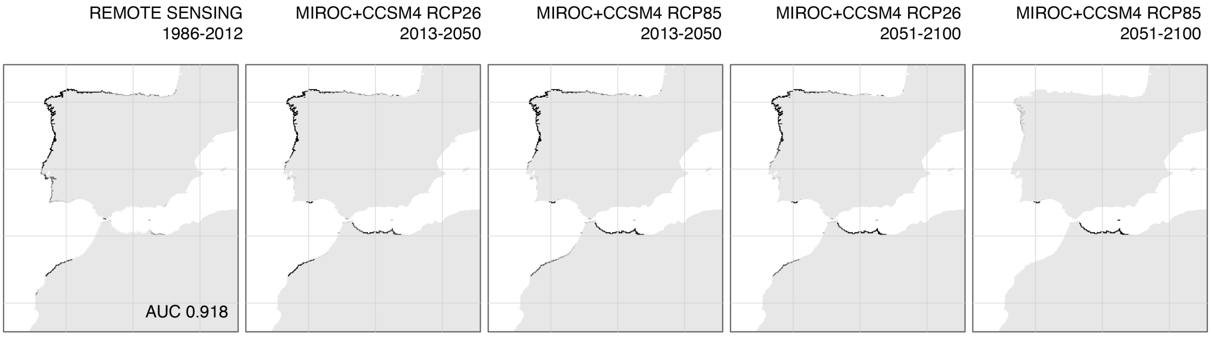
Appendix S2. Past and future distribution of *S. polyschides* (km of coastline) reconstructed with unlimited and no dispersal, predicted with remote sensing data (period 1986-2012) and AGCMs (MIROC5 and CCSM4) under two scenarios of greenhouse gas emissions (RCP2.6 and RCP8.5). Projections divided in those sites where *S. polyschides* occurred at any time and those sites where range-shifts were detected.

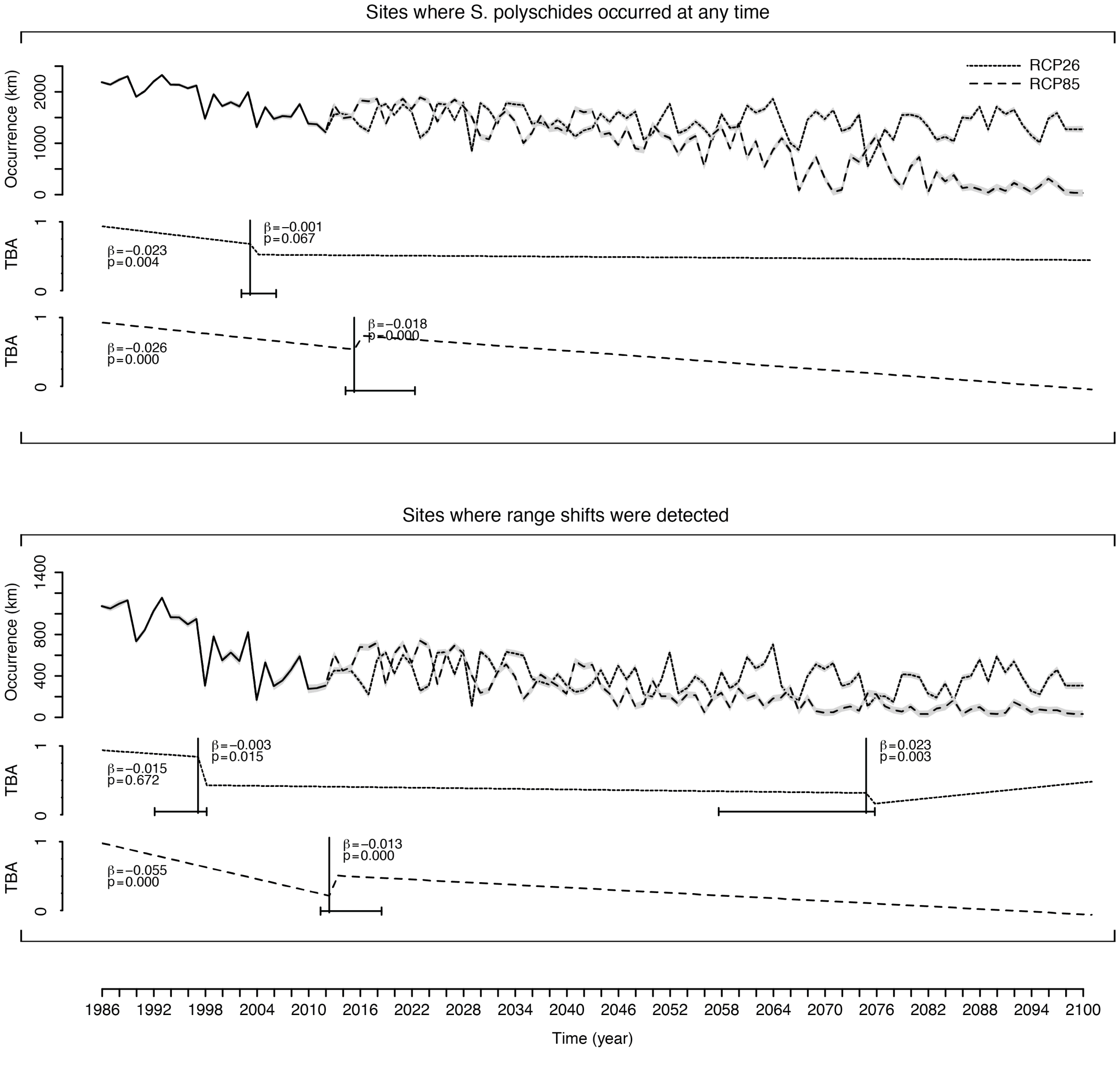
Reconstruction: No dispersal



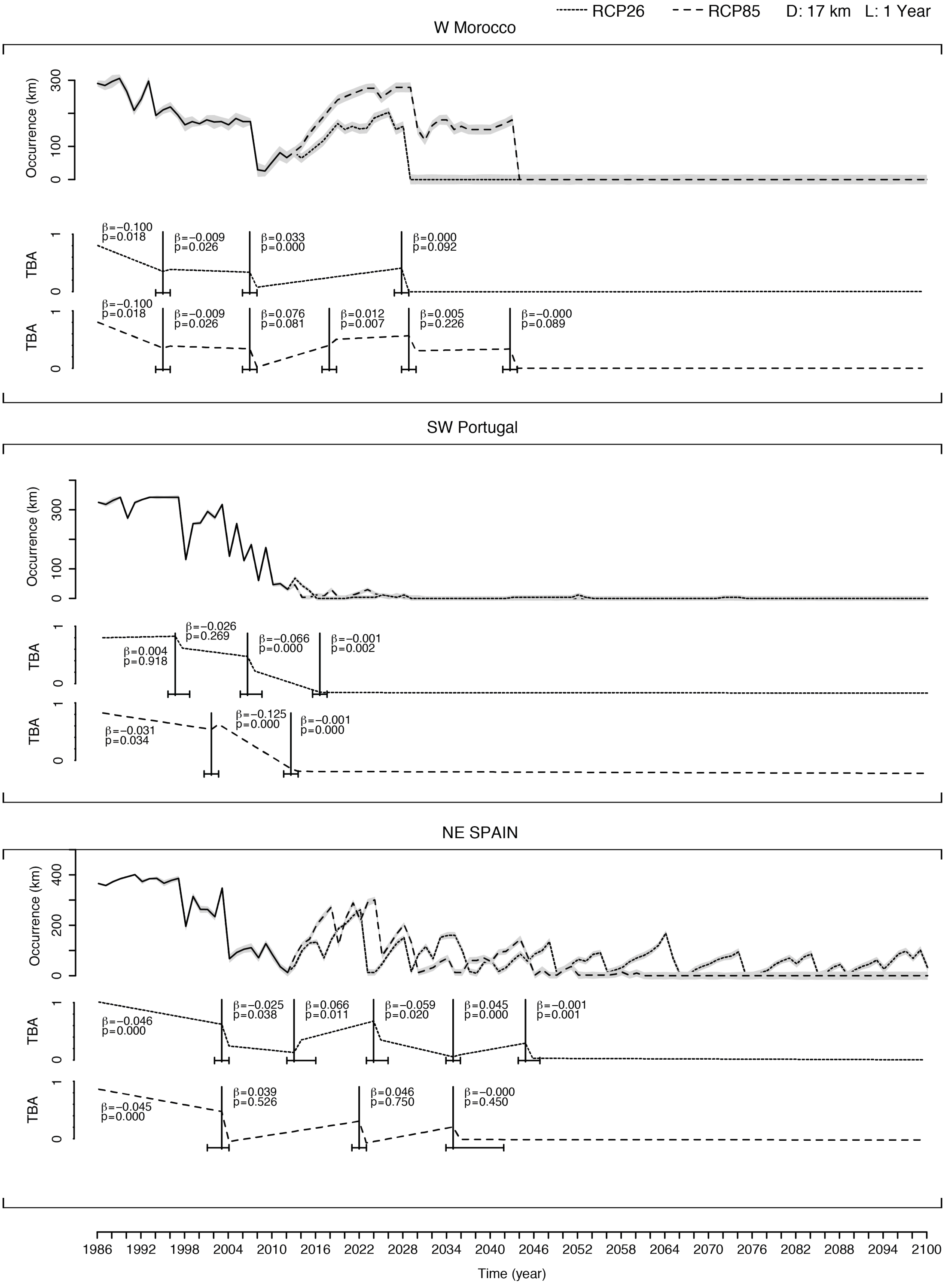


Reconstruction: Unlimited dispersal

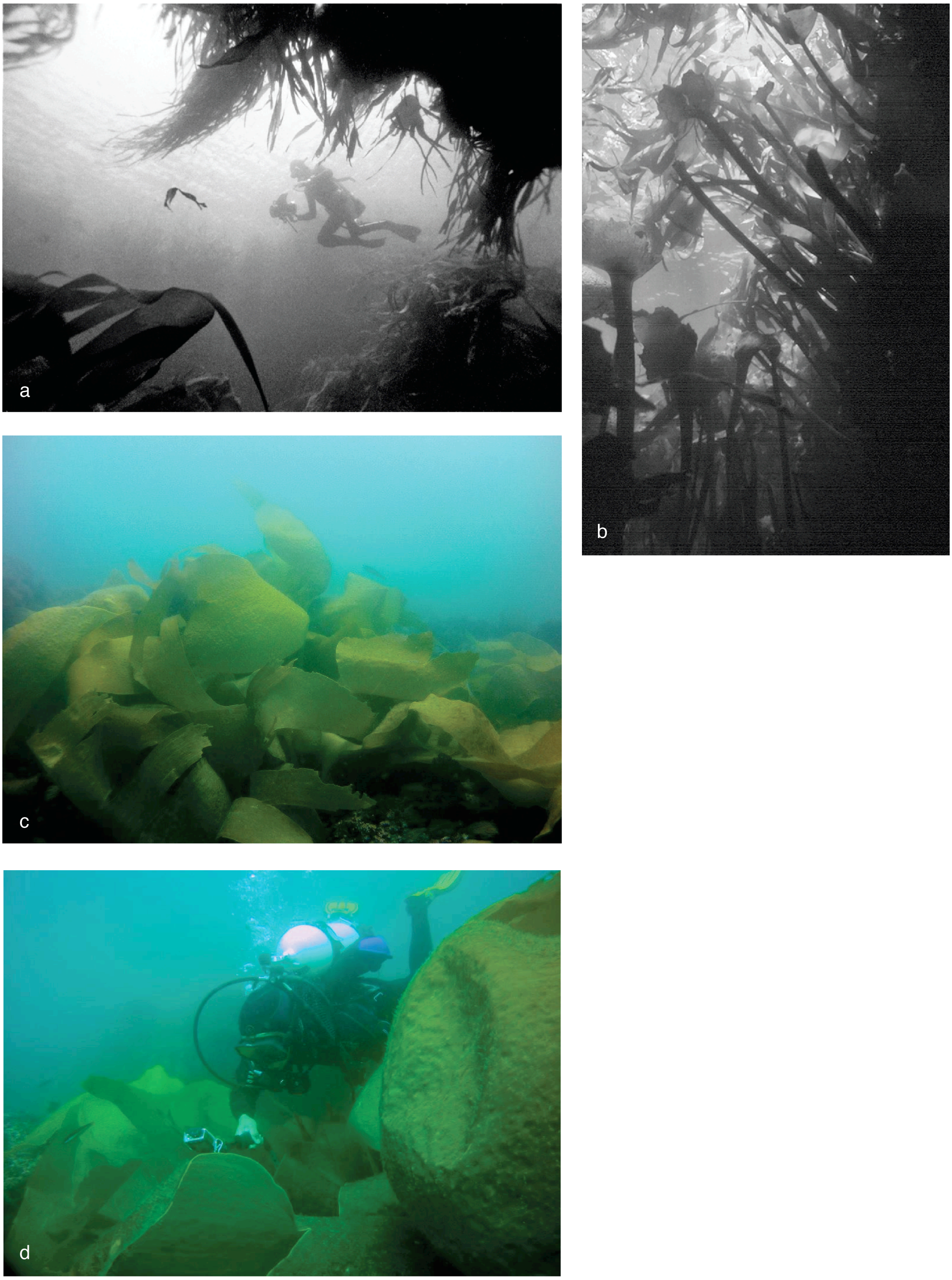




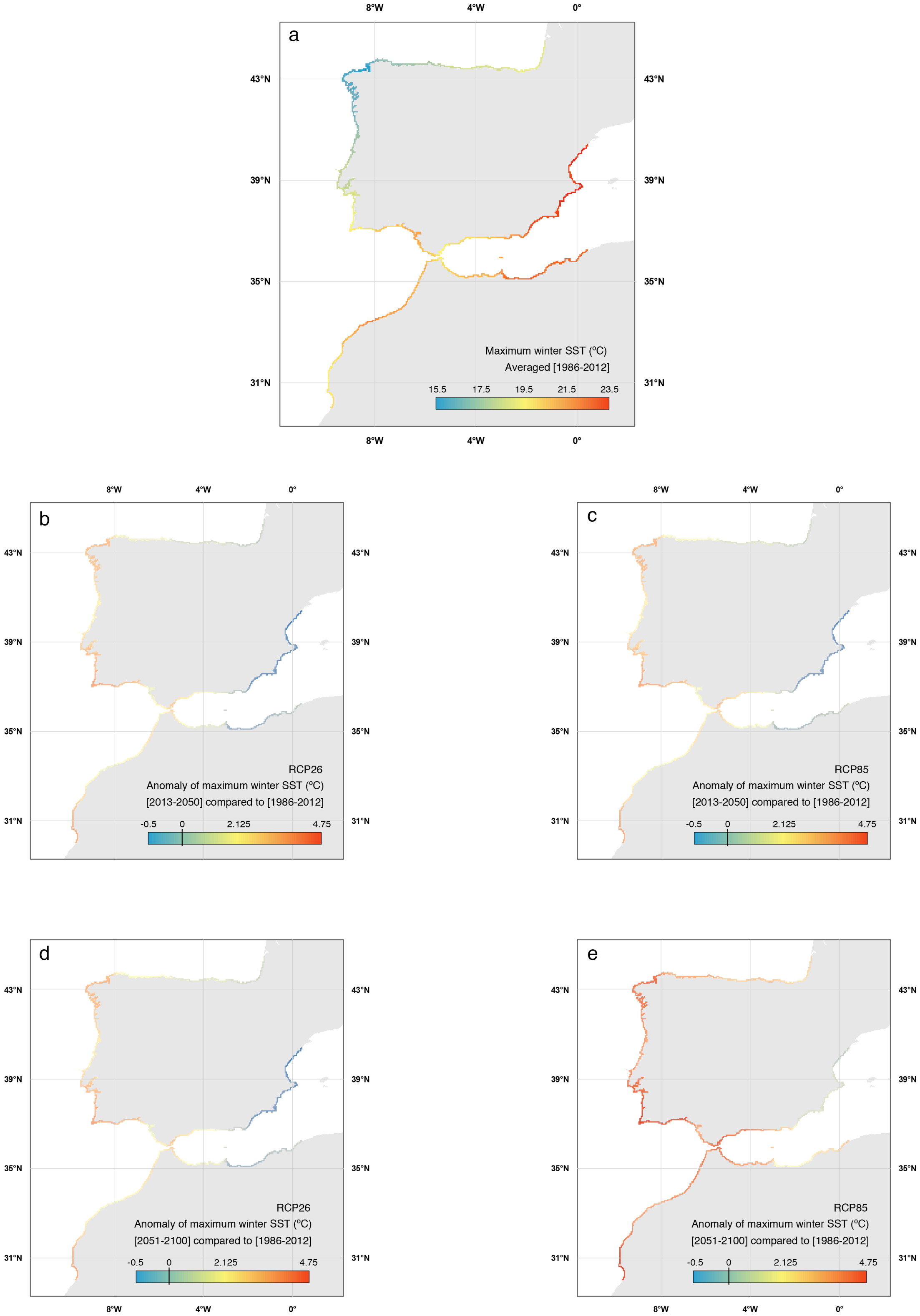
Appendix S3. Ensemble distribution models of *S. polyschides* for western Morocco, southwest of Portugal and northeast of Spain with specific measures of dispersal (D) and latency (L), generated with remote sensing data (period 1986-2012) and AGCMs (MIROC5 and CCSM4) under two scenarios of greenhouse gas emissions (RCP26 and RCP8.5). Shaded polygons represent the standard error of the ensembles. Trend break analysis by emission scenario. Vertical bars display the time of observed changes (break points with slope and p-value). Confidence intervals are also exhibited for each break point.



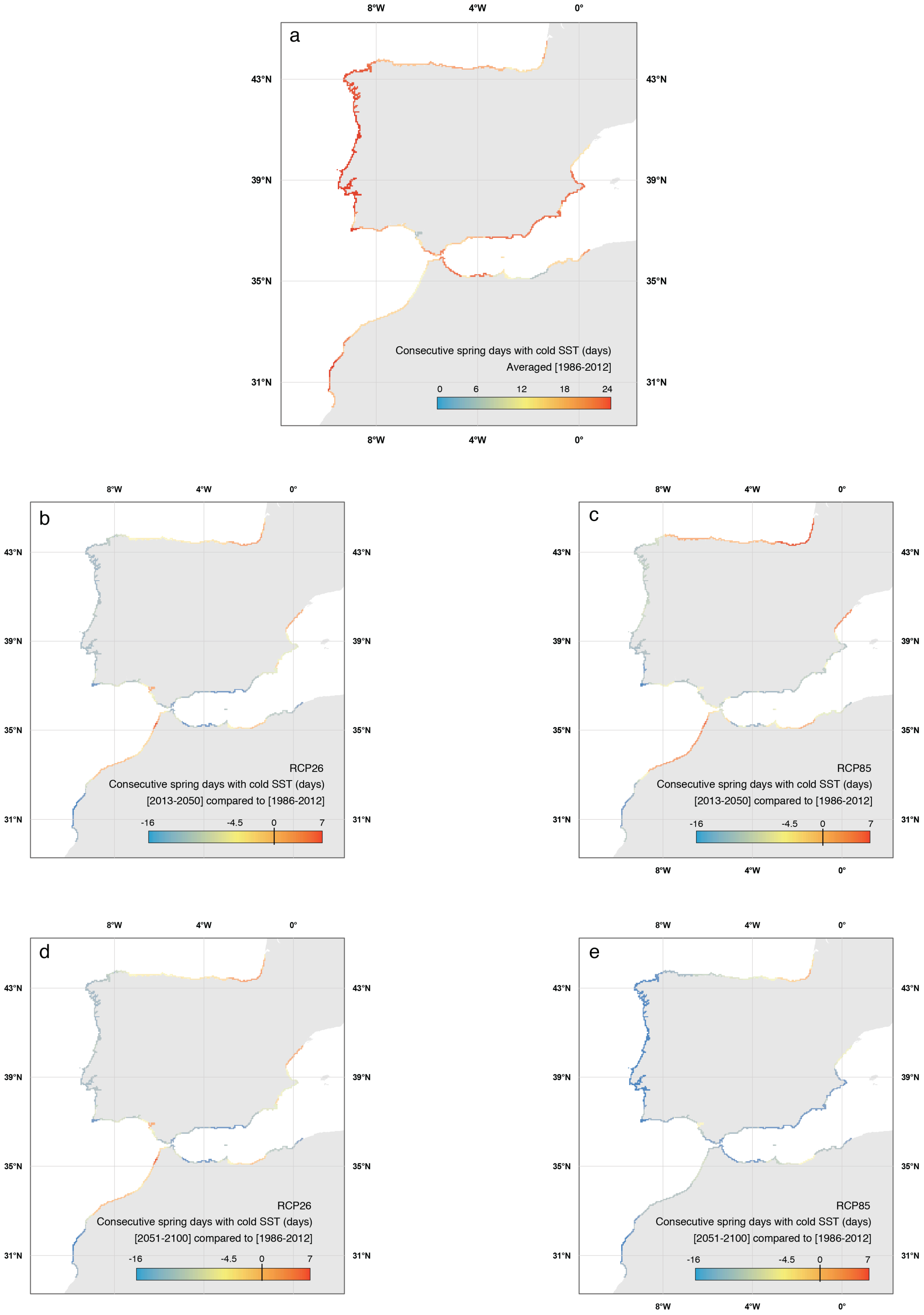
Appendix S4. Pictures taken in Arrábida (Setubal, Portugal) during field surveys performed on (a,b) the 1970s when abundat forests where distributed along this region (credits: Carlos Franco e Ester Serrão) and (c,d) on 2012 over the last known extant kelp forest of this site (credits: Diogo Paulo)



Appendix S5. (a) Maximum winter SST (averaged for the period 1986-2013) and related anomalies for the AGCMs simulations (MIROC5 and CCSM4) under two scenarios of greenhouse gas emissions (RCP26 and RCP85) for the periods (b,c) 2013 to 2050 and (d,e) 2051 to 2100.



Appendix S6. (a) Number of consecutive days with cold spring SST (averaged for the period 1986-2013) and related anomalies for the AGCMs simulations (MIROC5 and CCSM4) under two scenarios of greenhouse gas emissions (RCP26 and RCP85) for the periods (b,c) 2013 to 2050 and (d,e) 2051 to 2100.



CHAPTER IV » HIGH AND DISTINCT RANGE-EDGE GENETIC DIVERSITY DESPITE LOCAL BOTTLENECKS

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ABSTRACT

The genetic consequences of living on the edge of distributional ranges have been the subject of a largely unresolved debate. Populations occurring along persistent low latitude ranges (rear-edge) are expected to retain high and unique genetic diversity. In contrast, currently less favourable environmental conditions limiting population size at such range-edges may have caused genetic erosion that prevails over past historical effects, with potential consequences on reducing future adaptive capacity. The present study provides an empirical test of whether population declines towards a peripheral range might be reflected on decreasing diversity and increasing population isolation and differentiation. We compare population genetic differentiation and diversity with trends in abundance along a latitudinal gradient towards the peripheral distribution range of *Saccorhiza polyschides*, a large brown seaweed that is the main structural species of kelp forests in SW Europe. Signatures of recent bottleneck events were also evaluated to determine whether the recently recorded distributional shifts had a negative influence on effective population size. Our findings show decreasing population density and increasing spatial fragmentation and local extinctions towards the southern edge. Genetic data revealed two well-supported groups with a central contact zone. As predicted, higher differentiation and signs of bottlenecks were found at the southern edge region. However, a decrease in genetic diversity associated with this pattern was not verified. Surprisingly, genetic diversity increased towards the edge despite bottlenecks and much lower densities, suggesting that extinctions and recolonizations have not strongly reduced diversity or that diversity might have been even higher there in the past, a process of shifting genetic baselines.

INTRODUCTION

Understanding the processes shaping genetic diversity of range-edge populations is an important current challenge, particularly where rich former glacial refugia populations with high conservation value have become isolated in decreasing suitable habitat islands (Hampe & Petit, 2005). Accordingly, empirical data for populations at distributional edges do not all support the same general geographic pattern. These can vary from diverse persistent populations where habitat has remained favourable over the long term (Neiva et al., 2012a) to margins with small and low density populations where genetic diversity may be lower and clonal reproduction and inbreeding may prevail (Billingham et al., 2003; Arnaud-Haond et al., 2006). Such populations might represent the last refugia of threatened distinct genetic diversity (Diekmann & Serrão, 2012; Nicastro et al., 2013).

The genetic diversity of a population reflects both current and past events. The prediction of lower genetic diversity as a response to reductions in effective population size and gene flow towards edges (Vucetich & Waite, 2003; Eckert et al., 2008) assumes a current trend in abundance, from abundant central regions of distribution towards small and less dense populations; an assumption that has rarely been confirmed empirically. Many studies failed to find evidence for larger abundances at the centre of species distributions (Sagarin & Gaines, 2002) and the few that supported the hypothesis were limited to a small number of species (Jump & Woodward, 2003) and sites (Williams et al., 2003; Sorte & Hofmann, 2004). Yet, in most studies considering genetic diversity, a decrease in within population diversity and an increase in genetic differentiation between populations were observed towards the peripheral range (Eckert et al., 2008). The prevalence of effects of current population abundance patterns over past history in determining current genetic diversity might reflect the fact that extinction is forever, even when caused by unsuitable conditions that are temporary. Once lost, unique alleles occurring at range edges cannot reappear no matter how favourable the habitat becomes. The loss of adaptive variation towards range edges may compromise a population's ability to evolve (Pujol & Pannell, 2008; Pearson et al., 2009), thereby increasing the threat of extinction (Hoffmann & Blows, 1994; Young et al., 1996; Keller & Waller, 2010). This might be accentuated in isolated populations of annual species, which are naturally more prone to local bottlenecks and extinctions (Newman & Pilson, 1997). Thus, areas where past history created higher genetic diversity due to long term persistence of populations exposed to climatic refugia, or gene flow from differentiated populations (Garcia-Ramos & Kirkpatrick, 1997; Vucetich & Waite, 2003; Neiva et al., 2012b) are expected to be lost by current bottlenecks, although regional diversity might retain a diverse signature (Diekmann & Serrão, 2012).

The relationship between the geographic distributions of abundance and genetic diversity now appear more complex and interesting than previously assumed. This complexity strongly alters simplistic biogeographic predictions about population dynamics (Williams et al., 2003), genetic structure of populations, and species responses to climate change (Helmuth et al., 2005).

To move beyond simplistic assumptions it is necessary to integrate more sources of data (e.g., population demography and genetic structure) to narrow the range of viable hypotheses that explain the ecological and evolutionary mechanisms underlying species distribution (Sagarin et al., 2006). Moreover, studies frequently compare samples from sites with high abundances of focal species with very few in the peripheral range, assuming less abundance and higher levels of isolation without an empirical verification of demographic variables (Yakimowski & Eckert, 2008; Walser & Haag, 2012). This approach is unlikely to distinguish whether geographic variation in genetic structure covaries with contemporary population abundance and peripheral isolation, or is the result of historical processes (Vucetich & Waite, 2003).

An interesting model to study the genetic implications of distributional ranges from an abundant to a peripheral region is the Portuguese coast along western Iberia. This is a region with a biogeographical interface where a wide range of marine species show latitudinal clines in abundance, along a narrow strip of shoreline habitat essentially in one dimension, from North to South (Boaventura et al., 2002; Pereira et al., 2006). One such species is the annual kelp *Saccorhiza polyschides*, which is the main canopy species forming kelp forests in this region. This species sharply declines from being a highly abundant dominant species in the north to being rare near its distributional limit in the south. Such a spatially unidimensional model has previously proven effective in testing phylogeographic hypotheses in marine species (Sagarin & Gaines, 2002; Tellier et al., 2009).

This study addresses the genetic consequences of a sharp decline in abundance at the distributional margin of *S. polyschides*. This was achieved by quantifying the latitudinal gradient in population density towards the southern edge of distribution, and assessing whether it was related to decreasing genetic diversity and increasing differentiation. We used this information to test whether populations closer to the range boundary show no change in (1) relative densities, (2) fragmentation, (3) genetic differentiation, (4) genetic diversity and (5) signatures of recent bottleneck events (i.e., population turnover).

METHODS

FOCAL SPECIES, STUDY AREA AND SAMPLE COLLECTION

The annual kelp *S. polyschides* is an important ecosystem-building species in European waters (Coleman & Williams, 2002). This short-lived pioneer species is distributed from the western coast of Norway, extending southward to Scotland, Ireland, Wales, southwest England, Brittany, France and along the Spanish and Portuguese coasts, meeting its southern boundary in Morocco. It can also be found in few deep (~ 30m) isolated sites of the Western Mediterranean Sea (Norton, 1978).

Sampling sites for *S. polyschides* covered the entire west coast of Portugal, including searches in areas beyond the current southern limit of the species in mainland. This region, which happens to coincide with the boundaries of a political country, is an excellent model coastline to study the genetic implications of distributional ranges from an abundant to a peripheral region for 3 main reasons: 1) Gradual abundance gradient: It coincides perfectly with a sharp linear gradient from abundant continuous populations in the North, to small patchy fragmented populations in the center-southwest, to complete absence of the species along the southern coast. 2) Availability of long-term historical records of the species occurrence (particularly from Assis et al., 2009) showing recent range shifts along this coast. 3) Coastal southern limit: The southwest of Portugal is the southern range edge of the coastal distribution of *S. polyschides*. Beyond this region there are only 2 areas that support *S. polyschides*. Both are separated by hundreds to thousands of km in opposite directions (southwards, eastwards and westwards), are not part of the coastal distribution and thus are not useful to address the question of this paper. These two isolated areas are a) the strong upwelling points of Alboran (East) and Morocco (South), and b) the very deep offshore banks (e.g., Gorringe and Messina) where oceanic waters are so transparent that they allow the species to occur at depth ranges of about 40-80 m, much beyond the coastal depth ranges. Species distributions are not always linear with latitude and pockets or islands can occur beyond the limits of the linear latitudinal distribution, due to particular unique combinations of habitat conditions (Helmuth et al., 2002; Nicastro et al., 2013).

Along this sampled area populations recruit in spring and reach their highest abundance during summer. Adult individuals (sporophytes) die in the autumn and are absent during the winter, starting to recruit again in spring (Pereira et al., 2011). The Portuguese coastline was divided into 25 juxtaposed cells of 25 km from 42,0º N to 37,0º N, and for better resolution in North-South comparisons, the sampling effort was intensified at the 3 northernmost and 3 southernmost cells by dividing the 25 km cells into 5 sub-cells of 5 km. Forests of *S. polyschides* were sampled at the centroid sites of each cell, during the summers of 2008 and 2010, by means of SCUBA diving and snorkelling. If no kelp was found, at least two more randomly chosen sites in the same cell were surveyed with the same objective.

All sampling was conducted at comparable depths, shallower than 8 m, in order to avoid confounding latitude with the effects of depth, since the abundance of *S. polyschides* varies with depth (Santos, 1993). Species distribution was assessed in 2008 and 2010, by collecting presence and absence records at each sampling site. In the summer of 2010, the density of *S. polyschides* was also sampled and tissue was collected for genetic analysis. For density estimates, four quadrats (0.5 m x 0.5 m) were placed along three 20 m long transects haphazardly laid in an extant kelp forest, at 5, 10, 15 and 20 m (totalling 12 quadrats). In each quadrat all *S. polyschides* individuals were counted. For genetic analyses, 30 individuals were sampled along transects by removing a piece of the blade above the meristem. These were preserved in silica drying crystals until DNA extraction.

POPULATION DISTRIBUTION AND SPATIAL HETEROGENEITY

To evaluate inter-annual variability in the distribution and abundance of *S. polyschides*, the presence and absence records were plotted for both sampling years, together with an extensive list of historical geo-referenced occurrences gathered from literature (dataset and references can be obtained from the authors upon request). Furthermore, mean density of *S. polyschides* per site (expressed as individuals per m2) was calculated with the quadrat counts for 2010 samples. To infer the fragmentation level of kelp per site, the coefficient of variation among all quadrat counts was determined as a measure of dispersion that represents within site landscape spatial heterogeneity (Palmer et al., 1997) independently of the mean density. To test whether *S. polyschides* was less dense or more heterogeneous at sites towards the distributional edge, linear regression models were fitted between latitude and density, and between latitude and the coefficient of variation of density. Predictors were transformed if needed (log), homogeneity of variances and normality of models were assessed by graphical inspection of the residuals versus fitted values (Zuur et al., 2009) and by performing the Shapiro-Wilk test with H0: the residuals were normally distributed.

MICROSATELLITE AMPLIFICATION, SCORING AND CORRECTION

Genomic DNA was isolated from 5 to 10 mg of dried tissue using a CTAB method and Filter Plates (MSFBN6B10, Milllipore) as described in (Hoarau et al., 2006). A total of seven microsatellite loci (2F7, 1A1(2), 1E10, 3A10, 2A4, 3D12 and 2B3; Engel et al., 2008) were amplified for all sampling units. PCR reactions in 15 µl contained ±20 ng of DNA, 0.16 µM of forward 5' fluorochrome labeled primer and 0.33 µM of reverse primer, 0.8 mM of dNTPs (Bioline), 2.0 or 2.5 mM of MgCl2, 3.0 µl of 5x PCR Buffer and 0.4 U of GoTaq Polymerase (Promega, Madison, WI). Cycling conditions consisted of an initial denaturing step of 5 min at 95ºC, followed by 35 cycles of 30 s at 95ºC, 30 s at annealing temperature, 45 s at 72ºC, and a final elongation step at 72ºC for 20 minutes. All PCR reactions were performed on a GeneAmp 9700 thermocycler (PE Applied Biosystems, Foster City, California, USA). Fragment length was analyzed on an ABI PRISM 3130xl DNA analyzer (Applied Biosystems) using the GeneScan 500 LIZ standard.

Raw allele sizes were scored using the software STRand (Toonen & Hughes, 2001) and binned into allele classes using the MsatAllele package (Alberto, 2009) in the R software (R Development Core Team, 2012). Loci were tested for null alleles and scoring errors using the software Microchecker (van Oosterhout et al., 2004). Deviations from Hardy–Weinberg equilibrium and for linkage disequilibrium between pairs of loci were computed with FSTAT (Goudet, 2001).

ESTIMATES OF GENETIC DIVERSITY

Genetic diversity, as allelic richness (A) and Nei's gene diversity (expected heterozygosity; HE), were determined per locus and per site for all loci, using FSTAT. To test whether genetic diversity decreased towards the edge, a linear regression model was fitted between latitude and genetic diversity per site (A and HE). Homogeneity and normality of both models was assessed. Allelic richness was also computed for each genetic cluster (see below), standardised to the number of individuals and coastal distance range of the smallest cluster, using StandArich (Alberto et al., 2006). The number of unique alleles per genetic cluster was also determined.

POPULATION GENETIC STRUCTURE

The number of distinct genetic clusters (K) present in the studied region was inferred by running software Structure (Pritchard et al., 2000) with a burning time of 2x105 repetitions and 1x106 iterations exploring K from 1 to 8, with admixture allowed and without any a priori population assignments. The estimation of the likely number of clusters used the log probability of data Pr(X/K) (Pritchard et al., 2000) for each value of K and the DK criteria of (Evanno et al., 2005). For the most likely K, population assignment was graphically displayed with Distruct (Rosenberg, 2004). The patterns of genetic differentiation were illustrated through a Factorial Correspondence Analysis (FCA) of population multiscores computed using GENETIX 4.05 (Belkhir et al., 2004). Moreover, the association between the mean genetic similarity calculated over all loci and the geographic regions was shown by a consensus neighbour-joining (NJ) network based on Cavalli-Sforza & Edwards (Cavalli-Sforza & Edwards, 1967) genetic distances among all sites, computed using the software Populations (Langella, 1999) with $1x10^5$ bootstrap resamplings.

Levels of differentiation between sites were inferred using the FST estimator computed over loci, and within genetic groups using both FST and Jost's D (Weir & Cockerham, 1984). Hierarchical analysis of molecular variance (AMOVA) was computed using Genodive (Meirmans & Tienderen, 2004), based on allele frequency information under 999 permutations (Excoffier et al., 1992). Variance components were extracted for 3 hierarchical levels (1) among individuals within sites, (2) among sites within genetic groups and (3) among genetic groups. Genetic groups were partitioned following the outcomes of the FCA and the Bayesian clustering analysis.

Isolation by distance (IBD) was evaluated within groups, using pairwise estimates of mean genetic distance (FST ⁄ (1 – FST)) between sites, against pairwise minimum marine distances. Marine distances were computed with package gdistance for R (R Development Core Team, 2012) with least-cost distance between sites using land mass as an infinite resistance surface. The null hypothesis of no correlation between pairwise geographic distance and genetic distance matrices (Rousset, 1997; Rousset, 2000) was tested using Mantel non-parametric test (Mantel, 1967) based on 1x105 permutations as implemented in Genodive.

INFERENCE OF POPULATION BOTTLENECK

For each sampling site, evidence for recent bottleneck events was tested using two methods: (1) heterozygosity excess (Luikart & Cornuet, 1998) and (2) M-ratios (Garza & Williamson, 2001).

Populations that have experienced a recent bottleneck are predicted to temporarily lose allelic diversity at a significantly faster rate than heterozygosity (Luikart & Cornuet, 1998). This excess in heterozygosity was tested with software Bottleneck (Piry et al., 1999) using 9999 simulations. The Two-Phase Model (TPM) was used since it's more appropriate and realistic for microsatellites (Luikart & Cornuet, 1998; Piry et al., 1999). The frequency of step mutations was set to 0.9 (ps) and the variance of mutations to 12 (generic values, typical for many microsatellite markers; (Piry et al., 1999; Busch et al., 2007). Based on the number of loci in our dataset (less than 20), the Wilcoxon test was performed for the statistical analysis with the null hypothesis of no significant heterozygosity excess (on average) across loci (Luikart & Cornuet, 1998; Cornuet & Luikart, 1996).

The M-ratio test was performed with the software M_P_VAL (Garza & Williamson, 2001). This method is based on the premise that during a bottleneck, rare alleles are most likely to be lost, and the number of observed allelic states (k) reduces faster than the range of allele size (r), which results in a reduced M-ratio ($M = k/r$). Critical significance values (Mc), the lower boundary of the one-sided 95% confidence interval, were calculated using the software Critical_M (Garza & Williamson, 2001) with 10,000 randomizations (Garza, 2006). These calculations were made using ps, Dg (the size of non one-step changes) and Theta = $4Ne\mu$, three parameters known to influence the Mc results (Busch et al., 2007). Since there is no information on these parameters for the *S. polyschides* sampled sites, and to minimise type I errors, the Mc value for each site was calculated with the mean size of non-stepwise mutations = 3.5 and a highly conservative Theta = 10 (which assumes larger Ne and lower μ). The proportion of mutations was set to 0.9 as recommended by Garza & Williamson (Garza & Williamson, 2001). Observed M-ratios below Mc indicate a bottleneck.

RESULTS

SAMPLE COLLECTION AND MICROSATELLITE AMPLIFICATION

Along the Portuguese coast, presence-absence records of *S. polyschides* were performed on 48 visited cells (Table S1). At 23 of these cells, populations were sampled for density and genetic attributes. At one particular site (#8) only 16 individuals were found, precluding accurate density estimates within quadrats although samples could still be taken for genetic analysis.

All seven loci were polymorphic across all sites (see Table S2 for the details of gene diversity, allele richness and FIS values for each site and each locus). A total of 96 alleles were obtained from 676 genotyped individuals, ranging from 7 to 20 alleles per locus (mean = 13.71, SD = 4.39), and on a single site from 23 to 41 alleles (mean = 35.52, SD = 5.18). Significant FIS values were obtained, particularly in southern sites (#15, 17, 19, 20, 21, 22 and 23). No linkage disequilibrium was detected between all pairs of loci (Table S2). Microchecker analyses indicated no signs of stuttering error, but with the exception of one locus (3D12), all showed evidence of null alleles, particularly 2A4 (with 0.135 ± 0.078 null alleles on average, resulting in higher Fis values compared to other loci, Table S2). Yet, null alleles were uncommon to rare across loci (null alleles per locus < 0.2; Dakin & Avise, 2004), and had no consistency among sites. To account for possible null allele effects, all analyses of inter-population structure and bottleneck were run with and without locus 2A4, and its exclusion did not change the results. Hence, we did not exclude this locus from our analyses.

POPULATION ABUNDANCE AND SPATIAL HETEROGENEITY

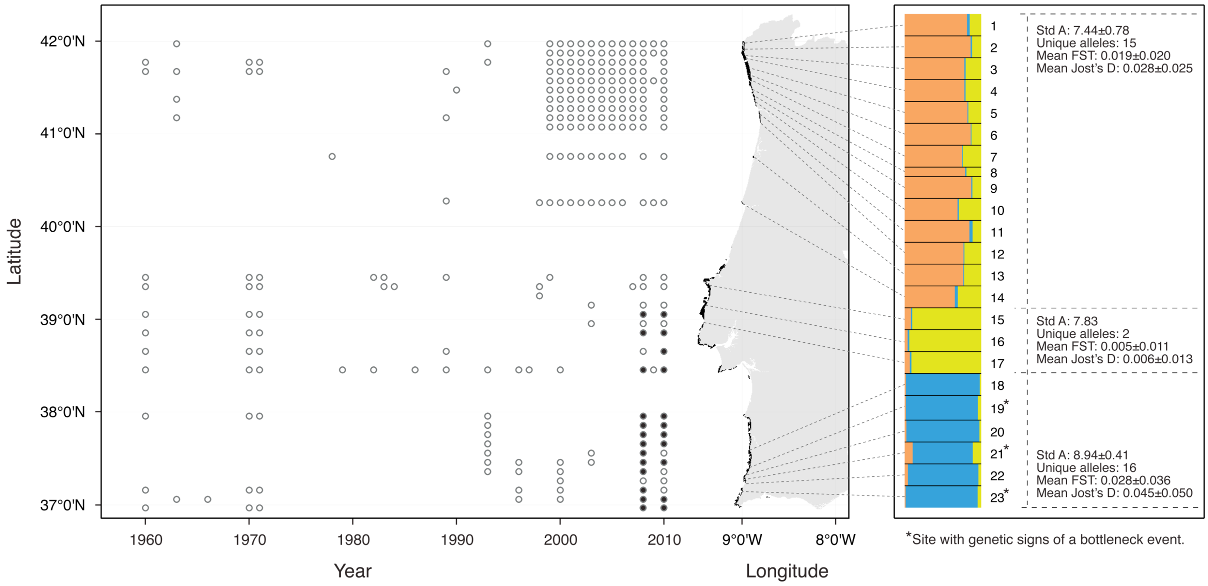

Fig 2. Historical distribution of *S. polyschides* based on surveys (2008 and 2010) and literature records (only comparable sites are shown; Open circle: presence, Black circle: absence). Habitat availability shown in black (Rocky reef; data from Portuguese sedimentary charts; Carvalho, 1992) along the coast for depths above 20 m (the observed depth distribution of *S. polyschides*; Assis et al., 2009). Genetic subdivision of *S. polyschides* based on STRUCTURE. The proportions of individual multilocus genotypes assigned to K=3 virtual clusters are indicated by the colours. Standardized allele richness (Std A), Mean FST, Mean Jost's D and number of unique alleles per genetic group.

S. polyschides was well established in the North of Portugal. North of 39º N, populations were present where there was suitable habitat and records were systematic throughout sampling years and literature references (Fig. 1). Conversely, south of this latitude, a large decline of *S. polyschides* was identified in recent years. Populations of *S. polyschides* at most southern sites where it was known to be present were extinct in 2008 and 2010, and the few extent populations were small and variable. Remarkably, at the southern range, some sites that were extinct in 2008 were recolonized from 2008 to 2010.

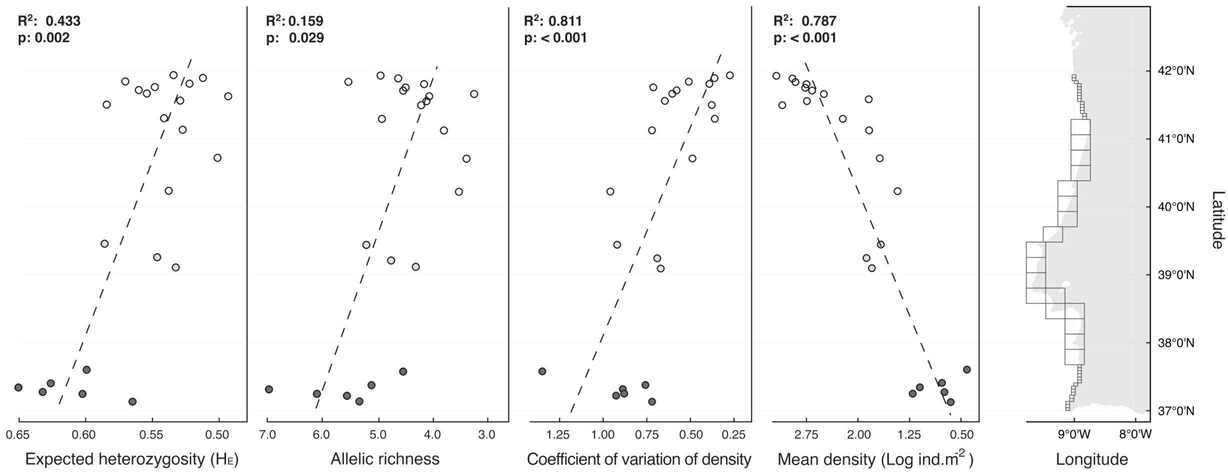

Figure 2. Sampling scheme for *S. polyschides* (cells represent the sampling units) within 25 km cells along the study range, and for detailed northern-southern comparisons within sub-cells of 5 km. Expected heterozygosity (HE), allele number, coefficient of variation of density and mean density (values increase from right to left; North: white circles, Center: grey circles, South: black circles) plotted against latitude (decimal degrees at WGS84). R-squared and p-values for linear models (dashed lines) fitted for sites with density records and genetic samples.

The density of kelp per sampling site varied between ca. 2 and 26 individuals·m^2 (Fig. 2). The highest densities were registered in the northern sites and a decline was found towards the South ($R^2 = 0.787$, $p < 0.001$). Below the dense northern kelp forests, two sharp declines in density were observed along the coast, the first below latitude 41º N (mean density < 10 individuals·m^2) followed by an even sparser region in the south (mean density < 5 individuals·m^2), below latitude 38º N. The among site variation in kelp density, quantified by the coefficient of variation of the densities, was lowest in the north, increasing significantly towards the south (Fig. 2; $R^2 = 0.811$, $p < 0.001$).

POPULATION GENETIC STRUCTURE

The Structure analyses, based on both the Evanno (Evanno et al., 2005) and the Pritchard (Pritchard et al., 2000) criteria, revealed 3 groups (K=3), separating the northern and the southern sites, plus a central region (Fig. 1, Appendix S4 in Supporting Information). When we analysed K=2 (data not shown), the distinct group in the central region appeared as an admixed zone, where alleles from the south and north appeared together (Appendix S5 in Supporting Information). Based on these results, we distinguished a central group and conducted analyses separately for 3 groups, hereafter designated North, Centre and South groups, composed by 14, 3 and 6 sites, respectively.

The genetic differentiation illustrated by the FCA and by the NJ network also revealed differentiation of three well-supported clusters (Appendix S6 in Supporting Information) corresponding to the same groups determined by the Structure analysis. Moreover, both FCA and NJ network revealed higher genetic distance between sites within the Centre and South than within the North.

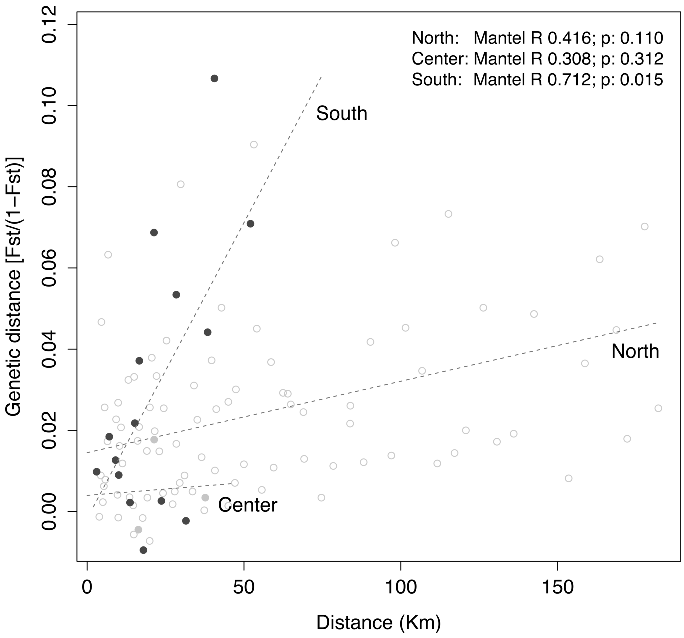

Fig 3. Isolation by distance of *S. polyschides*. Estimates of pairwise genetic differentiation (FST/(1-FST)) plotted against pairwise minimum site distance in kilometres for northern sites (white circles), central sites (grey circles) and southern sites (black circles). Mantel non-parametric tests based on $1x10^5$ permutations between pairwise genetic differentiation and pairwise site distance.

Pairwise mean FST and Jost's D levels of differentiation were higher between the southern sites than between the central or northern sites (Fig. 1). These values were significant among sites, among sites within genetic groups and among genetic groups (AMOVA; Appendix S3 in Supporting Information). The southern sites followed a model of isolation by distance (Mantel's R: 0.712, p = 0.015), that was not observed for the North and Center populations (Mantel's R: 0.416, p = 0.110 and R: 0.308, p = 0.312, respectively) (Fig. 3).

ESTIMATES OF GENETIC DIVERSITY

Allelic richness ranged from 3.28 to 7 alleles per site and expected heterozygosity from 0.490 to 0.648. These measures of diversity revealed a significant relation with latitude, increasing towards the south (A: $R^2 = 0.159$, p = 0.029; HE: $R^2 = 0.443$, p = 0.002; Fig. 2). Considering the two main groups, the allelic richness, standardised for 180 individuals within 52.2 km, was 8.94 ± 0.33 for the northern group and 10.62 for the southern. The North showed 17 unique alleles and the South showed 14 unique alleles. When the central admixture zone included, the within group allelic richness, standardised for 90 individuals within 37.6 km was 7.24 ± 0.38 for the North, 7.14 for the Center and 8.94 ± 0.41 for the South. The number of unique alleles was 15 in the North, 2 in the Center, and 14 in the South (Fig. 1).

INFERENCE OF POPULATION BOTTLENECK

The Wilcoxon test for the null hypothesis of no significant heterozygosity excess across loci showed no signs of bottleneck (Appendix S7 in Supporting Information). On the other hand, the M-ratio test retrieved bottleneck signs for three sites located in the Southern region (sites #19, 21 and 23; Fig. 1; S7). Our survey data show that the forests at sites #19 and #23 were locally extinct in 2008, but recolonized in 2010, the year when our genetic sampling took place.

DISCUSSION

Our results show persistence of high unique genetic diversity at a species range edge, despite evidence for strong demographic regressions, local extinctions, and extinctions followed by recolonizations. Although we found a decrease in density and an increase in fragmentation with latitude towards the distributional edge of *S. polyschides*, the hypothesis of a decrease in genetic diversity with decreasing density was not verified, contradicting expectations. Contrary to density and persistence data, allelic richness and heterozygosity increased towards the more sparsely populated southern range edge. Conversely, marginal southern sites were strongly genetically differentiated, inbreeding coefficients were higher and signs of recent genetic bottlenecks were detected, fitting expectations for small isolated populations undergoing distributional regression. These results raise the question as to why genetic diversity was higher at a low latitude edge despite low population density, fragmentation, genetic isolation, bottlenecks and inbreeding. Below we discuss several potential hypotheses that may explain this pattern.

PERIPHERAL POPULATION DECLINE

A north to south decline in density was evident as a set of latitudinal clines, decreasing density and increasing fragmentation (spatial heterogeneity of the population density). A considerable number of marine species also exhibit latitudinal abundance declines along this coast towards their distributional limits (Boaventura et al., 2002). Southern limits of some cold-water species have shifted north, possibly associated to recent warming associated with the sharp sea surface temperature gradient along this coast (Lima et al., 2007; Nicastro et al., 2013). However, in the case of *S. polyschides*, the decline in density towards the south has been magnified in recent decades, when local populations have been sharply reduced or even disappeared temporally or permanently. As a result, the genetic diversity of southern populations might thus be critically endangered.

PERIPHERAL POPULATION FRAGMENTATION

Significant and strong isolation by distance (IBD) was only present at the southern edge region, a likely consequence of habitat fragmentation as seen in other studies (Mandák et al., 2005; Lima et al., 2007; Diekmann & Serrão, 2012). Moreover, the levels of genetic differentiation between sites were higher and most were significant at the edge. These results show that the northern and central populations are highly connected within the region, whereas those towards the southern periphery of the range have lower gene flow between them, likely due to their occurrence as discrete, geographically isolated patches (Lawton, 1993; Young et al., 1996). The observed patterns of abundance can explain this result: *S. polyschides* tends to be less dense and more isolated towards the South, sharply increasing genetic distances and consequently IBD in this marginal zone. Such low densities may also increase the variation in mating success, which in turn explains the higher inbreeding values of the southern sites. Low sporophyte densities might be reflected in variable and patchy gametophyte densities, decreasing effective population size as only the spores that happen to settle in close proximity to others (within microscopic scales) will form gametophytes close enough to achieve reproductive success (Reed, 1990; Muth, 2012).

PHYLOGEOGRAPHIC INFLUENCES ON DIVERSITY

Along the studied range of western Iberia, our results reveal two major genetic groups, North and South, with an admixture region in the Centre. Their high genetic diversity and high number of unique alleles indicate that both regions represent populations that have been large, stable and persistent for long enough to accumulate unique mutations and maintain allelic diversity. They might thus represent genetic groups that were separated at distinct glacial refugia, a role that is also supported by their degree of differentiation from other populations from central Europe (Lamy et al, unpublished data), similarly to other marine species for which the Iberian Peninsula was a glacial refugium (Coyer et al., 2003; Neiva et al., 2012a; Diekmann & Serrão, 2012; Nicastro et al., 2013). Such reservoirs of unique genetic variation have high conservation value (Lesica & Allendorf, 1995; Hampe & Petit, 2005). The admixed genotypes in the central region and the rarity of unique alleles there, relative to the northern and southern regions, indicate that this is not an anciently diverged group but rather a more recent contact zone.

The geographical areas between the northern, central and southern forests were sampled and the absence of kelp forests reflected the paucity of suitable rocky habitat. Rocky reefs occur throughout the sampling region, but extensive sandy areas separate these kelp groups (Fig. 2; (Carvalho, 1992; Boaventura et al., 2002). Habitat discontinuity was associated with increased genetic differentiation between patches of the giant kelp Macrocystis pyrifera in southern California (Alberto et al., 2010) and *Laminaria digitata* in the English Channel (Billot et al., 2003), which is to be expected given the limits of spore dispersal of such species (Billot et al., 2003; Reed et al., 2006). Such limitations on dispersal are insufficient to assure regular connectivity between the spatially disconnected areas from our study. Yet, despite the breaks in suitable habitat between the genetic groups, some degree of north-south connectivity would be expected from the predominant spring wind and oceanographic circulation along the Portuguese coast (Oliveira et al., 2009). Surface currents could carry floating rafts of *S. polyschides*, with high dispersal potential in areas with strong unidirectional currents (Helmuth et al., 1994; Fraser et al., 2010). Such occasional large-scale dispersal across km scales must be possible, as it certainly occurred in the past during the colonization of distant available habitat. However, there is strong support for the idea that genetic groups have remained distinct over considerable time, as evidenced by the abundance of alleles unique to the north and south sites. Such genetic boundaries might also be explained by priority colonization effects, which block the spread of later colonizers, as recently proposed for other brown algae (Fraser et al., 2009; Tellier et al., 2011; Neiva et al., 2012a).

PERSISTENCE OF DIVERSITY DESPITE BOTTLENECKS

High genetic diversity is expected where populations have been large and persisted for long periods, without significant effects of drift, local extinctions and bottlenecks. Despite a possible glacial refugial origin of the ancient high and unique southern genetic diversity of *S. polyschides*, its recent history of regression and local extinctions recorded along this area was predicted to reflect lower diversity relative to northern Iberia. Conversely, recent bottlenecks and small population size with its associated drift effects, did not noticeably affect diversity patterns along this distributional edge.

How can genetic diversity survive over drastic population size reductions? We hypothesize possible non-exclusive mechanisms that could halt the loss of diversity of such marginal populations. One hypothesis is the occurrence of microscopic stages (such as gametophytes and very young sporophytes) able to persist over unfavourable periods. These could maintain genetic diversity in cryptic stages despite apparent temporary local extinctions and bottlenecks. Experiments on other kelp species, demonstrated that microscopic gametophytes can be maintained in culture for over 7 years (Neushul, 1983) and that when growth conditions become favourable, these produce adults faster and more reliably than gametophytes that had never been subject to developmental delay (Carney & Edwards, 2010; Carney, 2011). If such long developmental delays also occur in natural field conditions, then even at low densities of adult sporophytes, this delaying strategy may increase effective population size (Hock et al., 2008), by playing a role analogous to seed banks in plants, allowing temporal persistence of multiple cohorts of potential recruits that store genetic diversity and resume development in favourable years. This hypothesis is however not supported by the evidence from field studies, which identified arrested development stages only on the order of months, not years (e.g., Barradas et al., 2011) on this same coast, see also reviews by (Hoffmann & Santelices, 1991; Schiel & Foster, 2006; Carney & Edwards, 2010). Moreover, a temporal population genetic survey (covering 7-9 years) revealed that a local gametophyte "bank" might not be sufficient to prevent genetic instability of small and isolated populations of the European kelp *Laminaria digitata* (Valero et al., 2011). Furthermore, our findings of highest inbreeding coefficients in southern locations do not support the hypothesis of large effective population sizes hidden in cryptic stages.

An alternative hypothesis is the persistence of suitable habitat refugia at southern locations, namely deeper offshore habitats, where light penetration might still be sufficient for kelp persistence, as theoretically predicted for clearer offshore waters (Graham et al., 2007). Given the recent increase in sea temperature documented for this transitional zone, hypothetical deep offshore banks functioning as cold-water refugia, would provide better niche conditions than shallower warmer coastal sites (Graham et al., 2007). Such banks of high evolutionary significance (Riegl & Piller, 2003) connected to coastal sites (Glynn, 1996) could contribute with alleles periodically, thereby halting declines in genetic diversity. Although such deep offshore kelp forests with *S. polyschides* exist on underwater mounts (at ca. 40-80 m depths), these are located a few hundred km offshore of the southern distributional edge (Ormonde and Gettysburg bank; Gonçalves et al., 2004; Assis et al., 2009), and are genetically differentiated from these continental sites (Assis et al. unpublished data), rendering those unlikely to be frequent source populations for this annual species along its continental edge. Moreover, given the strong IBD found in the south, only a network of seamounts could explain the rescuing of diversity of such differentiated and isolated sites.

Local bottlenecks could also be rescued by connectivity from just the few neighbouring remaining patches in the area. Yet, once more, the higher levels of differentiation found between these patches do not support the idea that migration from local remaining sites would be a frequent process. Still, this hypothesis cannot be ruled out since it's difficult to survey the bottom of the ocean fully and extant populations might occur in areas that we are not aware of. In such a scenario, founder effects could lead to rapid differentiation of patches putatively recolonized by very few occasional migrants from other patches. Yet, this would have been associated with a strong reduction in diversity in such recolonized patches, which is not supported by the presence of many alleles and of alleles that are absent in their neighbours (S5).

A last, but not the least likely hypothesis, is that of shifting genetic baselines, whereby information about the past is lost with increasing extinctions, a problem already reported for other species along this coastline (Diekmann & Serrão, 2012; Nicastro et al., 2013). The higher southern diversity does not rule out that strong genetic diversity loss has occurred there. Our bottleneck results are congruent with the hypothesis that, although still richer in genetic diversity than denser northern populations, these southern patches could be the remnants of populations that once had greater genetic diversity.

Extinction of genetic variants is likely to happen frequently without it having been recorded to have ever existed before. This problem calls for studies of the potentially rich and unique genetic diversity that might still exist at pocket range edges. Rear edges below postglacial expansion zones are likely frequent along northern Atlantic shores, and in cases of expansion from introgressed genomes at contact zones, the rear edges may even represent the only surviving populations with the native genomes for the species, as has been reported for other brown algae (Neiva et al., 2010; Coyer et al., 2011). Marginal populations with such ancient private diversity raise concerns for future climate change predictions, particularly at the warmer edges of the distribution. Besides reporting unique allelic diversity, there is strong need to understand whether local adaptations exist in such endangered populations, increasing their conservation value. Although local adaptations are expected under high selective pressures in genetically distinct populations, their adaptive potential could be constrained in cases where native genetic diversity might have become limiting for their adaptive potential (Pearson et al., 2009).

Our results have clear implications for the conservation of *S. polyschides* in particular, in a context of future climate change where bottleneck events may prevail as a result of increasing environmental pressures (Parmesan & Yohe, 2003). In addition to the high conservation value of its genetically diverse and unique peripheral populations, which serve to halt local extinctions (Rogell et al., 2010) and preserve the evolutionary potential of *S. polyschides* (Pujol & Pannell, 2008; Pearson et al., 2009), the possible disappearance of these southern populations will also have direct ecological consequences. This kelp species functions as the most important ecosystem engineer of rocky shores along its southern distributional range, forming kelp forests that support a rich community. Thus the loss of kelp forest habitat caused by local extinctions of *S. polyschides* negatively affects the diversity and abundance of many associated species.

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REFERENCES

Alberto, F. (2009) MsatAllele_1.0: An R package to visualize the binning of microsatellite alleles. The Journal of heredity, 100, 394–397.

Alberto, F., Arnaud-haond, S., Duarte, C.M. & Serrão, E.A. (2006) Genetic diversity of a clonal angiosperm near its range limit: the case of Cymodocea nodosa at the Canary Islands. Marine Ecology Progress Series, 309, 117–129.

Alberto, F., Raimondi, P.P.T., Reed, D.D.C., Coelho, N.C., Leblois, R., Whitmer, A. & Serrão, E.A. (2010) Habitat continuity and geographic distance predict population genetic differentiation in giant kelp. Ecology, 91, 49–56.

Arnaud-Haond, S., Teixeira, S., Massa, S.I., Billot, C., Saenger, P., Coupland, G., Duarte, C.M. & Serrão, E.A. (2006) Genetic structure at range edge: low diversity and high inbreeding in Southeast Asian mangrove (Avicennia marina) populations. Molecular Ecology, 15, 3515–3525.

Assis, J., Tavares, D., Tavares, J., Cunha, A., Alberto, F., Serrão, E.A. & Ea (2009) Findkelp, a GIS-based community participation project to assess Portuguese kelp conservation status. Journal of Coastal Research, 3, 1469–1473.

Barradas, A. & Alberto, F. (2011) Fast sporophyte replacement after removal suggests banks of latent microscopic stages of Laminaria ochroleuca (Phaeophyceae) in tide pools in northern Portugal. CBM-Cahiers de Biologie, 52, 435–439.

Belkhir, K., Borsa, P., Chikhi, L., Raufaste, N. & Bonhomme, F. (2004) GENETIX 4.05, Population genetics software for Windows TM.

Billingham, Reusch, T., Alberto, F. & Serrão, E. (2003) Is asexual reproduction more important at geographical limits? A genetic study of the seagrass Zostera marina in the Ria Formosa, Portugal. Marine Ecology Progress Series, 265, 77–83.

Billot, C., Engel, C., Rousvoal, S., Kloareg, B. & Valero, M. (2003) Current patterns, habitat discontinuities and population genetic structure: the case of the kelp Laminaria digitata in the English Channel. Marine Ecology Progress Series, 253, 111–121.

Boaventura, D., Re, P., Cancela Da Fonseca, L., Hawkins, S.J., Ré, P. & Fonseca, L.C. Da (2002) Intertidal Rocky Shore Communities of the Continental Portuguese Coast: Analysis of Distribution. Marine Ecology, 23, 69–90.

Busch, J.D., Waser, P.M. & Dewoody, J.A. (2007) Recent demographic bottlenecks are not accompanied by a genetic signature in banner-tailed kangaroo rats (Dipodomys spectabilis). Molecular ecology, 16, 2450–62.

Carney, L.T. & Edwards, M.S. (2010) Role of Nutrient Fluctuations and Delayed Development in Gametophyte Reproduction By Macrocystis Pyrifera (Phaeophyceae) in Southern California1. Journal of Phycology, 46, 987–996.

Carney, L.T. (2011) A multispecies laboratory assessment of rapid sporophyte recruitment from delayed kelp gametophytes. Journal of Phycology, 47, 244-251.

Carvalho, D. (1992) Carta geológica de Portugal 1:500000. Directorate General for Fisheries, Lisbon.

Cavalli-Sforza, L.L. & Edwards, A.W.F. (1967) Phylogenetic analysis. Models and estimation procedures. The American Journal of Human Genetics, 19, 233–257.

Coleman, F.C. & Williams, S.L. (2002) Overexploiting marine ecosystem engineers: potential consequences for biodiversity. Trends in Ecology & Evolution, 17, 40–44.

Cornuet, J.M. & Luikart, G. (1996) Description and power analysis of two tests for detecting recent population bottlenecks from allele frequency data. Genetics, 144, 2001–2014.

Coyer, J. a., Peters, a. F., Stam, W.T. & Olsen, J.L. (2003) Post-ice age recolonization and differentiation of Fucus serratus L. (Phaeophyceae; Fucaceae) populations in Northern Europe. Molecular Ecology, 12, 1817–1829.

Coyer, J.A., Hoarau, G., Pearson, G., Mota, C., Jüterbock, A., Alpermann, T., John, U. & Olsen, J.L. (2011) Genomic scans detect signatures of selection along a salinity gradient in populations of the intertidal seaweed Fucus serratus on a 12 km scale. Marine genomics, 4, 41–49.

Dakin, E.E. & Avise, J.C. (2004) Microsatellite null alleles in parentage analysis. Heredity, 93, 504–9.

Diekmann, O.E. & Serrão, E.A. (2012) Range-edge genetic diversity: locally poor extant southern patches maintain a regionally diverse hotspot in the seagrass Zostera marina. Molecular ecology, 21, 1647–57.

Eckert, C.G., Samis, K.E. & Lougheed, S.C. (2008) Genetic variation across species' geographical ranges: the central-marginal hypothesis and beyond. Molecular ecology, 17, 1170–88.

Engel, C.R., Guillemin, M.-L., Jacob, A.-M., Valero, M. & Viard, F. (2008) Isolation of microsatellite loci from the kelp, Saccorhiza polyschides (Heterokontophyta, incertae sedis). Molecular ecology resources, 8, 406–408.

Evanno, G., Regnaut, S. & Goudet, J. (2005) Detecting the number of clusters of individuals using the software STRUCTURE: a simulation study. Molecular ecology, 14, 2611–20.

Excoffier, L., Smouse, P.E. & Quattro, J.M. (1992) Analysis of Molecular Variance Inferred from Metric Distances among DNA Haplotypes: Application to Human Mitochondrial DNA Restriction Data. Genetics, 131, 479–491.

Fraser, C.I., Hay, C.H., Spencer, H.G. & Waters, J.M. (2009) Genetic and Morphological Analyses of the Southern Bull Kelp Durvillaea Antarctica (Phaeophyceae: Durvillaeales) in New Zealand Reveal Cryptic Species. Journal of Phycology, 45, 436–443.

Fraser, C.I., Nikula, R. & Waters, J.M. (2011) Oceanic rafting by a coastal community. Proceedings of the Royal Society B: Biological Sciences, 278, 649–655.

Garcia-Ramos, G. & Kirkpatrick, M. (1997) Genetic models of adaptation and gene flow in peripheral populations. Evolution, 51, 21–28.

Garza, J.C. & Williamson, E.G., (2001) Detection of reduction in population size using data from microsatellite loci. Molecular Ecology, 10, 305–318.

Garza, J.C. (2006) Critical M. http://swfsc.noaa.gov/textblock.aspx?Division=FED&id=3298 (Consulted on Jan 2013)

Gaylord, B., Reed, D.C., Raimondi, P.T. & Washburn, L. (2006) Macroalgal spore dispersal in coastal environments: mechanistic insights revealed by theory and experiment. Ecological Monographs, 76, 481–502.

Glynn, P.W. (1996) Coral reef bleaching: facts, hypotheses and implications. Global Change Biology, 2, 495–509.

Gonçalves, J.M.S., Bispo, J. & Silva, J.A. (2004) Underwater survey of ichthyofauna of eastern Atlantic seamounts : Gettysburg and Ormond (Gorringe Bank). Archive of Fishery and Marine Research, 51, 233–240.

Goudet, J (2001) FSTAT, a program to estimate and test gene diversities and fixation indices (version 2.9.3). Available: http://www.unilch/izea/softwares/fstat.html. Accessed 2012 Dez 10.

Graham, M.H., Kinlan, B.P., Druehl, L.D., Garske, L.E. & Banks, S. (2007) Deep-water kelp refugia as potential hotspots of tropical marine diversity and productivity. Proceedings of the National Academy of Sciences of the United States of America, 104, 16576–16580.

Hampe, A. & Petit, R.J. (2005) Conserving biodiversity under climate change: the rear edge matters. Ecology letters, 8, 461–7.

Helmuth, B., Harley, C.D.G., Halpin, P.M., O'Donnell, M., Hofmann, G.E. & Blanchette, C.A. (2002) Climate change and latitudinal patterns of intertidal thermal stress. Science, 298, 1015–1017.

Helmuth, B., Kingsolver, J.G. & Carrington, E. (2005) Biophysics, physiological ecology, and climate change: does mechanism matter? Annual review of physiology, 67, 177–201.

Helmuth, B., Veit, R.R. & Holberton, R. (1994) Long-distance dispersal of a subantarctic brooding bivalve (Gaimardia trapesina) by kelp-rafting. Marine Biology, 120, 421–426.

Hoarau, G., Coyer, J.A., Stam, W.T. & Olsen, J.L. (2006) A fast and inexpensive DNA extraction/purification protocol for brown macroalgae. Molecular Ecology Notes, 7, 191–193.

Hock, Z., Szövényi, P., Schneller, J.J., Tóth, Z. & Urmi, E. (2008) Bryophyte diaspore bank: a genetic memory? Genetic structure and genetic diversity of surface populations and diaspore bank in the liverwort Mannia fragrans (Aytoniaceae). American Journal of Botany, 95, 542–548.

Hoffmann, A.A. & Blows, M.W. (1994) Species borders: ecological and evolutionary perspectives. Trends in Ecology & Evolution, 9, 223–227.

Hoffmann, A.J. & Santelices, B. (1991) Banks of algal microscopic forms: hypotheses on their functioning and comparisons with seed banks. Marine Ecology Progress Series, 79, 185–194.

Jump, A.S. & Woodward, F.I. (2003) Seed production and population density decline approaching the range-edge of Cirsium species. New Phytologist, 160, 349–358.

Keller, L. & Waller, D. (2002) Inbreeding effects in wild populations. Trends in Ecology & Evolution, 17, 19–23.

Langella, O. (1999) POPULATIONS 1.2.30 Population genetic software. Available: http://bioinformatics.org/*tryphon/populations/. Accessed 2012 Dez 10.

Lawton, J.H. (1993) Range, population abundance and conservation. Trends in ecology & evolution, 8, 409–13.

Lesica, P. & Allendorf, F.W. (1995) When Are Peripheral Populations Valuable for Conservation? Conservation Biology, 9, 753–760.

Letters, E., Sagarin, R.D. & Gaines, S.D. (2002) The “abundant centre” distribution: to what extent is it a biogeographical rule? Ecology Letters, 5, 137–147.

Lima, F.P., Ribeiro, P.A., Queiroz, N., Hawkins, S.J. & Santos, A.M. (2007) Do distributional shifts of northern and southern species of algae match the warming pattern? Global Change Biology, 13, 2592–2604.

Luikart, G., Cornuetm J.M. (1998) Empirical evaluation of a test for identifying recently bottlenecked populations from allele frequency data. Conservational Biology, 12, 228-237.

Mandák, B., Bímová, K., Pyšek, P., Štěpánek, J. & Plačková, I. (2005) Isoenzyme diversity in Reynoutria (Polygonaceae) taxa: escape from sterility by hybridization. Plant Systematics and Evolution, 253, 219–230.

Meirmans, P.G. & Van Tienderen, P.H. (2004) Genotype and Genodive: Two Programs for the Analysis of Genetic Diversity of Asexual Organisms. Molecular Ecology Notes, 4, 792–794.

Muth, A.F. (2012) Effects of Zoospore Aggregation and Substrate Rugosity on Kelp Recruitment Success. Journal of Phycology, n/a–n/a.

Neiva, J., Pearson, G. a., Valero, M. & Serrão, E. a. (2012a) Drifting fronds and drifting alleles: range dynamics, local dispersal and habitat isolation shape the population structure of the estuarine seaweed Fucus ceranoides. Journal of Biogeography, 39, 1167–1178.

Neiva, J., Pearson, G.A., Valero, M. & Serrão, E.A. (2012b) Fine-scale genetic breaks driven by historical range dynamics and ongoing density-barrier effects in the estuarine seaweed Fucus ceranoides L. BMC Evolutionary Biology, 12, 78.

Neiva, J., Pearson, G.A., Valero, M. & Serrão, E.A. (2010) Surfing the wave on a borrowed board: range expansion and spread of introgressed organellar genomes in the seaweed Fucus ceranoides L. Molecular Ecology, 19, 4812–4822.

Neushul, M. (1983) An overview of basic research on kelp and the kelp forest ecosystem. W Bascom. The Effects of Waste Disposal on Kelp Communities (ed. by Univ Calif Inst Mar Res), pp. 282–300. San Diego.

Newman, D. & Pilson, D. (1997) Increased probability of extinction due to decreased genetic effective population size: experimental populations of Clarkia pulchella. Evolution, 51, 354–362.

Nicastro, K.R., Zardi, G.I., Teixeira, S., Neiva, J., Serrão, E. a & Pearson, G. a (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.

Norton, T.A. (1978) The factors influencing the distribution of Saccorhiza polyschides in the region of Lough Ine. Journal of the Marine Biological Association of the United Kingdom, 58, 527–536.

Oliveira, P.B., Nolasco, R., Dubert, J., Moita, T. & Peliz, Á. (2009) Surface temperature, chlorophyll and advection patterns during a summer upwelling event off central Portugal. Continental Shelf Research, 29, 759–774.

Piry, S., Luikart, G., Cornuet, J.M. (1999) Bottleneck: a computer program for detecting recent reductions in the effective population size using allele frequency data. Journal of Heredity, 90, 502-503.

Van Oosterhout, C., Hutchinson, W.F., Wills, D.P.M. & Shipley, P. (2004) Micro-Checker: Software for Identifying and Correcting Genotyping Errors in Microsatellite Data. Molecular Ecology Notes, 4, 535–538.

Palmer, M.A., Hakenkamp, C.C. & Nelson-baker, K. Ecological heterogeneity in streams : why variance matters.

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

Pearson, G.A., 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. Journal of Ecology, 97, 450–462.

Pereira, S.G., Lima, F.P., Queiroz, N.C., Ribeiro, P.A. & Santos, A.M. (2006) Biogeographic Patterns of Intertidal Macroinvertebrates and their Association with Macroalgae Distribution along the Portuguese Coast. Hydrobiologia, 555, 185–192.

Pereira, T. & Engelen, A. (2011) Temperature effects on the microscopic haploid stage development of Laminaria ochroleuca and Sacchoriza polyschides, kelps with contrasting life histories. CBM-Cahiers de Biologie, 52, 395–403.

Pritchard, J.K., Stephens, M. & Donnelly, P. (2000) Inference of population structure using multilocus genotype data. Genetics, 155, 945–959.

Pujol, B. & Pannell, J.R. (2008) Reduced responses to selection after species range expansion. Science, 321, 96.

R Development Core Team (2013) R: A Language and Environment for Statistical Computing.

Reed, D.C. (1990) The effects of variable settlement and early competition on patterns of kelp recruitment. Ecology, 71, 776-787.

Reed, D.C., Kinlan, B.P., Raimondi, P.T., Washburn, L., Gaylord, B., Drake, P.T., Jacob, P.K. & Peter, F.S. (2006) A metapopulation perspective on patch dynamics and connectivity of giant kelp. Marine Metapopulations (ed. by J.P. Kritzer Sale Pf), pp. 353–386. Academic Press, San Diego.

Riegl, B. & Piller, W.E. (2003) Possible refugia for reefs in times of environmental stress. International Journal of Earth Sciences, 92, 520–531.

Rogell, B., Thörngren, H., Laurila, A. & Höglund, J. (2010) Fitness costs associated with low genetic variation are reduced in a harsher environment in amphibian island populations. Conservation Genetics, 11, 489–496.

Rosenberg, N.A. (2003) Distruct: a Program for the Graphical Display of Population Structure. Molecular Ecology Notes, 4, 137–138.

Rousset, F. (1997) Genetic Differentiation and Estimation of Gene Flow from FStatistics Under Isolation by Distance. Genetics, 1228, 1219–1228.

Rousset, F. (2000) Genetic differentiation between individuals. Journal of Evolutionary Biology, 13, 58–62.

Sagarin, R.D., Gaines, S.D. & Gaylord, B. (2006) Moving beyond assumptions to understand abundance distributions across the ranges of species. Trends in ecology evolution, 21, 524–30.

Santos, R. (1993) A multivariate study of biotic and abiotic relationships in a subtidal algal stand. Marine Ecology Progress Series, 94, 181–190.

Schiel, D.R. & Foster, M.S. (2006) The Population Biology of Large Brown Seaweeds: Ecological Consequences of Multiphase Life Histories in Dynamic Coastal Environments. Annual Review of Ecology Evolution and Systematics, 37, 343–372.

Sorte, C. & Hofmann, G. (2004) Changes in latitudes, changes in aptitudes: Nucella canaliculata (Mollusca: Gastropoda) is more stressed at its range edge. Marine Ecology Progress Series, 274, 263–268.

Tellier, F., Meynard, A.P., Correa, J. a, Faugeron, S. & Valero, M. (2009) Phylogeographic analyses of the 30 degrees S south-east Pacific biogeographic transition zone establish the occurrence of a sharp genetic discontinuity in the kelp Lessonia nigrescens: vicariance or parapatry? Molecular phylogenetics and evolution, 53, 679–93.

Tellier, F., Tapia, J., Faugeron, S., Destombe, C. & Valero, M. (2011) the Lessonia Nigrescens Species Complex (Laminariales, Phaeophyceae) Shows Strict Parapatry and Complete Reproductive Isolation in a Secondary Contact Zone1. Journal of Phycology, 47, 894–903.

Toonen, R.J. & Hughes, S. (2001) Increased throughput for fragment analysis on an ABI PRISM 377 automated sequencer using a membrane comb and STRand software. Biotechniques, 31, 1320–1324.

Valero, M., Destombe, C., Mauger, S., Ribout, C., Engel, C.R., Daguin-thiebaut, C. & Tellier, F. (2011) Using genetic tools for sustainable management of kelps: a literature review and the example of Laminaria digitata. Cahiers de Biologie Marine, 52, 467–483.

Version, U., Articles, C. & Mantel, N. (1967) The detection of disease clustering and a generalized regression approach. Cancer Research, 27, 209–220.

Vucetich, J.A.J. & Waite, T.A.T. (2003) Spatial patterns of demography and genetic processes across the species' range: Null hypotheses for landscape conservation genetics. Conservation Genetics, 4, 639 – 645.

Walser, B. & Haag, C.R. (2012) Strong intraspecific variation in genetic diversity and genetic differentiation in Daphnia magna: the effects of population turnover and population size. Molecular ecology, 21, 851–61.

Weir, B.S. & Cockerham, C.C. (1984) Estimating F-statistics for the analysis of population structure. Evolution, 38, 1358–1370.

Williams, C.K., Ives, A.R., Applegate, R.D., Illiams, C.H.K.W. & Ves, A.N.R.I. (2003) Population dynamics across geographical ranges: time-series analyses of three small game species. Ecology, 84, 2654–2667.

Yakimowski, S.B. & Eckert, C.G. (2008) Populations do not become less genetically diverse or more differentiated towards the northern limit of the geographical range in clonal Vaccinium stamineum (Ericaceae). The New phytologist, 180, 534–44.

Young, A., Boyle, T. & Brown, T. (1996) The population genetic consequences of habitat fragmentation for plants. Trends in Ecology & Evolution, 11, 413–418.

Zuur, A.F., Ieno, E.N., Walker, N., Saveliev, A.A. & Smith, G.M. (2009) Mixed effects models and extensions in ecology with R, Springer New York, New York, NY.

SUPPORTING INFORMATION

Appendix S1. Number, name, latitude (LAT) and longitude (LON) of site. Records of presence and absence of *S. polyschides* for sampling years 2008 and 2010. Mean density records for the 2010 survey.

Cell 25km	Cell 5km	Location	Site	LAT	LON	2008 P	2010 P	2010 D (Ind/m^2)
1	1	Vila Praia de Ancora	1	41,82	-8,87	1	1	24,83
1	2	Afife	2	41,78	-8,87	1	1	19,58
1	3	Carreço	3	41,74	-8,87	1	1	18,75
1	4	Viana do Castelo	4	41,69	-8,85	1	1	15,92
1	5	Praia Amorosa	5	41,64	-8,82	1	1	16,25
2	1	Belinho	6	41,59	-8,80	1	1	14,67
2	2	Cepaes	7	41,55	-8,79	1	1	12,33
2	3	Ofir	8	41,51	-8,78	1	1	-
2	4	Rio Alto	9	41,46	-8,77	1	1	15,83
2	5	Estela	-	41,45	-8,77	0	0	-
3	1	A ver o Mar	10	41,39	-8,78	1	1	22,75
3	2	Póvoa	-	41,37	-8,76	0	0	-
3	3	Vila do Conde	-	41,32	-8,73	0	0	-
3	4	Angueiras	-	41,26	-8,72	0	0	-
3	5	Leca da Palmeira	11	41,20	-8,71	1	1	9,33
4	-	Granja	12	41,03	-8,65	1	1	6,33
5	-	Paramos	-	40,97	-8,65	0	0	-
5	-	Esmoriz	-	40,95	-8,65	0	0	-
5	-	Furadouro	-	40,87	-8,67	0	0	-
6	-	Aveiro	13	40,64	-8,76	1	1	5,42
7	-	Vagos	-	40,50	-8,79	0	0	-
7	-	Mira	-	40,44	-8,81	0	0	-
7	-	Tocha	-	40,31	-8,85	0	0	-
8	-	Figueira da Foz	14	40,16	-8,88	1	1	4,17
9	-	Costa de Lavos	-	40,08	-8,87	0	0	-
9	-	Leirosa	-	40,05	-8,89	0	0	-
9	-	Alhais	-	40,00	-8,91	0	0	-
10	-	Praia da Vieira	-	39,87	-8,97	0	0	-
10	-	Valeiras	-	39,74	-9,03	0	0	-
10	-	Pedra d'Ouro	-	39,72	-9,04	0	0	-
11	-	Nazaré	-	39,60	-9,08	0	0	-
11	-	São Martinho	-	39,51	-9,14	0	0	-
11	-	Foz do Arelho	-	39,43	-9,23	0	0	-
12	-	Consolacão	15	39,32	-9,35	1	1	5,33
13	-	Praia Formosa	16	39,13	-9,38	1	1	6,58
14	-	Ribeira de Ilhas	17	38,98	-9,42	1	1	6,83
15	-	Cabo Raso		38,70	-9,48	0	0	-
15	-	Boca do inferno		38,69	-9,43	1	0	-
15	-	Parede		38,68	-9,36	0	0	-
16	-	Caxias		38,69	-9,27	0	0	-
16	-	Costa da caparica		38,64	-9,23	0	0	-
16	-	Lagoa de Albufeira		38,51	-9,18	0	0	-
17	-	Cabo Espichel		38,41	-9,21	0	0	-
17	-	Sesimbra		38,43	-9,09	0	0	-
17	-	Cabo Afonço		38,44	-9,04	0	0	-
18	-	Portinho da Arrábida		38,47	-8,97	0	0	-
18	-	Troia		38,46	-8,88	0	0	-
18	-	Pego		38,29	-8,78	0	0	-
19	-	Aberta Nova		38,17	-8,78	0	0	-
19	-	Santo André		38,10	-8,80	0	0	-
19	-	Santo André (Sul)		38,08	-8,80	0	0	-
20	-	Praia do Norte		37,96	-8,87	0	0	-
20	-	Sines		37,95	-8,88	0	0	-
20	-	São Torpes		37,91	-8,80	0	0	-
21	-	Porto Covo		37,84	-8,79	0	0	-
21	-	Ilha do Pessegueiro		37,83	-8,79	0	0	-
21	-	Praia do Malhão		37,78	-8,80	0	0	-
22	1	Almograve		37,65	-8,80	0	0	-
22	2	Cavaleiro		37,59	-8,81	0	0	-

Cell 25km	Cell 5km	Location	Site	LAT	LON	2008 P	2010 P	2010 D (Ind/m^2)
22	3	Porto das Barcas	18	37,54	-8,79	0	1	1,50
22	4	Zambujeira		37,52	-8,78	0	0	-
22	5	Carvalhal		37,49	-8,79	0	0	-
23	1	Asseiceira		37,46	-8,80	0	0	-
23	2	Odeceixe	19	37,44	-8,80	0	1	2,17
23	3	Alzejur (Norte)	20	37,32	-8,87	1	1	3,22
23	4	Alzejur (Arrifana)	21	37,29	-8,87	1	1	2,83
23	5	Alzejur (Arrifana Sul)	22	37,29	-8,86	1	1	3,33
24	1	Praia de Vale		37,24	-8,87	0	0	-
24	2	Carrapateira	23	37,16	-8,91	0	1	1,92
24	3	Praia da Barriga		37,12	-8,93	0	0	-
24	4	Ponta Ruiva		37,06	-8,97	0	0	-
24	5	Sagres		37,02	-8,99	0	0	-

Appendix S2. Genetic diversity as allelic richness (A) and Nei's gene diversity (HE), per site and loci. Inbreeding coefficients (FIS) per site and per loci and deviations from Hardy–Weinberg equilibrium and for linkage disequilibrium between pairs of loci.

	HE	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**20**	**21**	**22**	**23**
	1E 10	0.613	0.526	0.557	0.516	0.584	0.553	0.58	0.657	0.598	0.643	0.535	0.449	0.529	0.501	0.674	0.603	0.595	0.188	0.404	0.42	0.521	0.324	0.441
	2A4	0.435	0.234	0.671	0.558	0.647	0.584	0.678	0.583	0.442	0.742	0.406	0.57	0.665	0.585	0.463	0.406	0.496	0.9	0.638	0.65	0.667	0.667	0.581
	3A10	0.723	0.713	0.648	0.67	0.744	0.728	0.672	0.647	0.559	0.699	0.679	0.718	0.629	0.657	0.56	0.613	0.583	0.763	0.785	0.811	0.784	0.829	0.82
Loci	**3D12**	0.384	0.421	0.403	0.46	0.407	0.345	0.303	0.381	0.432	0.389	0.612	0.373	0.213	0.459	0.513	0.131	0.328	0.632	0.551	0.538	0.511	0.634	0.399
	1A1(2)	0.66	0.714	0.708	0.696	0.712	0.679	0.679	0.689	0.743	0.634	0.684	0.668	0.652	0.554	0.665	0.604	0.535	0.749	0.789	0.821	0.704	0.696	0.732
	2B3	0.489	0.491	0.556	0.44	0.335	0.583	0.552	0	0.553	0.455	0.372	0.432	0.266	0.501	0.633	0.635	0.572	0.432	0.56	0.753	0.711	0.577	0.493
	2F7	0.57	0.607	0.52	0.542	0.547	0.451	0.509	0.474	0.564	0.558	0.535	0.566	0.592	0.498	0.539	0.533	0.542	0.575	0.5	0.575	0.536	0.569	0.601
	A	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**20**	**21**	**22**	**23**
	1E 10	3.024	2.652	2.611	2.736	2.78	2.498	2.757	3.399	2.945	3.331	2.483	2.608	2.65	1.999	2.947	2.926	2.851	1.861	2.103	2.15	2.721	2.16	2.421
	2A4	2.595	1.997	4.116	3.261	3.596	3.686	3.949	2.669	2.991	4.117	2.975	3.266	3.571	3.041	2.906	2.617	3.266	4	3.066	3.572	2.978	3.107	2.507
	3A10	3.965	3.863	3.317	3.578	4.169	3.861	3.425	3.255	2.824	3.833	3.58	3.626	3.089	3.335	3.343	3.575	3.244	4.569	4.712	4.924	4.707	5.221	5.194
Loci	**3D12**	2.904	2.792	2.388	2.84	2.532	2.406	1.891	2.318	2.673	2.505	3.141	2.52	1.849	2.784	3.348	1.541	2.293	3.044	3.311	3.518	3.343	3.808	2.739
	1A1(2)	3.082	3.76	3.762	3.899	3.57	3.355	3.307	3.55	4.056	3.055	3.411	3.326	3.048	2.967	3.96	4.092	3.136	4.541	5.394	5.593	4.577	4.685	4.765
	2B3	2.483	2.16	2.733	2.155	2.39	3.055	2.498	1	2.749	1.99	2.353	2.144	2.066	2.196	2.944	3.164	2.583	2.378	2.837	5.197	4.224	2.607	2.702
	2F7	2.632	2.942	2.171	2.316	2.438	2.296	1.999	1.996	2.639	2.426	2.191	2.613	2.723	1.998	2.6	2.305	2.316	2.674	2.146	2.61	2.698	2.62	2.926
	Fis	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**20**	**21**	**22**	**23**
	1E 10	0.129	-0.141	-0.077	-0.099	-0.313	-0.024	0.081	-0.054	0.052	0.015	0.227	-0.04	0.243	-0.238	0.555	0.143	0.048	-0.064	0.199	0.207	0.503	0.042	0.471
	2A4	0.425	0.643	0.369	0.68	0.287	0.366	0.717	0	0.33	0.501	0.121	0.561	0.436	0.474	0.52	0.211	0.702	1	0.804	1	0.786	0.906	1
	3A10	0.308	0.033	0.074	0.204	0.193	-0.053	0.008	-0.307	-0.014	0.142	0.34	0.026	-0.136	0.055	0.048	0.268	-0.03	0.039	0.101	-0.068	0.117	-0.006	-0.057
Loci	**3D12**	0.22	0.05	0.091	0.275	-0.227	-0.16	-0.208	-0.21	-0.236	-0.028	0.211	0.196	-0.097	0.129	0.026	-0.057	-0.158	0.05	0.063	0.071	0.103	-0.218	0.165
	1A1(2)	-0.111	0.227	0.041	0.01	-0.163	0.034	0.019	0.442	0.057	0.001	0.06	0.003	-0.023	-0.059	0.326	-0.104	-0.031	0.021	0.117	0.087	0.112	0.138	0.057
	2B3	-0.023	-0.221	0.068	-0.137	0.485	0.171	-0.388	NA	-0.206	-0.177	0.247	0.123	0.166	-0.438	0.436	0.395	0.636	0.201	0.692	0.478	0.297	0.635	0.517
	2F7	0.092	-0.044	0.137	0.045	0.543	0.129	0.149	0.189	-0.36	0.283	0.641	-0.12	0.822	-0.178	0.424	0.124	0.301	0.073	0.516	0.16	0.004	0.212	0.197
	Per population	0.139	0.04	0.105	0.145	0.1	0.073	0.088	0.023	-0.053	0.133	0.263	0.101	0.234	-0.023	0.34	0.165	0.224	0.258	0.342	0.272	0.276	0.246	0.301
	P-value for Fis per population		Adjusted P-value for 5% nominal level is: 0.00031																					
	P-value	0.004	0.2109	0.018	0.0016	0.0354	0.0761	0.0543	0.4127	0.8596	0.005	0.0013	0.0236	0.0006	0.6503	0.0003	0.0025	0.0003	0.0006	0.0003	0.0003	0.0003	0.0003	0.0003

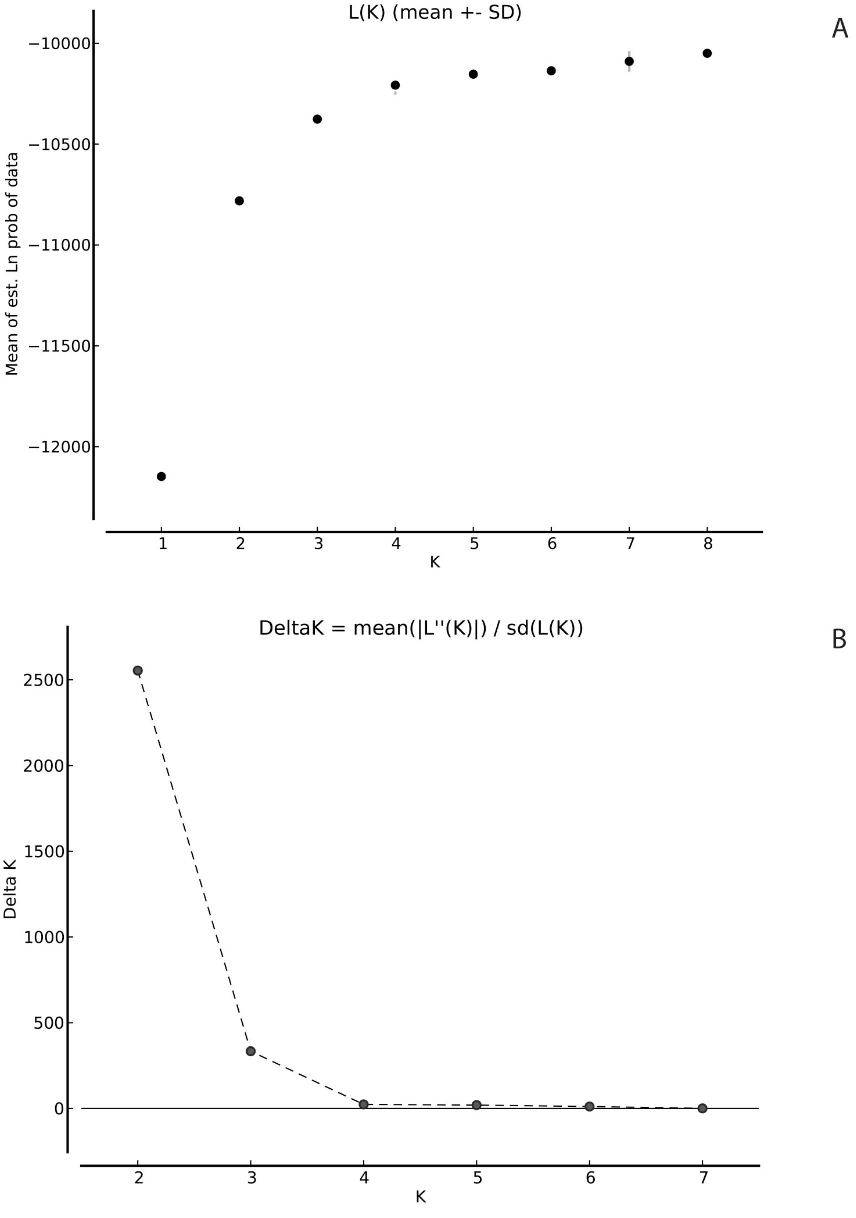
P-value for genotypic disequilibrium	
Adjusted P-value:	0.002381
Loci pairs	P-value
1E10 X 2A4	0.02143
1E10 X 3A10	0.1381
1E10 X 3D12	0.00338
1E10 X 1A1(2)	0.4619
1E10 X 2B3	0.75714
1E10 X 2F7	0.08333
2A4 X 3A10	0.08095
2A4 X 3D12	0.4
2A4 X 1A1(2)	0.02857
2A4 X 2B3	0.11429
2A4 X 2F7	0.0619
3A10 X 3D12	0.00714
3A10 X 1A1(2)	0.01667
3A10 X 2B3	0.8119
3A10 X 2F7	0.09048
3D12 X 1A1(2)	0.46667
3D12 X 2B3	0.13095
3D12 X 2F7	0.02857
1A1(2) X 2B3	0.68571
1A1(2) X 2F7	0.0619
2B3 X 2F7	0.05952

Appendix S3. Pairwise FST between sites. Hierarchical analysis of molecular variance (AMOVA) under 999 permutations with 3 hierarchical levels.

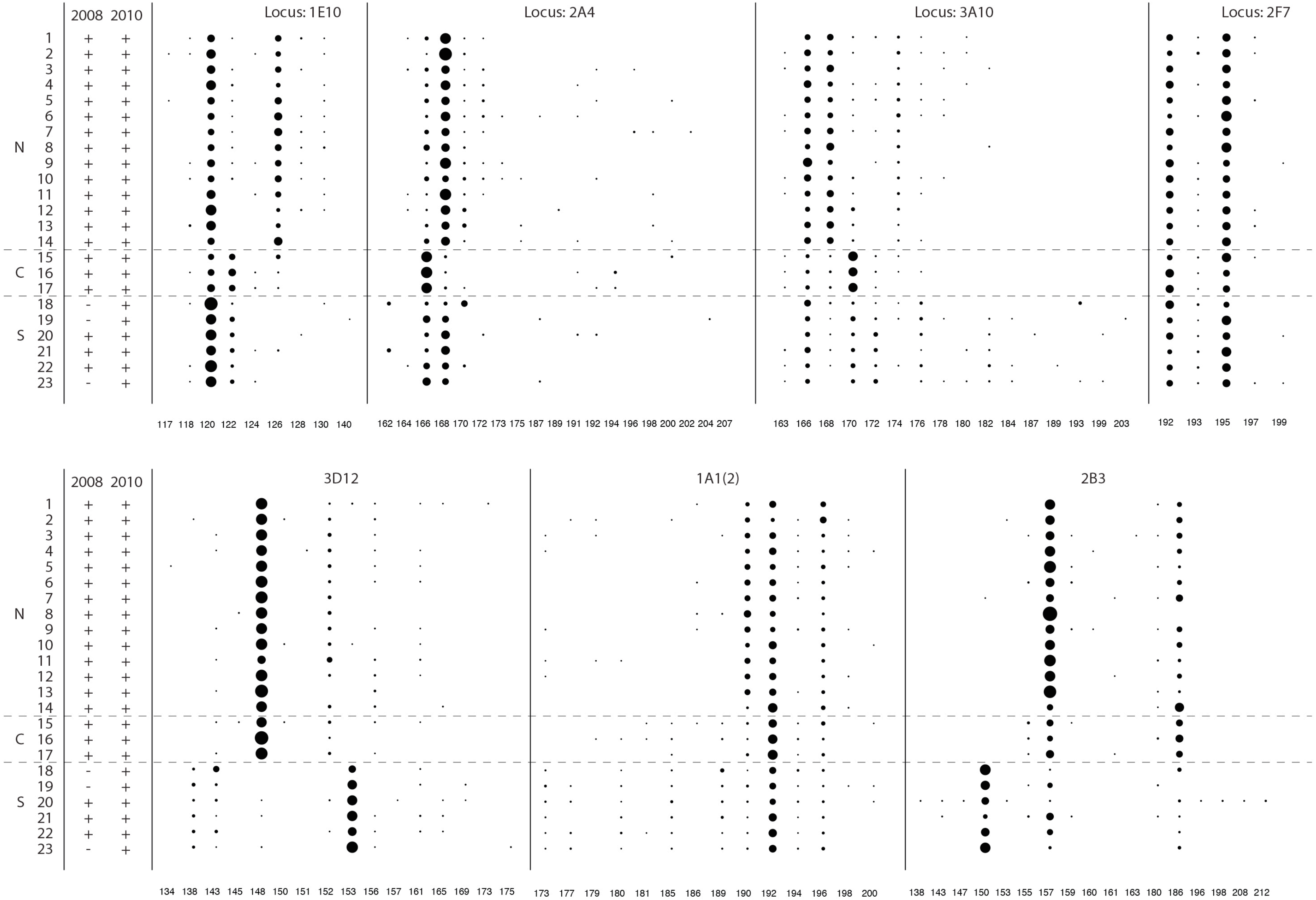
		North														Center			South					
	Fst	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**20**	**21**	**22**	**23**
North	**1**	0	0.009	-0.001	0.003	0.003	0.004	0.007	0.03	0.01	0.007	0.013	0.012	0.017	0.025	0.141	0.186	0.148	0.265	0.215	0.201	0.162	0.196	0.239
	2	0.009	0	0.025	0.022	0.032	0.025	0.04	0.075	0.013	0.048	0.026	0.025	0.048	0.066	0.191	0.246	0.205	0.282	0.241	0.216	0.188	0.22	0.267
	3	-0.001	0.025	0	-0.001	0.004	0.002	-0.007	0.025	0.009	0	0.011	0.011	0.02	0.018	0.127	0.168	0.132	0.24	0.208	0.194	0.164	0.19	0.232
	4	0.003	0.022	-0.001	0	0.008	0.02	0.017	0.036	0.002	0.005	0.005	0.003	0.014	0.043	0.141	0.174	0.131	0.231	0.197	0.185	0.148	0.176	0.227
	5	0.003	0.032	0.004	0.008	0	0.002	0.016	-0.006	0.019	0.005	0.011	0.024	0.012	0.058	0.133	0.191	0.146	0.269	0.212	0.213	0.165	0.199	0.248
	6	0.004	0.025	0.002	0.02	0.002	0	0.006	0.026	0.02	0.015	0.026	0.028	0.033	0.035	0.144	0.203	0.168	0.277	0.227	0.218	0.177	0.214	0.258
	7	0.007	0.04	-0.007	0.017	0.016	0.006	0	0.045	0.012	-0.002	0.036	0.036	0.043	0.008	0.123	0.161	0.134	0.256	0.23	0.213	0.189	0.216	0.248
	8	0.03	0.075	0.025	0.036	-0.006	0.026	0.045	0	0.06	0.031	0.022	0.043	0.014	0.106	0.166	0.234	0.182	0.315	0.238	0.253	0.199	0.233	0.289
	9	0.01	0.013	0.009	0.002	0.019	0.02	0.012	0.06	0	0.017	0.016	0.029	0.04	0.046	0.174	0.214	0.178	0.255	0.228	0.204	0.181	0.213	0.254
	10	0.007	0.048	0	0.005	0.005	0.015	-0.002	0.031	0.017	0	0.032	0.025	0.021	0.019	0.097	0.134	0.097	0.23	0.206	0.2	0.161	0.186	0.229
	11	0.013	0.026	0.011	0.005	0.011	0.026	0.036	0.022	0.016	0.032	0	0.015	0.028	0.068	0.187	0.241	0.19	0.264	0.216	0.203	0.161	0.194	0.253
	12	0.012	0.025	0.011	0.003	0.024	0.028	0.036	0.043	0.029	0.025	0.015	0	0.001	0.062	0.15	0.187	0.14	0.243	0.215	0.205	0.167	0.187	0.247
	13	0.017	0.048	0.02	0.014	0.012	0.033	0.043	0.014	0.04	0.021	0.028	0.001	0	0.083	0.167	0.206	0.157	0.272	0.238	0.241	0.19	0.217	0.276
	14	0.025	0.066	0.018	0.043	0.058	0.035	0.008	0.106	0.046	0.019	0.068	0.062	0.083	0	0.116	0.159	0.134	0.255	0.231	0.211	0.188	0.21	0.243
Center	**15**	0.141	0.191	0.127	0.141	0.133	0.144	0.123	0.166	0.174	0.097	0.187	0.15	0.167	0.116	0	0.017	0.003	0.261	0.186	0.206	0.181	0.182	0.206
	16	0.186	0.246	0.168	0.174	0.191	0.203	0.161	0.234	0.214	0.134	0.241	0.187	0.206	0.159	0.017	0	-0.004	0.294	0.234	0.244	0.241	0.233	0.247
	17	0.148	0.205	0.132	0.131	0.146	0.168	0.134	0.182	0.178	0.097	0.19	0.14	0.157	0.134	0.003	-0.004	0	0.265	0.202	0.22	0.201	0.193	0.223
South	**18**	0.265	0.282	0.24	0.231	0.269	0.277	0.256	0.315	0.255	0.23	0.264	0.243	0.272	0.255	0.261	0.294	0.265	0	0.07	0.051	0.096	0.042	0.066
	19	0.215	0.241	0.208	0.197	0.212	0.227	0.23	0.238	0.228	0.206	0.216	0.215	0.238	0.231	0.186	0.234	0.202	0.07	0	0.011	0.018	-0.008	0.001
	20	0.201	0.216	0.194	0.185	0.213	0.218	0.213	0.253	0.204	0.2	0.203	0.205	0.241	0.211	0.206	0.244	0.22	0.051	0.011	0	0.018	0.009	0.003
	21	0.162	0.188	0.164	0.148	0.165	0.177	0.189	0.199	0.181	0.161	0.161	0.167	0.19	0.188	0.181	0.241	0.201	0.096	0.018	0.018	0	0.01	0.036
	22	0.196	0.22	0.19	0.176	0.199	0.214	0.216	0.233	0.213	0.186	0.194	0.187	0.217	0.21	0.182	0.233	0.193	0.042	-0.008	0.009	0.01	0	0.002
	23	0.239	0.267	0.232	0.227	0.248	0.258	0.248	0.289	0.254	0.229	0.253	0.247	0.276	0.243	0.206	0.247	0.223	0.066	0.001	0.003	0.036	0.002	0

AMOVA table				
Source	**Nested**	**SSD**	**F**	**p**
Among Individual	Sites	1484.811	0.137	0.001
Among Sites	Clusters	93.977	0.02	0.001
Among Clusters	--	310.642	0.164	0.001

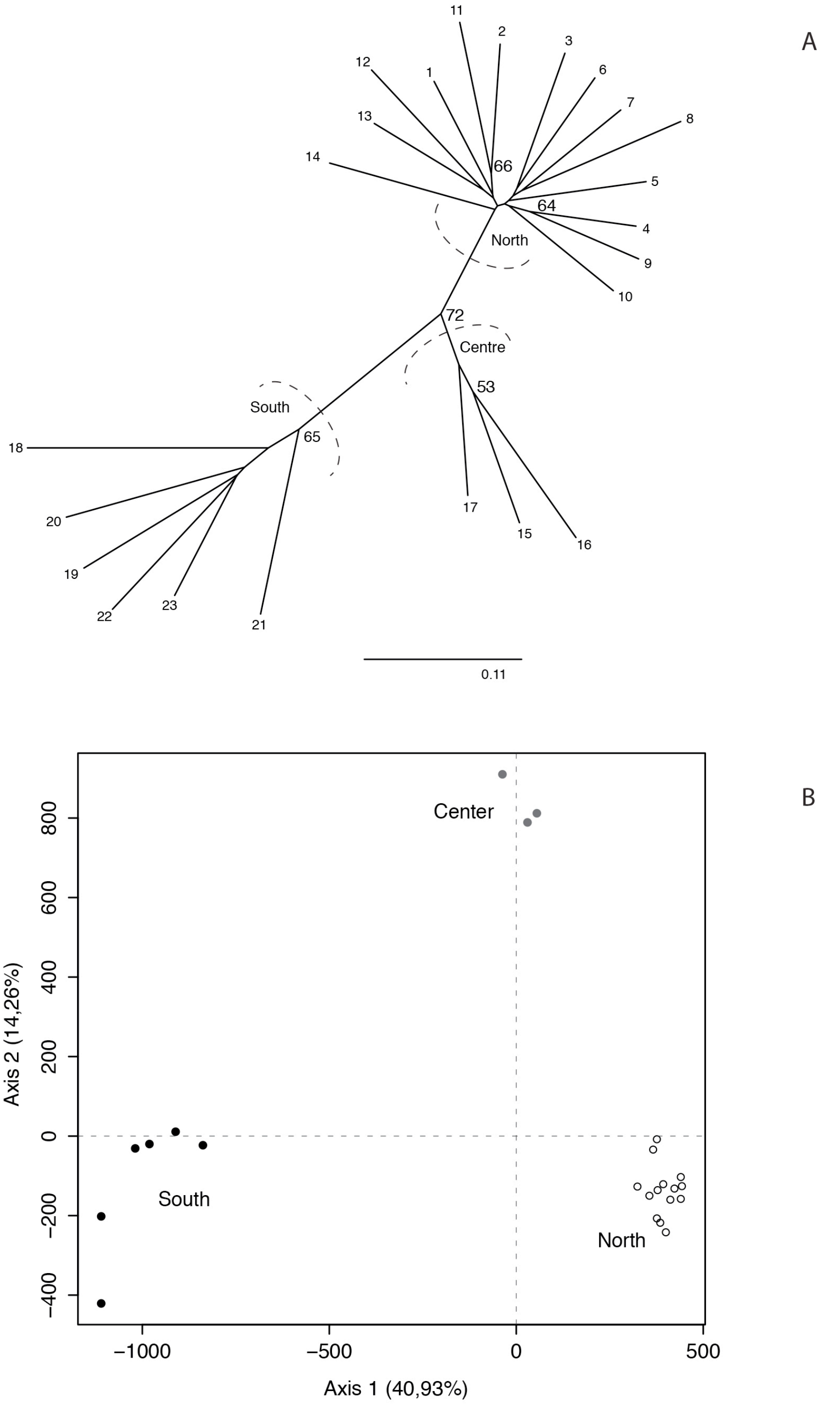
Appendix S4. Estimation of the most probable number of groups (K) based on Bayesian clustering for K = 1 to 8 and 25 runs each (STRUCTURE). (A) Mean log-likelihood of the data per K, i.e., standard output from Structure. (B) Mean absolute difference of the second order rate of change with respect to K (Pritchard et al., 2000).



Appendix S5. Allele frequencies for each locus represented by dots of varying diameter. Allele sizes are indicated on the x axis and sites on the y axis. Presence (+) and absence (-) of *S. polyschides* per site for the 2008 and 2010 surveys.



Appendix S6. Genetic differentiation of *S. polyschides* ilustrated by a (A) neighbour-joining network of genotypes using Cavalli-Sforza & Edwards (Belkhir et al., 2004) pairwise distances. Numbers above the branches are Bayesian posterior probabilities (> 0.50). Inferred groups are divided by dotted lines; and by (B) a Factorial Correspondence Analysis of population multiscores.



Appendix S7. Inference of bottleneck for each sampling site using the Wilcoxon test for heterozygosity excess over all loci and M-ratio method. Site number, number of samples per site (n), Wilcoxon test probability (one tail; Wp), Critical MC value, M-ratio (M) and the probability of a smaller M Ratio under equilibrium (Mp).

Site	n		Wp	Mc	M	Mp
1	30		0.96094	0.659998	0.774922	0.00560000000000002
2	30		0.98047	0.659998	0.783301	0.2656
3	30		0.98047	0.659998	0.682986	0.5456
4	30		0.97266	0.659998	0.675183	0.0574
5	30		0.8125	0.659998	0.667347	0.0075
6	30		0.8125	0.659998	0.771651	0.00359999999999999
7	30		0.53125	0.659998	0.733083	0.0856
8	16		0.28125	0.594372	0.837302	0.00560000000000002
9	30		0.98828	0.659998	0.774542	0.1156
10	30		0.59375	0.659998	0.752041	0.7856
11	30		0.97266	0.659998	0.778571	0.00790000000000006
12	30		0.59375	0.659998	0.720094	0.0779999999999999
13	30		0.46875	0.659998	0.665146	0.2729
14	30		0.23438	0.659998	0.687202	0.00560000000000002
15	30		0.94531	0.659998	0.731973	0.000900000000000034
16	30		0.96094	0.659998	0.811905	0.000100000000000051
17	30		0.94531	0.659998	0.777211	0.5809
18	30		0.28906	0.659998	0.677046	0.000100000000000051
19	30		0.76563	0.681872	0.549608	0.000799999999999983
20	30		0.94531	0.659998	0.661641	0.000100000000000051
21	30		0.85156	0.659998	0.640693	0.00560000000000002
22	30		0.97266	0.659998	0.815073	0.000600000000000023
23	30		0.65625	0.659998	0.617908	0.000100000000000051

CHAPTER V » MTDNA PHYLOGEOGRAPHY AND SPECIES DISTRIBUTION MODELS REVEAL AN EXTENSIVE BIOGEOGRAPHIC SHIFT IN THE HIGH-INTERTIDAL SEAWEED *PELVETIA CANALICULATA*

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ABSTRACT

Evidence suggests that latitudinal range shifts, involving both spatial expansions and trailing-edge contractions, may represent a common response to climatic change in the marine realm. The biogeographical histories of coastal organisms however have been inferred primarily using molecular markers, potentially overlooking past range dynamics beyond contemporary rear edges. We combine mtDNA data and distribution models to investigate marine biogeographic shifts using as a model the high-intertidal seaweed *Pelvetia canaliculata*. We investigate the hypotheses that its distribution is set by both marine and terrestrial variables and that its range has globally shifted northwards since the LGM. The advantages of combining SDM and phylogeographic approaches are also discussed. Individuals belonging to 27 sites covering the extant range of *Pelvetia canaliculata* were sampled and sequenced for a ca. 500 bp mtDNA intergenic spacer. A niche model was developed using marine and terrestrial variables. Range dynamics were reconstructed based on the geographical patterns of genetic variation and on the SDM projections for the LGM and the present. The best distribution models incorporated both marine and terrestrial variables. Projections for the LGM revealed a potential distribution between southern Morocco and the periglacial shorelines of the Celtic Sea. *Pelvetia canaliculata* was subdivided in three largely disjunct lineages, two of them endemic to Iberia. The central / northern European lineage exhibited the highest haplotypic diversity and showed a consistent latitudinal decline in nucleotide diversity and haplotypic richness. Range projections imply an extensive post-glacial poleward expansion concurrently with an important southern contraction, supporting the view that coastal species may track migrating climatic envelops along the shorelines instead of suffering global range contractions/expansions into / from classic refugia. SDM and phylogeographical data supported the long-term presence between NW Iberia and Ireland, and molecular variation further allowed the identification of the sources and putative pathways of colonization. The low variability within Iberian lineages suggested more complex range dynamics that are not captured by projecting distributions for the LGM and the present. Integrating independent SDM and phylogeographic approaches improves inferences regarding the patterns and evolutionary implications of climate-driven marine range shifts.

INTRODUCTION

The bio- and phylogeographical significance of the Pleistocene glacial-interglacial cycles is well recognized in terrestrial systems, where abundant paleontological, archaeological and molecular evidence reveal major changes in the spatial distribution of biomes, ecosystems and individual organisms in response to climatic shifts (Hewitt, 1999, Provan & Bennett, 2008, Hofreiter & Stewart, 2009, Stewart et al., 2010). Phylogeographic evidence from northern (Maggs et al., 2008, Ilves et al., 2010, Marko et al., 2010) and southern (Fraser et al., 2009) cold-temperate shores show that the latitudinal shifts in seawater isotherms and sea-ice extension across the glacial-interglacial cycles also exerted a strong and direct influence on the distribution of coastal species. In the NW Atlantic, the compression of isotherms and the loss of ice-free rocky intertidal substrate led to the regional extirpation of many taxa during the Last Glacial Maximum (LGM, ~21000 KYBP; Ilves et al., 2010, Waltari & Hickerson, 2012). In the NE Atlantic, the ice sheets reached as far south as the British Isles and the dramatic drop in sea level resulted in the complete emersion of several shallow seas, including the North Sea, Baltic Sea, Irish Sea and the English Channel (Ménot et al., 2006). Consequently, the littoral communities currently found in these areas could only colonize them after the LGM, originating from periglacial or more southern glacial refugia (Provan et al., 2005, Hoarau et al., 2007, Remerie et al., 2009, Provan & Maggs, 2012).

The range dynamics of coastal species have been inferred primarily using molecular data, in part because most marine taxonomic groups leave an extremely fragmentary fossil record and because the Holocene transgression has submerged potential fossil deposits from colder periods (when sea levels were lower by as much as 120m; Lambeck & Chappell, 2001). The interpretation of genetic patterns is not always straightforward though. Organisms with high dispersal abilities tend to approach new genetic equilibria relatively fast, so that the genetic signals of past demographic histories and contemporary gene flow can be severely confounded (Pelc et al., 2009). Genetic patterns may also reflect stochastic or selective processes rather than signal relevant biogeographic and demographic events, particularly when assessed using a single marker such as mitochondrial DNA (mtDNA; Ilves et al., 2010, Rato et al., 2011). Since genes can only be sampled from extant populations, even geographically comprehensive multi-locus data-sets will fail to estimate past range dynamics beyond contemporary rear-edges. This inherent limitation of molecular markers is particularly relevant for coastal species because evidence suggests that responses to climatic oscillations in the marine realm often involves range shifts at both distribution margins rather than contractions/expansions into/from classic refugia (Sunday et al., 2012).

A major challenge in marine biogeography is to infer temporal changes in the distribution of organisms in the absence of a fossil record. Species distribution models (SDM) are a useful approach to generate spatially explicit information and can be used to validate and/or complement biogeographic inferences based on molecular markers. SDMs build a mathematical representation of the realized niche of species based on their known distribution in environmental space, allowing predictions of the potential species distributional range across time periods for which empirical or modelled environmental data are available (Elith & Leathwick, 2009). A variety of terrestrial studies have successfully combined phylogeographical and hindcasting SDM data to investigate climate-driven range dynamics (Hugall et al., 2002, Knowles et al., 2007, Waltari et al., 2007, Carnaval et al., 2009, Schorr et al., 2012), but only very recently have the advantages of such integrative approaches been applied in the marine realm (Bigg et al., 2008, Provan & Maggs, 2012, Waltari & Hickerson, 2012).

SDMs are generally based on climatic descriptors (e.g., temperature, precipitation), not only because climate is considered predominant in setting species distributions at coarse (e.g., latitudinal) spatial scales (Breeman, 1990, Pearson & Dawson, 2003, Araújo & Pearson, 2005), but also because these variables often represent the only predictors available for different periods of time (Svenning et al., 2011). SDMs assume that species niches are constant across space and time (i.e., niche conservatism) and that the current species distributions are not severely constrained by historical, geographical, biotic (e.g., competition) or anthropogenic-related factors (i.e., they assume species-climate equilibrium). SDMs are expected to be accurate for organisms with climatically-defined distributional ranges and living in landscapes with steep environmental gradients, so that non-climatic factors (e.g., substrate type, biotic interactions) can be assumed to have negligible effects on predicted distributions at a biogeographical scale (Sinclair et al., 2010). Strictly intertidal seaweeds are good models to infer the effects of past climatic events on species distributional range shifts as they meet the SDM criteria and have particularly good distributional records. Most importantly, seaweeds commonly display strong phylogeographical structures that can be linked to their past range dynamics (Hoarau et al., 2007, Fraser et al., 2009, Coyer et al., 2010, Neiva et al., 2010). In this paper we use an intertidal fucoid seaweed to investigate marine biogeographic shifts along the NE Atlantic by integrating SDM and phylogeographic approaches.

The high-intertidal species *Pelvetia canaliculata* is hypothesized to have experienced important range shifts across the glacial-interglacial cycles, since its modern distribution from Northern Portugal (40ºN Lat.) to European Russia (71ºN Lat; Toxopeus et al., 2011) encompasses both ice-free and previously glaciated regions of the NE Atlantic. At its southern distributional limit in NW Iberia, recent studies have found high levels of genetic diversity and/or endemism for other algae (Neiva et al., 2012b, Provan & Maggs, 2012). Biogeographic distributions of seaweed species have traditionally been linked to ocean sea surface temperature (SST) isotherms, with their range boundaries set by lethal or sub-lethal conditions limiting growth, reproduction or survival (Hoek, 1982, Breeman, 1988, Breeman, 1990, Luning, 1990). For intertidal species subjected to daily immersion – emersion cycles, the terrestrial climate (e.g., air temperature) may play an additional role in setting distributional boundaries (Helmuth et al., 2002, Martinez et al., 2012), but this possibility has seldom been tested.

In this study we develop a SDM for *P. canaliculata* based on marine and terrestrial climatic variables and transfer it for the LGM. We compare range projections with the historical biogeography of *P. canaliculata* inferred from mtDNA data and assess the congruence and complementarity of the two approaches. We hypothesize that the range is 1) set by both marine and terrestrial climate variables, 2) has suffered a northern expansion and southern compression since the LGM, and 3) will exhibit higher genetic diversity where the LGM and modern ranges overlap. Finally, we discuss the usefulness of integrating SDM and phylogeographic data to infer the palaeo-distributions of species in shallow marine environments and the evolutionary consequences of marine range-shifts.

METHODS

MODEL ORGANISM

Pelvetia canaliculata (L.) Decaisne & Thuret (channelled wrack) is a medium-sized (< 16 cm) perennial brown alga and the single extant representative of its genus. It forms, together with Fucus serratus, Ascophyllum nodosum, Himanthalia elongata, Laminaria hyperborea and other kelp/fucoid seaweeds, an endemic cold-temperate seaweed assemblage that typifies the

NE Atlantic shores and that has a southern distributional limit in NW Iberia. *P. canaliculata* is hermaphroditic and restricted to the upper littoral zone where it forms a narrow and often monospecific belt above *Fucus spiralis* in sheltered to semi-exposed rocky shores. This seaweed is particularly tolerant to desiccation and can survive emerged for several days during neap tides. As other fucoid seaweeds, it has direct development and lacks dispersive (planktonic) developmental stages. Fucoid eggs and zygotes disperse only locally, typically less than 5 m from the spawning parent (Chapman, 1995, Pearson & Serrao, 2006). Non-local dispersal is more likely to occur via rafting of detached fragments that retain the capacity to release gametes before senescence (Norton, 1992, McKenzie & Bellgrove, 2008, Neiva et al., 2012a).

OCCURRENCE AND ENVIRONMENTAL DATA

Presence data for *P. canaliculata* was collated from several sources, including field observations from the authors and collaborators, research articles, reports and online databases [the latter mainly for the British Isles, NBN Gateway (http://www.nbn.org.uk/)]. This seaweed is easily identified based on morphology and position on the shore and misidentification is very unlikely. Records were only considered when geographical locations were unequivocal and explicit down to shore/beach level. A variable number of geographically close occurrences were removed from non-marginal regions to ensure a similar record density and spacing throughout the species “core” range, thus reducing the effects of spatial autocorrelation (Beatty & Provan, 2011). The final dataset and references can be obtained from the authors upon request.

Current climatic data were obtained from several databases provided by the National Oceanic and Atmospheric Administration (NOAA/OAR/ESRL PSD, Boulder, Colorado, USA, www.esrl.noaa.gov/psd/). Raw data were summarized in several long-term (1980-2010) monthly mean metrics describing the seasonal range variation of salinity, sea surface temperature (SST), air temperature (AT) and relative air humidity (see Appendix S1 in Supporting Information for selected variables, data sources, references and types of data). Tidal amplitude and estimated intertidal availability (calculated using bathymetric and tidal amplitude data) were also included in the models. The climatic data for the LGM period were derived from two atmospheric circulation models - the Community Climate System Model (CCSM4) and the Model for Interdisciplinary Research on Climate (MIROC5; available from the Earth System Grid Federation, www.esgf.org). Simulated tidal amplitudes were derived from Egbert et al. (2004) and intertidal availability recalculated for -120 m depth. These predictors were gridded by bilinear interpolation to match the distribution data (Carnaval & Moritz, 2008).

SDMS AND LGM PROJECTIONS

Species niche models based on presence/absence data typically outperform those based on presence-data only (Elith et al., 2006). Pseudo-absences were computed with the package Biomod (R Development Core Team, 2012). Presences and pseudo-absences were gridded (0.25º resolution cells) and divided in two independent data sets. The first, for model training, was generated by randomly selecting 70% of the data. The second, for testing model results, was generated with the remaining 30%. Collinearity between predictors can hinder the interpretation of models, particularly if predictors were not correlated in the past (Kivinen et al., 2008). Therefore, highly correlated pairs of predictors were identified using Pearson’s correlation matrices ($R^2 \geq |0.70|$) and discarded (Giovanelli et al., 2010). SDMs were computed with the training data and all the combinations of non-correlated predictors using four methods with high predictive performance: Boosted Regression Trees (BRT; De'ath, 2007)], Maximum Entropy (Maxent; Phillips et al., 2006), Multivariate Adaptive Regression Splines (MARS; Leathwick et al., 2005)] and Generalized Additive Models (GAM; Ferrier et al., 2002), using the packages gbm, dismo, mda and gam (R software), respectively. This iterative approach was performed 50 times for each method, and at each step, pseudo-absences were regenerated along with the randomization of training and testing data. For each model a predictive map was generated and reclassified into a binary presence-absence surface based on a threshold that maximized the sum of sensitivity and specificity (Manel et al., 2001, Thuiller et al., 2009). Model predictions were evaluated in terms of discriminatory power against testing data by the Area Under the receiver-operated characteristic Curve (AUC) and True Skill Statistic (TSS, Allouche et al., 2006).

The sub-set of predictors that were eventually used to project the distribution of *P. canaliculata* in the present and LGM environments were selected as those with the highest mean AUC value per modeling method (Tyberghein et al., 2012), using paired Wilcoxon tests between the mean AUC values of all combinations of predictors (Guisan et al., 2007) under H0: no differences in discriminatory power between subset of predictors. The hindcasted LGM distributions were generated by merging the resulting surfaces of each method with both circulation models as a function of its mean AUC (i.e., Ensemble modeling; Roura-

Pascual et al., 2004, Araújo & New, 2007, Buisson et al., 2010). Therefore, the resulting distribution maps represent those areas predicted with highest discrimination among methods, with consensus for different estimates of climate. These maps were reclassified into probability of occurrence, and glacial ice (for LGM prediction) was added following the reconstruction of Peltier (1994). To evaluate transferability to CCSM4 and MIROC5 model simulations, projections were generated with the current climate conditions driven from remote sensing, and compared using TSS statistics with projections made with the circulation models for the present time (1980-2010).

SAMPLING AND MOLECULAR ANALYSES

Table I. *Pelvetia canaliculata* sampled populations (S: map code; Text: text code), location, number od sampled individuals (n), clade (C), mtIGS haplotype frequencies, number of haplotypes (Nhap), haplotype diversity (H: $H\,(10^{-3})$) and nucleotide diversity (π: $\pi\,(10^{-5})$) for each geographic region and sampling site. PT: Portugal; ES: Spain; FR: France; IE: Ireland; UK: United Kingdom; NL: The Netherlands; DK: Denmark; NO: Norway; IS: Iceland.

Population, country	**S**	**Text**	**Lat, Lon**	**n**	**C**	**Haplotypes**	$\mathbf{N_{hap}}$	**H**	**π**
Viana do Castelo, PT	1	VIA	41º42'N, 8º51'W	16	A	A2(16)	1	-	-
Samieira, ES	2	RPO	42º25'N, 8º44'W	16	A	A2(16)	1	-	-
Lires, ES	3	LIR	43º00'N, 9º15'W	16	A	A1(13), A3(2), A4	3	342	72
A Coruña, ES	4	RCO	43º22'N, 8º23'W	16	A	A1(16)	1	-	-
Porcia, ES	5	POR	43º34 N, 6º53'W	16	A	A1(16)	1	-	-
Lastres, ES	6	LAS	43º30'N, 5º16'W	16	A	A1(16)	1	-	-
Noja, ES	7	NOJ	43º29'N, 3º32'W	16	A,B	A1(3), A6(4), B1(9)	3	625	293
Txatxarramendi/Ea, ES	8	BCO	43º23'N, 2º35'W	16	A,B	A1, B1(3), B2(8), B3(4)	4	692	194
Piriac-sur-Mer, FR	9	PSM	47º23'N, 2º33'W	15	C	C2(2), C18(12), C19	3	362	147
Le Cabellou, FR	10	CON	47º51'N, 3º55'W	16	C	C1(15), C3	2	125	19
Roscoff, FR	11	ROS	48º44'N, 3º59'W	16	C	C4(9), C5(2), C6, C7, C8, C29, C30	7	692	271
Saint-Briac-sur-Mer, FR	12	SBM	48º38'N, 2º08'W	15	C	C1(2), C21(11), C22, C23	4	467	127
Plymouth, UK	13	PLY	50º21'N, 4º10'W	16	C	C1(16)	1	-	-
St. Ives, UK	14	STI	50º13'N, 5º29'W	16	C	C9(16)	1	-	-
Dunworley, IE	15	COR	51º35'N, 8º46'W	16	C	C1(14), C11(2)	2	233	35
Gleninagh Quay, IE	16	GAL	53º08'N, 9º13'W	16	C	C1(16)	1	-	-
Ballyhoorisky, IE	19	DON	55º15'N, 7º45'W	16	C	C1(3), C24(8), C25(2), C26, C27, C28	6	733	184
Rhosneigr, UK	17	WAL	53º09'N, 4º17'W	16	C	C1(16)	1	-	-
Easdale, UK	20	OBA	56º17'N, 5º39'W	16	C	C1(11), C29(3), C31(2)	3	508	103
Orkneys, UK	21	ORK	58º57'N, 3º15'W	16	C	C17(16)	1	-	-
Aberdeen, UK	22	ABE	57º08'N, 2º05'W	16	C	C12, C17(12), C18, C20(2)	4	442	90
Tholen, NL	18	NED	51º36'N, 4º06'E	16	C	C10(16)	1	-	-
Faroe Islands, DK	23	FAR	61º55'N, 6º55'W	16	C	C13(6), C17(10)	2	500	149
Mildevegen, NO	24	HOR	60º14'N, -4º59'W	16	C	C1(14), C14, C15	3	242	37
Hylla, NO	25	TRO	63º50'N, 11º25'E	15	C	C1(15)	1	-	-
Fauske (Saltfjord), NO	26	NOR	67º15'N, 15º20º E	16	C	C1(12), C16(3), C17	3	425	67
Herdisarvik, IS	27	ICE	63º51'N, 21º46'W	16	C	C1(16)	1	-	-

Populations of *Pelvetia canaliculata* (n = 27) were sampled throughout the entire distributional range of the species in the NE Atlantic, from northern Portugal (41º Lat.) to northern Norway (67º Lat.; Fig. 1 and Table I). At each site, 3-5 cm tips of apical vegetative tissue was excised from 16 individuals sampled along a 50-200 m linear transect or random walk; tissue samples were individually stored dehydrated in silica-gel crystals until DNA extraction. Genomic DNA was extracted from approximately 8 mg of dried tissue using the Nucleospin® Multi-96 plant kit (Macherey-Nagel Duren, Germany), according to the manufacturer's protocol.

An "universal" fucoid/kelp primer pair targeting the 23S/trnK intergenic spacer (mtIGS) was developed based on the partial alignment of the mitochondrial (mtDNA) genomes of Fucus vesiculosus (Secq et al., 2006; GenBank accession no AY494079), Laminaria digitata (Secq et al., 2002; GenBank accession no AJ344328) and Saccharina spp. (Yotsukura et al., 2010; GenBank accession nos AP011493-99). Primers (F: 5′- TGGGTAGTTTGACTGGGGCGGT-3′, R: 5′- ACGGTTCCAATACCCACACCTGC -3′) were designed in conserved flanking regions to amplify a large, 1500 bp fragment spanning the mtIGS. After sequencing, new primers specific to the mtIGS of *P. canaliculata* were designed (F 5′-GGAGGTGCAAGAGCTGCAAGGT-3′; R 5′- TCGAACTCCCGTCTTCGTGCTT-3′). Polymerase chain reactions (PCRs) were performed in a 20 μL volume containing 1 X GoTaq Flexi buffer (Promega), 2.0 mM MgCl2, 125 μM each dNTP, 0.5 μM each primer, 1 U GoTaq® Flexi DNA Polymerase (Promega) and 2 μL of 1:100 diluted DNA template. An initial denaturation step (94º C, 5 min) was followed by 35 cycles of 94º C for 30 s, 60º C for 30 s and 72º C for 1 min, and a final extension step (72º C, 10 min). MtIGS amplicons were cleaned with ExoSap (Fermentas) and sequenced in an automated capillary sequencer (Applied Biosystems) at CCMAR (Portugal).

The geographic distribution of haplotypes was mapped and their genealogic relationships were inferred using the median-joining algorithm implemented in Network v4.6 (Bandelt et al., 1999). Haplotype (Hhap) and nucleotide diversities (πhap) within populations and selected geographic regions were calculated with DnaSP v5 (Librado & Rozas, 2009).

RESULTS

SDM FOR *PELVETIA CANALICULATA*

The modeling methods used to predict the distribution of *P. canaliculata* had mixed performances, with mean AUC values ranging from acceptable to outstanding (mean AUC range from > 0.7 to 0.981). BRT had the highest discriminatory power (mean AUC 0.900±0.071; max AUC 0.981) followed by Maxent (0.848±0.058; max AUC 0.973), MARS (mean AUC 0.815±0.069; max AUC 0.953) and GAM (mean AUC 0.659±0.116; max AUC 0.928). The predictors which had more explanatory value were Maximum Summer Air Temperature (MaxS-AT), Minimum Winter Sea Surface Temperature (MinW-SST), Maximum Summer Sea Surface Temperature (MaxS-SST) and Tidal Coefficient (TC, mean AUC 0.913±0.029). This subset of predictors was the most accurate for BRT, Maxent and MARS (mean AUC 0.948±0.019, 0.897±0.009 and 0.883±0.011, respectively), whereas for GAM the highest AUC values were obtained only with MaxS-AT, MinW-SST and MaxS-SST predictors (mean AUC 0.855±0.021). Since the second best prediction for the latter method included the TC, and GAM had the lowest AUC values, these four predictors were considered in all models for Ensemble purposes. The comparison of remote sensed data with both CCM4 and MIROC5 circulation models revealed an excellent transferability for such simulations (CCSM4: TSS = 0.874; MIROC5: TSS = 0.891).

HINDCASTED DISTRIBUTIONS

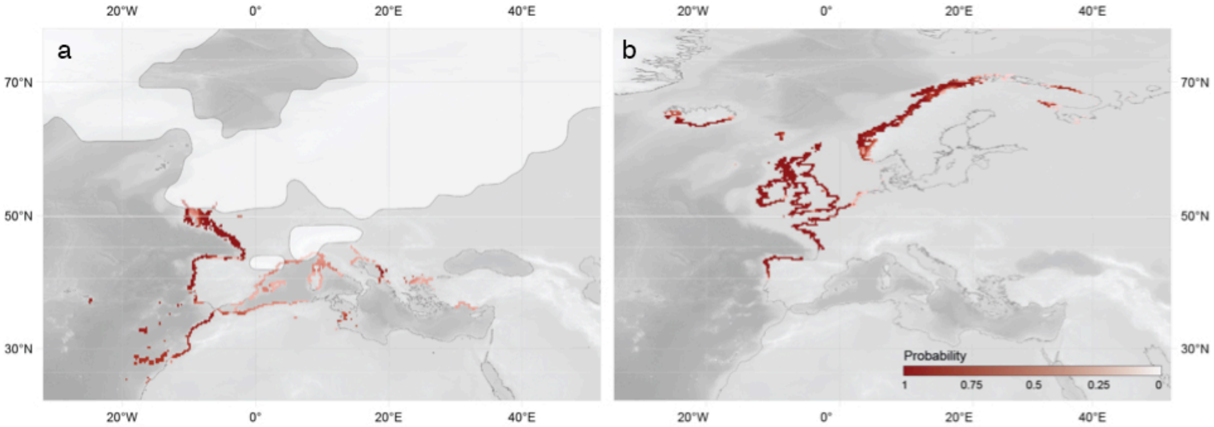

Figure 1. Species distribution modeling for *Pelvetia canaliculata* during a) the Last Glacial Maximum and b) the present. Shaded areas along the shorelines indicate the predicted probability of occurrence. In a) the stripped line depicts the maximum extension of ice-sheets and the shoreline was modeled to a lower sea level (-120 m).

The Ensemble hindcast supported a significant change in the distribution of *P. canaliculata* between the LGM and today (Fig. 1). As expected, projections revealed that northern glaciated regions were unsuitable, although its presence would have been possible in marginal periglacial regions such as the palaeo-shorelines of the Celtic Sea and western Ireland (Fig. 1a). On the opposite range margin, during full glacial conditions the distribution of *P. canaliculata* could potentially extend far beyond its current southern limit in NW Iberia.

Suitable habitat was present throughout southern Portugal, the Moroccan Atlantic coast and the Canary and Madeira archipelagos. Conditions may have been similarly favourable in the western Mediterranean, although high probabilities of occurrence were only supported for the regions with higher tidal coefficients. Taken together, the comparison of modern and hindcasted distributions implies that *P. canaliculata* has experienced an extensive post-glacial range expansion into northern latitudes concurrently with an important contraction at southern latitudes. The regions with higher probability of occurrence during both the LGM and the present were located between NW Iberia and the moving shorelines of the Celtic Sea, with the exception of the Cantabrian Sea, where the probability of occurrence was spatially variable across the two periods.

MTDNA PHYLOGEOGRAPHY

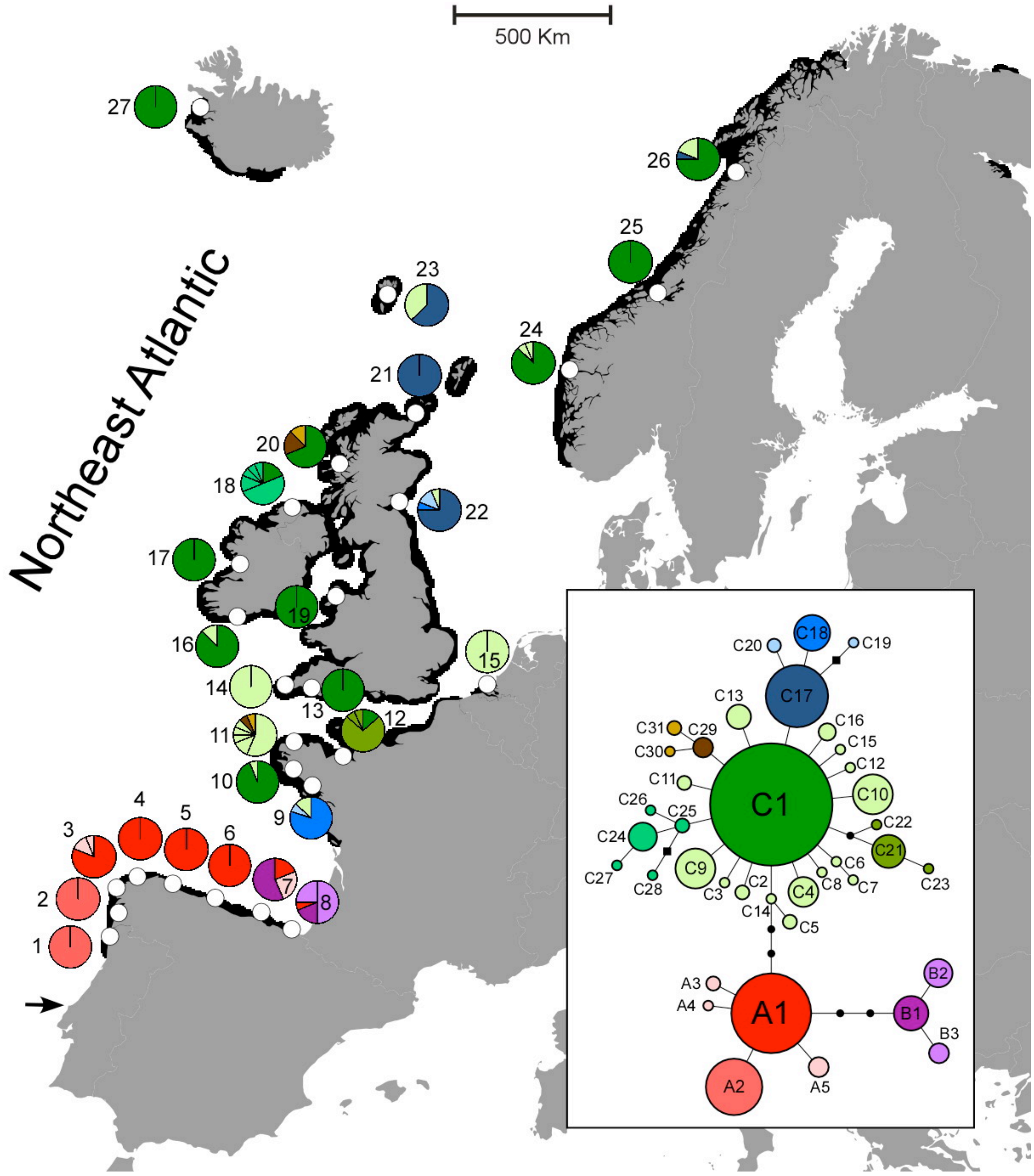

Figure 2. Genealogy and distribution of mtIGS haplotypes throughout the range of *Pelvetia canaliculata*. (a) Contemporary range of *Pelvetia canaliculata* in the northeast Atlantic (black shoreline) and location of sampling sites (white circles). Pie charts depict haplotype frequencies at each site (see Table I for location and haplotype ID's). Haplotypes are colored as in (b). The black arrow on the low left corner marks the historical southern limit by 1990. (b) Parsimony network of mtIGS haplotypes. Sampled haplotypes are represented by circles sized to their global frequency. Links represent a single nucleotide change, black dots represent inferred, unsampled haplotypes, and black squares represent small indels. Shared haplotypes (A1, A2, B1, C1, C17, C18 and C29) are depicted in strong colours, whereas private haplotypes (within each lineage) are represented by pale colours. Two haplotype radiations within lineage C are also depicted in specific green shades.

A total of 39 mtIGS haplotypes (GenBank accession nos KC143772-KC143810) were identified in the 429 individuals of *Pelvetia canaliculata*. The median-joining network revealed three major mtIGS lineages displaying well-defined, largely disjunct geographical distributions (Table I and Fig. 2). Phylogroup A, composed of haplotypes A1 and 4 related ones, was present throughout Iberia. A second Iberian phylogroup, B, composed of B1 and 2 related haplotypes, was restricted to the easternmost part of the Cantabrian Sea. Phylogroup C, composed of C1 and 30 related haplotypes, was vastly distributed along Central and Northern European shores, from NW France to Norway and Iceland.

Phylogroups were defined by one interior and widespread (within the respective phylogroup range) haplotype (A1, B1 and C1), although a few derived haplotypes dominated in more restricted geographical regions (e.g., A2 in W Iberia and C17 in Scotland/Faroes region) or single populations (e.g., C9 in St. Ives and C10 in Netherlands). Distinct lineages were only found mixed in the eastern Cantabrian populations of NOJ and BCO (lineages A and B). Lineage A was interior in the network, and its divergence from lineage B and C was of the same order of magnitude. Globally, only the three interior haplotypes (A1, B1 and C1) plus four derived ones (A2, C17, C18 and C29) were shared among at least two populations. Haplotypes A2 and C17 were shared between neighbouring populations whereas C18 and C29 were shared between distant populations from Brittany and Scotland. The remaining 32 haplotypes were population-specific and among these 16 represented non-singleton variants. Haplotypic diversity within populations was commonly very low; 12 populations (44%) were fixed for a single haplotype, and in only two populations (ROS and DON) were more than 5 haplotypes detected. These latter populations had the highest haplotypic diversities (H= 0.692 and 0.733 respectively), but NOJ exhibited the highest nucleotide diversity (π= 0.00293), as it was composed of two distinct haplotype lineages (A and B) with similar frequencies.

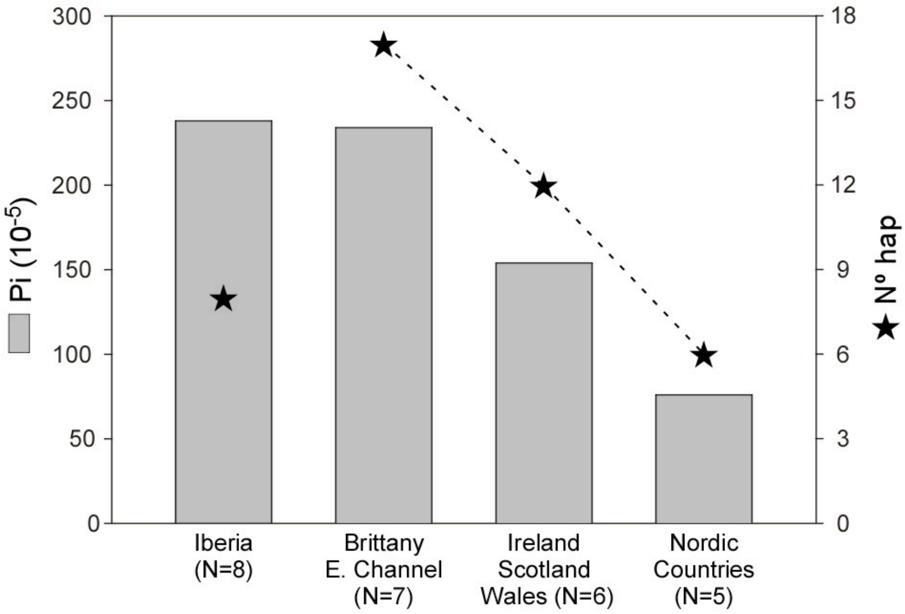

Figure 3. Nucleotide diversity (Pi, columns) and number of haplotypes (stars) of *Pelvetia canaliculata* within four selected geographic regions.

Haplotypic diversity but not nucleotide diversity was lower in Iberia (Lineages A & B: n= 128, Nhap= 8, H= 0.670, π= 0.00238) than in Central/Northern Europe (Lineage C: n= 304, Nhap= 31, H= 0.726, π= 0.00180). Within the former, π was highest in the Brittany/Channel region (0.00233) and lowest (0.00076) in the Nordic Countries (Table I; Fig. 3).

DISCUSSION

SDM ANALYSES

Pelvetia canaliculata is presently distributed throughout regions with a mild oceanic or marine-influenced terrestrial climate. As hypothesized from its strictly high-intertidal habitat, the niche model developed revealed that at a biogeographical scale its distribution is set by both marine and terrestrial climatic conditions, particularly those related with temperature. The southern distributional limit of *P. canaliculata* in northern Portugal is shared with many intertidal/shallow subtidal cold-temperate seaweeds (Lima et al., 2007). In NW Iberia (including N Portugal), where such cold-temperate species are rather ubiquitous, summer SSTs are atypically low relative to central Portugal or the inner Cantabrian Sea, due to persistent (and often intense) upwelling. Contrary to other cold-temperate seaweeds, however, *P. canaliculata* extends its distribution into the inner Cantabrian Sea (Basque Country), where summer SSTs can reach 20ºC (Diez et al., 2012). In central Portugal, where *P. canaliculata* is currently absent, mean summer SSTs are slightly lower but a Mediterranean terrestrial climate prevails. *P. canaliculata* was present in the Berlenga Island (off central Portugal) at least until 1992 (personal observation, Appendix S2 in Supporting Information) and its ~240 km northwards retreat may be related with the SST warming trend observed in this already marginal (and mostly sandy) shoreline during the past decades (Lima et al., 2007, Nicastro et al., 2013). Similar SST warming trends along the Cantabrian Sea (Gomez-Gesteira et al., 2008, Diez et al., 2012) have not been accompanied by a westward displacement, suggesting synergistic effects of air and SSTs at the southern limit. At more local spatial scales, non-climatic variables are also important in determining the potential occurrence of *P. canaliculata*, particularly the availability of relatively sheltered rocky substrata (Martinez et al., 2012). The scarcity of rocky substrata helps to explain its distributional gap along the southern Atlantic shores of France, between the Basque Country and La Rochelle, in addition to being a climatically marginal area.

The projected LGM distribution of *P. canaliculata* implies that with post-glacial warming, it expanded vastly into previously glaciated/elevated northern latitudes (ca. 18º Lat., from the palaeoshorelines of the Celtic Sea into Northern Norway) while suffering a marked range compression at its southern trailing edge (ca. 14º in Lat, from Morocco and possibly the Mediterranean to its present rear edge in northern Portugal). Fore- and hindcasting SDMs for coastal fish, invertebrates and other seaweeds commonly predict analogous shifts at both distributional margins (though not necessarily to the same extent) in response to climatic perturbations (Lenoir et al., 2011, Provan & Maggs, 2012, Waltari & Hickerson, 2012). Empirical data also support the generality of marine biogeographic shifts. Archaeological remains establish the presence of fish species that are currently exclusive of cold areas, such as salmon and cod, in the Western Mediterranean around the LGM (Cortes-Sanchez et al., 2008, Kettle et al., 2011), implying that significant southern range contractions occurred as these species expanded northwards. Documented range shifts attributable to the ongoing warming trend similarly show northward expansions of cold-sensitive species but also noticeable relocations of southern range boundaries in warm-sensitive species (Beaugrand et al., 2002, Perry et al., 2005, Wernberg et al., 2011, Jones et al., 2012, Nicastro et al., 2013).

Taken together, this and other studies suggest that coastal species often track migrating climatic envelops along the shorelines instead of suffering global range contractions / expansions into / from classic refugia (see Bennett & Provan, 2008, Stewart et al., 2010). The high responsiveness of both range margins has been attributed to the fact that the distribution of marine species matches very closely their limits of thermal tolerance (Sunday et al., 2012). This insufficiently recognized difference between marine (range-shift) and terrestrial (contraction-expansion) responses of temperate species has important theoretical and practical implications. Genetically diverse regions in marine species such as *P. canaliculata* are expected to be found where glacial and interglacial distributions overlap, the long term climatic refugia over the species' history, rather than corresponding to their maximum range contractions as in common definitions of terrestrial refugia (Hewitt, 2000, Stewart et al., 2010).

MTDNA PHYLOGEOGRAPHY

Pelvetia canaliculata consists of three divergent genetic clusters displaying largely disjunct geographical distributions. The existence of distinct Iberian and Central/Northern phylogroups, physically separated by the large distributional gap in the south-western French coast, represents the most striking feature of the mtDNA phylogeography of *P. canaliculata*. The two endemic mtDNA lineages indicate that globally Iberia has provided a long-term climatic refugium for *P. canaliculata*, since unique genetic variation was able to evolve and persist there, but also that this region had a very limited (if any) contribution to the colonization of Northern Europe following the LGM. The refugial status of Iberia is puzzling however when considering the low haplotypic diversity within the widespread phylogroup A. This lineage is far less diverse when compared to phylogroup C within its southern (refugial) distributional range around Brittany and the English Channel (see below), or to endemic Iberian lineages of other cold-temperate fucoid species with similar distributions and inferred Iberian refugia (Neiva et al., 2012b).

A hypothetical population bottleneck in Iberia, that would explain the current low diversity within widespread lineage A, cannot be attributed to glacial periods, as in even colder periglacial latitudes lineage C clearly persisted. Furthermore, SDMs projected an extended distribution of *P. canaliculata* throughout southern latitudes suggesting that Iberia was a central climatic optimum. A more plausible hypothesis is that Iberian *P. canaliculata* regressed during warmer periods such as the Holocene Climatic Optimum (HCO, 9-5 ka BP). The summer air temperatures during the HCO were on average warmer than today in northern and central Europe, but similar or colder in SW Europe (Cheddadi et al., 1996, Davis et al., 2003, Wanner et al., 2008). Some palaeoclimatic simulations however fail to reproduce this

HCO scenario in Iberia (Bonfils et al., 2004, Brewer et al., 2007), and environmental reconstructions based on marine proxies actually suggest a cooling trend since this period (Marchal et al., 2002). Archaeological evidence from seafood shells (Clark, 1971, Bailey & Craighead, 2003)) and subtropical monk seal bones (Marin et al., 2011) found in northern Spain are consistent with warmer SST during the mid-Holocene. The molecular variation in the cold-temperate fucoid seaweed *F. ceranoides* is also consistent with a recent westward colonization from an Eastern Cantabrian refugium (Neiva et al., 2012b), further suggesting the existence of unsuitable climatic conditions throughout most of Northern Iberia in the recent past.

Unstable range dynamics attributable to contemporary decadal-scale meteorological events may offer an alternative explanation. Several fucoid and kelp species have been experiencing regional range shifts along the Cantabrian Sea in the last century, including range expansions and contractions from/into colder NW Iberia (Arrontes, 2002, Fernández & Anadón, 2008, Fernandez, 2011). Himanthalia elongata, for instance, has retreated ca. 200 km from Cantabria to Western Asturias since 1960, and its range has been contracting further west in the past several years. By 2000 *F. serratus* was expanding its range eastwards along the Asturian coastline, but has more recently accompanied *H. elongata* in its most recent westward contraction. Similar contraction/expansion cycles along northern Iberia have not been observed in *P. canaliculata* in modern times, but may have occurred during earlier periods. If so, they would certainly contribute to the observed genetic depletion in this region, as recurrent extinctions and leading-edge colonisations are expected to eliminate most regional genetic diversity despite the long-term regional presence of a species.

Whether resulting from a mid-Holocene warm phase or/and from more recent range instability, identifying the location of putative “warm-phase” refugia is complicated by the low levels of variation throughout this entire coast. Local hotspots of genetic diversity within lineages can be very restricted geographically (Neiva et al., 2012b) and may have passed undetected by the relatively coarse sampling adopted. Putative refugial areas for phylogroup A may alternatively have been located beyond the contemporary distributional range of *P. canaliculata*, i.e., in central Portugal or beyond. Rear-edge populations have long been acknowledged as important repositories of genetic diversity (Hampe & Petit, 2005), and several ancient DNA studies reveal that long-vanished trailing-edge populations often possessed unique genetic variation (Dalen et al., 2007, Calvignac et al., 2008). Contemporary southern extinctions along Moroccan and Iberian shorelines have also been accompanied by the loss of unique genetic diversity in a range of cold temperate marine species (Diekmann & Serrao, 2012, Nicastro et al., 2013, Assis et al., in press). In the absence of aDNA or pre-extinction samples, it will remain purely speculative whether the putative extinct S Iberian/ Moroccan populations of *P. canaliculata* belonged to phylogroup A or whether they were genetically more diverse than extant Iberian populations.

The same applies to phylogroup B. It is conceivable, although difficult to test with data at hand, that this phylogroup was at times more widespread in the past, for instance along northern Iberia or southern France, and that the inner Cantabrian Sea represents only a smaller refugial area where it has been able to experience a more stable persistence. The limited number of populations sampled and their average diversity in particular do not allow much inference about its demographical past. In any case, it would be interesting to investigate if the nuclear background of this lineage is similarly unique. If differentiation proved to be genome-wide, it would confirm the independent evolution of this phylogroup by excluding stochastic or selective sweep underlying the regional fixation for type-B mtDNA haplotypes in this geographically and ecologically marginal region. The loss of these relict populations, for instance as a result of ongoing climatic change, would then have a major effect on the overall genetic diversity of this species.

In sharp contrast with Iberian phylogroups A and B, phylogroup C was both widespread and diverse. Its vast distribution throughout central and northern Europe indicates that refugial populations belonging to this lineage have been the source of the post-glacial poleward colonization. A clear decrease of haplotypic richness and nucleotide diversity (but not haplotypic diversity) was observed between the Brittany/Channel region and the Nordic countries. The former region has been reported as a diversity hotspot in several other seaweed taxa (Provan et al., 2005, Hoarau et al., 2007, Olsen et al., 2010) which should reflect its proximity to refugial periglacial shorelines. The higher genetic diversity and differentiation found in Brittany and to a lesser extent further north, illustrated by the large number of private haplotypes and even small haplotype radiations, suggests that this refugial region was in the long-term larger and more stable than those located in northern Iberia. The distribution of the most common haplotypes along the northern range (C1 and C17) suggests that the post-glacial colonization of northern Europe proceeded via two distinct phases and routes, as in the estuarine mysid *Neomysis integer* (Remerie et al., 2009) and the seaweeds *Palmaria palmata*, *F. ceranoides* and *F. serratus* (Provan et al., 2005, Hoarau et al., 2007, Neiva et al., 2012a). The first wave migrated westwards and northwards following the submersion of the English Channel and the Celtic and Irish seas, allowing the central haplotype C1 to spread along the southern English shores and into Ireland and Western Scotland. After the re-establishment of the passage between the Channel and the North Sea (c. 7.5 ka), a second wave expanded along the east coast of England, where the derived haplotype C17 eventually spread further north along eastern Scotland, where it eventually contacted with the descendents of the first wave. This first wave apparently arrived earlier to Norway, as this region is dominated by haplotype C1. Similarly, the mtDNA haplotypes found in Iceland are consistent with colonization via Norway or Scotland, and not via the shortest (and thus expected) route provided by the Faeroes archipelago.

CONGRUENCE OF APPROACHES AND EVOLUTIONARY CONSEQUENCES OF RANGE SHIFTS

The explicit spatial approach of SDMs allows the estimation of past range dynamics beyond modern distributions and provides an independent source of information to contrast with phylogeographic data. The SDM projections for modern and full glacial conditions implied a relatively stable presence of *P. canaliculata* between NW Iberia and the dynamic shorelines of the Celtic Sea (currently Brittany, the English Channel and S Ireland), which is in agreement with the refugial areas inferred with molecular markers. Some discrepancies between SDM and molecular data were apparent however. The existence of two endemic lineages supported the status of Iberia as a long-term refugium, but the lack of intra-lineage variation suggested a more dynamic past characterized by a recent (re)colonization event from a more restricted (yet undetected) area within or south of the Iberian range. Regional extinction/recolonization dynamics along marginal shorelines can be swift and often transitory in response to extreme or short-scale (years to decades) meteorological variation (Arrontes, 2002, Henriques et al., 2007, Wethey et al., 2011). These patterns highlight the general sensitivity and response capacity of coastal species to changes in environmental conditions, particularly along marginal regions. They further imply that the distribution of *P. canaliculata* has changed more dynamically than can be captured by projecting its range for the LGM and the present, which is not particularly unexpected if the large climatic instability observed during the last millennia is taken into account (Bond et al., 1997, Ganopolski & Rahmstorf, 2001, Overpeck & Cole, 2006). Projecting the ranges for additional time steps would potentially increase the resolution of the spatial dynamics experienced by this seaweed in Iberia and beyond, as recent studies show (Espindola et al., 2012).

The evolutionary success of a given species is related to its ability to track suitable conditions in a changing environment, but also with the maintenance of its adaptive capacity. As for many low-dispersal marine organisms, *P. canaliculata* is subdivided into well-defined phylogeographic groups whose contribution to the global range/niche occupancy differs markedly. Phylogroup B for instance is restricted to a short stretch of coastline in the inner Cantabrian Sea whereas phylogroup C occupies the entire range above 45º Lat. These differences, under strict niche conservatism, are assumed to reflect primarily the effects of demographic history acting on pre-existing patterns of lineage distribution and divergence. However, the distinct evolutionary histories and selective regimes experienced by lineages occupying different geographic/environmental spaces are likely to promote the regional accumulation of unique and potentially adaptive genetic variability (Pearman et al., 2010). Perhaps the biggest limitation of species-based SDMs such as the one here developed for *P. canaliculata* is that they do not take into account these historical components of diversity and their potential importance for the overall functional diversity (and thus evolutionary potential) of species (Jump & Penuelas, 2005). Acknowledging the existence of multiple phylogeographic lineages is especially important in the context of climate-induced range shifts. As inferred by SDM and phylogeographic data, the demographic behaviours and fate of regional populations of *P. canaliculata* at the glacial-interglacial transition were quite diverse. Phylogroup C survived along peri-glacial shorelines and its proximity to newly suitable habitats favoured its northward post-glacial expansion. Southern lineages on the contrary were inferred to have suffered a global range reduction. Thus, even if the extirpation of populations at the trailing edge is counteracted by the establishment of others at the leading edge, such spatial rearrangements of lineages may result in severe losses in overall levels of genetic diversity, particularly if the contracting range is old and exhibits high levels of genetic diversity or endemism (e.g., Nicastro et al., 2013).

In a future scenario of increased air and SST temperatures, the complete extirpation of the evolutionarily divergent lineage B is a reasonable concern. The fate of contracting lineages of *P. canaliculata* may be further complicated by density-barrier effects. When regional environmental conditions become too extreme, the genetic variants harboured by vanishing populations will necessarily be lost unless these were allowed to disperse into remaining suitable areas. *P. canaliculata* is presumably able to disperse non-locally via drifting fragments and, as the extensive post-glacial expansion that resulted in the spread of lineage C demonstrates, to keep track of its habitat. The colonization of Iceland and the existence of a few shared haplotypes between distant population pairs from Brittany and Scotland further support the existence of long-distance dispersal events. Despite this, the southern haplotypes were never detected north of Iberia, nor were C-derived haplotypes found south of Brittany. Furthermore, the absence of shared haplotypes in genetically diverse regions such as Brittany and the existence of many shallow phylogeographic breaks throughout the range of *P. canaliculata* imply that gene-flow is often negligible even at relatively small spatial scales. These obviously contrasting outcomes of dispersal into newly available (colonization) and into occupied (immigration) habitats imply important density-barrier effects (De Meester et al., 2002, Ishida & Taylor, 2007) and typically result, as in *P. canaliculata*, in the formation of homogenous and persistent genetic sectors. These are expected when non-local dispersal is rare and local population sizes are large compared to the number of immigrants, and have been shown to occur in range of structural seaweed species (Fraser et al., 2009, Neiva et al., 2012b). Because of distance and density-barrier effects, the unique genetic variation harboured by Iberian populations may be trapped between unsuitable conditions at the warming trailing-edge and more northern regions where lineage C has long been established.

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REFERENCES

Allouche, O., Tsoar, A. & Kadmon, R. (2006) Assessing the accuracy of species distribution models: prevalence, kappa and the true skill statistic (TSS). Journal of Applied Ecology, 43, 1223-1232.

Araujo, M.B. & Pearson, R.G. (2005) Equilibrium of species' distributions with climate. Ecography, 28, 693-695.

Araújo, M.B. & New, M. (2007) Ensemble forecasting of species distributions. Trends in Ecology & Evolution, 22, 42-47.

Arrontes, J. (2002) Mechanisms of range expansion in the intertidal brown alga Fucus serratus in northern Spain. Marine Biology, 141, 1059-1067.

Assis, J., Coelho, N.C., Alberto, F., Valero, M., Raimondi, P., Reed, D. & Serrão E.A. (2013) High and distinct range-edge genetic diversity despite local bottlenecks. PLoS ONE 8(7): e68646

Bailey, G.N. & Craighead, A.S. (2003) Late Pleistocene and Holocene coastal palaeoeconomies: A reconsideration of the molluscan evidence from northern Spain. Geoarchaeology-an International Journal, 18, 175-204.

Bandelt, H.J., Forster, P. & Rohl, A. (1999) Median-joining networks for inferring intraspecific phylogenies. Molecular Biology and Evolution, 16, 37-48.

Beatty, G.E. & Provan, J. (2011) Comparative phylogeography of two related plant species with overlapping ranges in Europe, and the potential effects of climate change on their intraspecific genetic diversity. BMC Evolutionary Biology, 11.

Beaugrand, G., Reid, P.C., Ibanez, F., Lindley, J.A. & Edwards, M. (2002) Reorganization of North Atlantic marine copepod biodiversity and climate. Science, 296, 1692-1694.

Bennett, K.D. & Provan, J. (2008) What do we mean by 'refugia? Quaternary Science Reviews, 27, 2449-2455.

Bigg, G.R., Cunningham, C.W., Ottersen, G., Pogson, G.H., Wadley, M.R. & Williamson, P. (2008) Ice-age survival of Atlantic cod: agreement between palaeoecology models and genetics. Proceedings of the Royal Society B-Biological Sciences, 275, 163-U113.

Bond, G., Showers, W., Cheseby, M., Lotti, R., Almasi, P., deMenocal, P., Priore, P., Cullen, H., Hajdas, I. & Bonani, G. (1997) A pervasive millennial-scale cycle in North Atlantic Holocene and glacial climates. Science, 278, 1257-1266.

Bonfils, C., de Noblet-Ducoudre, N., Guiot, J. & Bartlein, P. (2004) Some mechanisms of mid-Holocene climate change in Europe, inferred from comparing PMIP models to data. Climate Dynamics, 23, 79-98.

Breeman, A.M. (1988) Relative importance of temperature and other factors in determining geographic boundaries of seaweeds - Experimental and phenological evidence. Helgolander Meeresuntersuchungen, 42, 199-241.

Breeman, A.M. (1990) Expected effects of changing seawater temperatures on the geographic distribution of seaweed species. Expected effects of climatic change on marine coastal ecosystems. (ed. by J. J. Beukeuma), pp. 69-76. Kluwer Academic Publishers, The Netherlands.

Brewer, S., Guiot, J. & Torre, F. (2007) Mid-Holocene climate change in Europe: a data-model comparison. Climate of the Past, 3, 499-512.

Buisson, L., Thuiller, W., Casajus, N., Lek, S. & Grenouillet, G. (2010) Uncertainty in ensemble forecasting of species distribution. Global Change Biology, 16, 1145-1157.

Calvignac, S., Hughes, S., Tougard, C., Michaux, J., Thevenot, M., Philippe, M., Hamdine, W. & Hanni, C. (2008) Ancient DNA evidence for the loss of a highly divergent brown bear clade during historical times. Molecular Ecology, 17, 1962-1970.

Carnaval, A.C. & Moritz, C. (2008) Historical climate modeling predicts patterns of current biodiversity in the Brazilian Atlantic forest. Journal of Biogeography, 35, 1187-1201.

Carnaval, A.C., Hickerson, M.J., Haddad, C.F.B., Rodrigues, M.T. & Moritz, C. (2009) Stability Predicts Genetic Diversity in the Brazilian Atlantic Forest Hotspot. Science, 323, 785-789.

Chapman, A.R.O. (1995) Functional ecology of Fucoid algae - 23 years of progress. Phycologia, 34, 1-32.

Cheddadi, R., Yu, G., Guiot, J., Harrison, S.P. & Prentice, I.C. (1996) The climate of Europe 6000 years ago. Climate Dynamics, 13, 1-9.

Clark, G.A. (1971) Asturian of Cantabria - Subsistence Base and Evidence for Post-Pleistocene Climatic Shifts. American Anthropologist, 73, 1244.

Cortes-Sanchez, M., Morales-Muniz, A., Simon-Vallejo, M.D., Bergada-Zapata, M.M., Delgado-Huertas, A., Lopez-Garcia, P., Lopez-Saez, J.A., Lozano-Francisco, M.C., Riquelme-Cantal, J.A., Rosello-Izquierdo, E., Sanchez-Marco, A. & Vera-Pelaez, J.L. (2008) Palaeoenvironmental and cultural dynamics of the coast of Malaga (Andalusia, Spain) during the Upper Pleistocene and early Holocene. Quaternary Science Reviews, 27, 2176-2193.

Coyer, J.A., Hoarau, G., Van Schaik, J., Luijckx, P. & Olsen, J.L. (2010) Trans-Pacific and trans-Arctic pathways of the intertidal macroalga Fucus distichus L. reveal multiple glacial refugia and colonizations from the North Pacific to the North Atlantic. Journal of Biogeography, 38, 756-771.

Dalen, L., Nystrom, V., Valdiosera, C., Germonpre, M., Sablin, M., Turner, E., Angerbjorn, A., Arsuaga, J.L. & Gotherstrom, A. (2007) Ancient DNA reveals lack of postglacial habitat tracking in the arctic fox. Proceedings of the National Academy of Sciences of the United States of America, 104, 6726-6729.

Davis, B.A.S., Brewer, S., Stevenson, A.C. & Guiot, J. (2003) The temperature of Europe during the Holocene reconstructed from pollen data. Quaternary Science Reviews, 22, 1701-1716.

De'ath, G. (2007) Boosted trees for ecological modeling and prediction. Ecology, 88, 243-251.

De Meester, L., Gomez, A., Okamura, B. & Schwenk, K. (2002) The Monopolization Hypothesis and the dispersal-gene flow paradox in aquatic organisms. Acta Oecologica, 23, 121-135.

Diekmann, O.E. & Serrao, E.A. (2012) Range-edge genetic diversity: locally poor extant southern patches maintain a regionally diverse hotspot in the seagrass Zostera marina. Molecular Ecology, 21, 1647-1657.

Diez, I., Muguerza, N., Santolaria, A., Ganzedo, U. & Gorostiaga, J.M. (2012) Seaweed assemblage changes in the eastern Cantabrian Sea and their potential relationship to climate change. Estuarine Coastal and Shelf Science, 99, 108-120.

Egbert, G.D., Ray, R.D. & Bills, B.G. (2004) Numerical modeling of the global semidiurnal tide in the present day and in the last glacial maximum. Journal of Geophysical Research-Oceans, 109.

Elith, J., Graham, C.H., Anderson, R.P., Dudik, M., Ferrier, S., Guisan, A., Hijmans, R.J., Huettmann, F., Leathwick, J.R., Lehmann, A., Li, J., Lohmann, L.G., Loiselle, B.A., Manion, G., Moritz, C., Nakamura, M., Nakazawa, Y., Overton, J.M., Peterson, A.T., Phillips, S.J., Richardson, K., Scachetti-Pereira, R., Schapire, R.E., Soberon, J., Williams, S., Wisz, M.S. & Zimmermann, N.E. (2006) Novel methods improve prediction of species' distributions from occurrence data. Ecography, 29, 129-151.

Elith, J. & Leathwick, J.R. (2009) Species Distribution Models: Ecological Explanation and Prediction Across Space and Time. Annual Review of Ecology Evolution and Systematics pp. 677-697.

Espindola, A., Pellissier, L., Maiorano, L., Hordijk, W., Guisan, A. & Alvarez, N. (2012) Predicting present and future intra-specific genetic structure through niche hindcasting across 24 millennia. Ecology Letters, 15, 649-657.

Fernandez, C. (2011) The retreat of large brown seaweeds on the north coast of Spain: the case of Saccorhiza polyschides. European Journal of Phycology, 46, 352-360.

Fernández, C. & Anadón, R. (2008) La cornisa Cantábrica: un escenario de cambios de distribución de comunidades intermareales. Algas, 39, 30-32.

Ferrier, S., Watson, G., Pearce, J. & Drielsma, M. (2002) Extended statistical approaches to modeling spatial pattern in biodiversity in northeast New South Wales. I. Species-level modeling. Biodiversity and Conservation, 11, 2275-2307.

Fraser, C.I., Nikula, R., Spencer, H.G. & Waters, J.M. (2009) Kelp genes reveal effects of subantarctic sea ice during the Last Glacial Maximum. Proceedings of the National Academy of Sciences of the United States of America, 106, 3249-3253.

Ganopolski, A. & Rahmstorf, S. (2001) Rapid changes of glacial climate simulated in a coupled climate model. Nature, 409, 153-158.

Giovanelli, J.G.R., de Siqueira, M.F., Haddad, C.F.B. & Alexandrino, J. (2010) Modeling a spatially restricted distribution in the Neotropics: How the size of calibration area affects the performance of five presence-only methods. Ecological Modeling, 221, 215-224.

Gomez-Gesteira, M., Decastro, M., Alvaez, I. & Gomez-Gesteira, J.L. (2008) Coastal sea surface temperature warming trend along the continental part of the Atlantic Arc (1985-2005). Journal of Geophysical Research-Oceans, 113.

Guisan, A., Graham, C.H., Elith, J. & Huettmann, F. (2007) Sensitivity of predictive species distribution models to change in grain size. Diversity and Distributions, 13, 332-340.

Hampe, A. & Petit, R.J. (2005) Conserving biodiversity under climate change: the rear edge matters. Ecology Letters, 8, 461-467.

Helmuth, B., Harley, C.D.G., Halpin, P.M., O'Donnell, M., Hofmann, G.E. & Blanchette, C.A. (2002) Climate change and latitudinal patterns of intertidal thermal stress. Science, 298, 1015-1017.

Henriques, M., Goncalves, E.J. & Almada, V.C. (2007) Rapid shifts in a marine fish assemblage follow fluctuations in winter sea conditions. Marine Ecology Progress Series, 340, 259-270.

Hewitt, G. (2000) The genetic legacy of the Quaternary ice ages. Nature, 405, 907-913.

Hewitt, G.M. (1999) Post-glacial re-colonization of European biota. Biological Journal of the Linnean Society, 68, 87-112.

Hoarau, G., Coyer, J.A., Veldsink, J.H., Stam, W.T. & Olsen, J.L. (2007) Glacial refugia and recolonization pathways in the brown seaweed Fucus serratus. Molecular Ecology, 16, 3606-3616.

Hoek, C.v.d. (1982) The distribution of benthic marine algae in relation to the temperature regulation of their life histories. Biological Journal of the Linnean Society, 18, 81-144.

Hofreiter, M. & Stewart, J. (2009) Ecological change, range fluctuations and population dynamics during the Pleistocene. Current Biology, 19, R584-R594.

Hugall, A., Moritz, C., Moussalli, A. & Stanisic, J. (2002) Reconciling paleodistribution models and comparative phylogeography in the Wet Tropics rainforest land snail Gnarosophia bellendenkerensis (Brazier 1875). Proceedings of the National Academy of Sciences of the United States of America, 99, 6112-6117.

Ilves, K.L., Huang, W., Wares, J.P. & Hickerson, M.J. (2010) Colonization and/or mitochondrial selective sweeps across the North Atlantic intertidal assemblage revealed by multi-taxa approximate Bayesian computation. Molecular Ecology, 19, 4505-4519.

Ishida, S. & Taylor, D.J. (2007) Mature habitats associated with genetic divergence despite strong dispersal ability in an arthropod. BMC Evolutionary Biology, 7.

Jones, S.J., Southward, A.J. & Wethey, D.S. (2012) Climate change and historical biogeography of the barnacle Semibalanus balanoides. Global Ecology and Biogeography, 21, 716-724.

Jump, A.S. & Penuelas, J. (2005) Running to stand still: adaptation and the response of plants to rapid climate change. Ecology Letters, 8, 1010-1020.

Kettle, A.J., Morales-Muniz, A., Rosello-Izquierdo, E., Heinrich, D. & Vollestad, L.A. (2011) Refugia of marine fish in the northeast Atlantic during the last glacial maximum: concordant assessment from archaeozoology and palaeotemperature reconstructions. Climate of the Past, 7, 181-201.

Kivinen, S., Luoto, M., Heikkinen, R.K., Saarinen, K. & Ryttari, T. (2008) Threat spots and environmental determinants of red-listed plant, butterfly and bird species in boreal agricultural environments. Biodiversity and Conservation, 17, 3289-3305.

Knowles, L.L., Carstens, B.C. & Keat, M.L. (2007) Coupling genetic and ecological-niche models to examine how past population distributions contribute to divergence. Current Biology, 17, 940-946.

Lambeck, K. & Chappell, J. (2001) Sea level change through the last glacial cycle. Science, 292, 679-686.

Leathwick, J.R., Rowe, D., Richardson, J., Elith, J. & Hastie, T. (2005) Using multivariate adaptive regression splines to predict the distributions of New Zealand's freshwater diadromous fish. Freshwater Biology, 50, 2034-2052.

Lenoir, S., Beaugrand, G. & Lecuyer, E. (2011) Modelled spatial distribution of marine fish and projected modifications in the North Atlantic Ocean. Global Change Biology, 17, 115-129.

Librado, P. & Rozas, J. (2009) DnaSP v5: a software for comprehensive analysis of DNA polymorphism data. Bioinformatics, 25, 1451-1452.

Lima, F.P., Ribeiro, P.A., Queiroz, N., Hawkins, S.J. & Santos, A.M. (2007) Do distributional shifts of northern and southern species of algae match the warming pattern? Global Change Biology, 13, 2592-2604.

Luning, K. (1990) Seaweeds. Their Environment, Biogeography and Ecophysiology., Wiley-Interscience, New York, USA.

Maggs, C.A., Castilho, R., Foltz, D., Henzler, C., Jolly, M.T., Kelly, J., Olsen, J., Perez, K.E., Stam, W., Vainola, R., Viard, F. & Wares, J. (2008) Evaluating signatures of glacial refugia for north Atlantic benthic marine taxa. Ecology, 89, 108-122.

Manel, S., Williams, H.C. & Ormerod, S.J. (2001) Evaluating presence-absence models in ecology: the need to account for prevalence. Journal of Applied Ecology, 38, 921-931.

Marchal, O., Cacho, I., Stocker, T.F., Grimalt, J.O., Calvo, E., Martrat, B., Shackleton, N., Vautravers, M., Cortijo, E., van Kreveld, S., Andersson, C., Koc, N., Chapman, M., Sbaffi, L., Duplessy, J.C., Sarnthein, M., Turon, J.L., Duprat, J. & Jansen, E. (2002) Apparent long-term cooling of the sea surface in the northeast Atlantic and Mediterranean during the Holocene. Quaternary Science Reviews, 21, 455-483.

Marin, A.B., Gonzalez-Morales, M.R. & Estevez, J. (2011) Paleoclimatic inference of the mid-Holocene record of monk seal (Monachus monachus) in the Cantabrian Coast. Proceedings of the Geologists Association, 122, 113-124.

Marko, P.B., Hoffman, J.M., Emme, S.A., McGovern, T.M., Keever, C.C. & Cox, L.N. (2010) The 'Expansion-Contraction' model of Pleistocene biogeography: rocky shores suffer a sea change? Molecular Ecology, 19, 146-169.

Martinez, B., Viejo, R.M., Carreno, F. & Aranda, S.C. (2012) Habitat distribution models for intertidal seaweeds: responses to climatic and non-climatic drivers. Journal of Biogeography, 39, 1877-1890.

McKenzie, P.F. & Bellgrove, A. (2008) Dispersal of Hormosira banksii (Phaeophyceae) via detached fragments: Reproductive viability and longevity. Journal of Phycology, 44, 1108-1115.

Ménot, G., Bard, E., Rostek, F., Weijers, J.W.H., Hopmans, E.C., Schouten, S. & Damste, J.S.S. (2006) Early reactivation of European rivers during the last deglaciation. Science, 313, 1623-1625.

Neiva, J., Pearson, G.A., Valero, M. & Serrão, E.A. (2010) Surfing the wave on a borrowed board: range expansion and spread of introgressed organellar genomes in the seaweed Fucus ceranoides L. Molecular Ecology, 19, 4812-4822.

Neiva, J., Pearson, G.A., Valero, M. & Serrão, E.A. (2012a) Drifting fronds and drifting alleles: range dynamics, local dispersal and habitat isolation shape the population structure of the estuarine seaweed Fucus ceranoides. Journal of Biogeography, 39, 1167-1178.

Neiva, J., Pearson, G.A., Valero, M. & Serrao, E.A. (2012b) Fine-scale genetic breaks driven by historical range dynamics and ongoing density-barrier effects in the estuarine seaweed Fucus ceranoides L. BMC Evolutionary Biology, 12, 78.

Nicastro, K.R., Zardi, G.I., Teixeira, S., Neiva, J., Serrão, E.A. & Pearson, G.A. (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.

Norton, T.A. (1992) Dispersal by macroalgae. British Phycological Journal, 27, 293-301.

Olsen, J.L., Zechman, F.W., Hoarau, G., Coyer, J.A., Stam, W.T., Valero, M. & Aberg, P. (2010) The phylogeographic architecture of the fucoid seaweed Ascophyllum nodosum: an intertidal 'marine tree' and survivor of more than one glacial-interglacial cycle. Journal of Biogeography, 37, 842-856.

Overpeck, J.T. & Cole, J.E. (2006) Abrupt change in Earth's climate system. Annual Review of Environment and Resources pp. 1-31.

Pearman, P.B., D'Amen, M., Graham, C.H., Thuiller, W. & Zimmermann, N.E. (2010) Within-taxon niche structure: niche conservatism, divergence and predicted effects of climate change. Ecography, 33, 990-1003.

Pearson, G.A. & Serrao, E.A. (2006) Revisiting synchronous gamete release by fucoid algae in the intertidal zone: fertilization success and beyond? Integrative and Comparative Biology, 46, 587-597.

Pearson, R.G. & Dawson, T.P. (2003) Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? Global Ecology and Biogeography, 12, 361-371.

Pelc, R.A., Warner, R.R. & Gaines, S.D. (2009) Geographical patterns of genetic structure in marine species with contrasting life histories. Journal of Biogeography, 36, 1881-1890.
Peltier, W.R. (1994) Ice-Age Paleotopography. Science, 265, 195-201.

Perry, A.L., Low, P.J., Ellis, J.R. & Reynolds, J.D. (2005) Climate change and distribution shifts in marine fishes. Science, 308, 1912-1915.

Phillips, S.J., Anderson, R.P. & Schapire, R.E. (2006) Maximum entropy modeling of species geographic distributions. Ecological Modeling, 190, 231-259.

Provan, J., Wattier, R.A. & Maggs, C.A. (2005) Phylogeographic analysis of the red seaweed Palmaria palmata reveals a Pleistocene marine glacial refugium in the English Channel. Molecular Ecology, 14, 793-803.

Provan, J. & Bennett, K.D. (2008) Phylogeographic insights into cryptic glacial refugia. Trends in Ecology & Evolution, 23, 564-571.

Provan, J. & Maggs, C.A. (2012) Unique genetic variation at a species' rear edge is under threat from global climate change. Proceedings of the Royal Society B-Biological Sciences, 279, 39-47.

R Development Core Team (2012) R: A language and environment for statistical computing. Vienna, Austria.

Rato, C., Carranza, S. & Harris, D.J. (2011) When selection deceives phylogeographic interpretation: The case of the Mediterranean house gecko, Hemidactylus turcicus (Linnaeus, 1758). Molecular Phylogenetics and Evolution, 58, 365-373.

Remerie, T., Vierstraete, A., Weekers, P.H.H., Vanfleteren, J.R. & Vanreusel, A. (2009) Phylogeography of an estuarine mysid, Neomysis integer (Crustacea, Mysida), along the north-east Atlantic coasts. Journal of Biogeography, 36, 39-54.

Roura-Pascual, N., Suarez, A.V., Gomez, C., Pons, P., Touyama, Y., Wild, A.L. & Peterson, A.T. (2004) Geographical potential of Argentine ants (Linepithema humile Mayr) in the face of global climate change. Proceedings of the Royal Society B-Biological Sciences, 271, 2527-2534.

Schorr, G., Holstein, N., Pearman, P.B., Guisan, A. & Kadereit, J.W. (2012) Integrating species distribution models (SDMs) and phylogeography for two species of Alpine Primula. Ecology and Evolution, 2, 1260-1277.

Secq, M.P.O., Kloareg, B. & Loiseaux-de Goer, S. (2002) The mitochondrial genome of the brown alga Laminaria digitata: a comparative analysis. European Journal of Phycology, 37, 163-172.

Secq, M.P.O., Goer, S.L., Stam, W.T. & Olsen, J.L. (2006) Complete mitochondrial genomes of the three brown algae (Heterokonta : Phaeophyceae) Dictyota dichotoma, Fucus vesiculosus and Desmarestia viridis. Current Genetics, 49, 47-58.

Sinclair, S.J., White, M.D. & Newell, G.R. (2010) How Useful Are Species Distribution Models for Managing Biodiversity under Future Climates? Ecology and Society, 15.

Stewart, J.R., Lister, A.M., Barnes, I. & Dalen, L. (2010) Refugia revisited: individualistic responses of species in space and time. Proceedings of the Royal Society B-Biological Sciences, 277, 661-671.

Sunday, J.M., Bates, A.E. & Dulvy, N.K. (2012) Thermal tolerance and the global redistribution of animals. Nature Climate Change, 2, 686-690.

Svenning, J.-C., Flojgaard, C., Marske, K.A., Nogues-Bravo, D. & Normand, S. (2011) Applications of species distribution modeling to paleobiology. Quaternary Science Reviews, 30, 2930-2947.

Thuiller, W., Lafourcade, B., Engler, R. & Araújo, M.B. (2009) BIOMOD - a platform for ensemble forecasting of species distributions. Ecography, 32, 369-373.

Toxopeus, J., Kozera, C.J., O'Leary, S.J.B. & Garbary, D.J. (2011) A reclassification of Mycophycias ascophylli (Ascomycota) based on nuclear large ribosomal subunit DNA sequences. Botanica Marina, 54, 325-334.

Tyberghein, L., Verbruggen, H., Pauly, K., Troupin, C., Mineur, F. & De Clerck, O. (2012) Bio-ORACLE: a global environmental dataset for marine species distribution modeling. Global Ecology and Biogeography, 21, 272-281.

Waltari, E., Hijmans, R.J., Peterson, A.T., Nyari, A.S., Perkins, S.L. & Guralnick, R.P. (2007) Locating Pleistocene Refugia: Comparing Phylogeographic and Ecological Niche Model Predictions. PLoS ONE, 2, e563.

Waltari, E. & Hickerson, M.J. (2012) Late Pleistocene species distribution modeling of North Atlantic intertidal invertebrates. Journal of Biogeography, 40, 249-260.

Wanner, H., Beer, J., Buetikofer, J., Crowley, T.J., Cubasch, U., Flueckiger, J., Goosse, H., Grosjean, M., Joos, F., Kaplan, J.O., Kuettel, M., Mueller, S.A., Prentice, I.C., Solomina, O., Stocker, T.F., Tarasov, P., Wagner, M. & Widmann, M. (2008) Mid- to Late Holocene climate change: an overview. Quaternary Science Reviews, 27, 1791-1828.

Wernberg, T., Russell, B.D., Thomsen, M.S., Gurgel, C.F.D., Bradshaw, C.J.A., Poloczanska, E.S. & Connell, S.D. (2011) Seaweed communities in retreat from ocean warming. Current Biology, 21, 1828-1832.

Wethey, D.S., Woodin, S.A., Hilbish, T.J., Jones, S.J., Lima, F.P. & Brannock, P.M. (2011) Response of intertidal populations to climate: Effects of extreme events versus long term change. Journal of Experimental Marine Biology and Ecology, 400, 132-144.

Yotsukura, N., Shimizu, T., Katayama, T. & Druehl, L.D. (2010) Mitochondrial DNA sequence variation of four Saccharina species (Laminariales, Phaeophyceae) growing in Japan. Journal of Applied Phycology, 22, 243-251.

SUPPORTING INFORMATION

Appendix S1. Environmental predictors used for modeling the distribution of *Pelvetia canaliculata*, including sources of data, derived metrics (monthly mean 1980-2010), types of data (RS: Remote sensing; DO: Direct observation; OM: Ocean model) and predictor units.

Environmental predictor **Source**	**Type**	**Units**
Ocean Salinity NCEP Global Ocean Data Assimilation System [1]		
Long term mean of winter’ salinity Long term mean of summer’ salinity	RS, DO	PPM
Sea Surface Temperature OI SST V2 High Resolution Dataset [2]		
Long term mean of the highest SST winter month Long term mean of the lower SST winter month Long term mean of the highest SST summer month Long term mean of the lower SST summer month	RS, DO	ºC
Air Temperature CPC Surface Air Temperature Data Set [3]		
Long term air temperature mean of the hottest winter month Long term air temperature mean of the coldest winter month Long term air temperature mean of the hottest summer month Long term air temperature mean of the coldest summer month	RS, DO	ºC
Air Relative Humidity NCEP/NCAR Reanalysis 1: Surface [4]		
Long term air relative humidity mean of the moisterest winter month Long term air relative humidity mean of the moisterless winter month Long term air relative humidity mean of the moisterest summer month Long term air relative humidity mean of the moisterless summer month	RS, DO	%
Intertidal Habitat Global Inverse Tide Model: Medium-resolution TPXO7.1 [5] Global General Bathymetric Chart of the Oceans [6]		
Tidal amplitude	OM	cm
Intertidal availability (hydrographic zero (0m bathymetry) + tidal amplitude	OM, DO	m^2

[1] Ji, M., Leetmaa, A. & Derber, J. (1995) An Ocean Analysis System for Seasonal to Interannual Climate Studies. *Monthly Weather Review*, **123**, 460-481.

[2] Reynolds, R.W., Smith, T.M., Liu, C., Chelton, D.B., Casey, K.S. & Schlax, M.G. (2007) Daily high-resolution-blended analyses for sea surface temperature. *Journal of Climate*, **20**, 5473-5496.

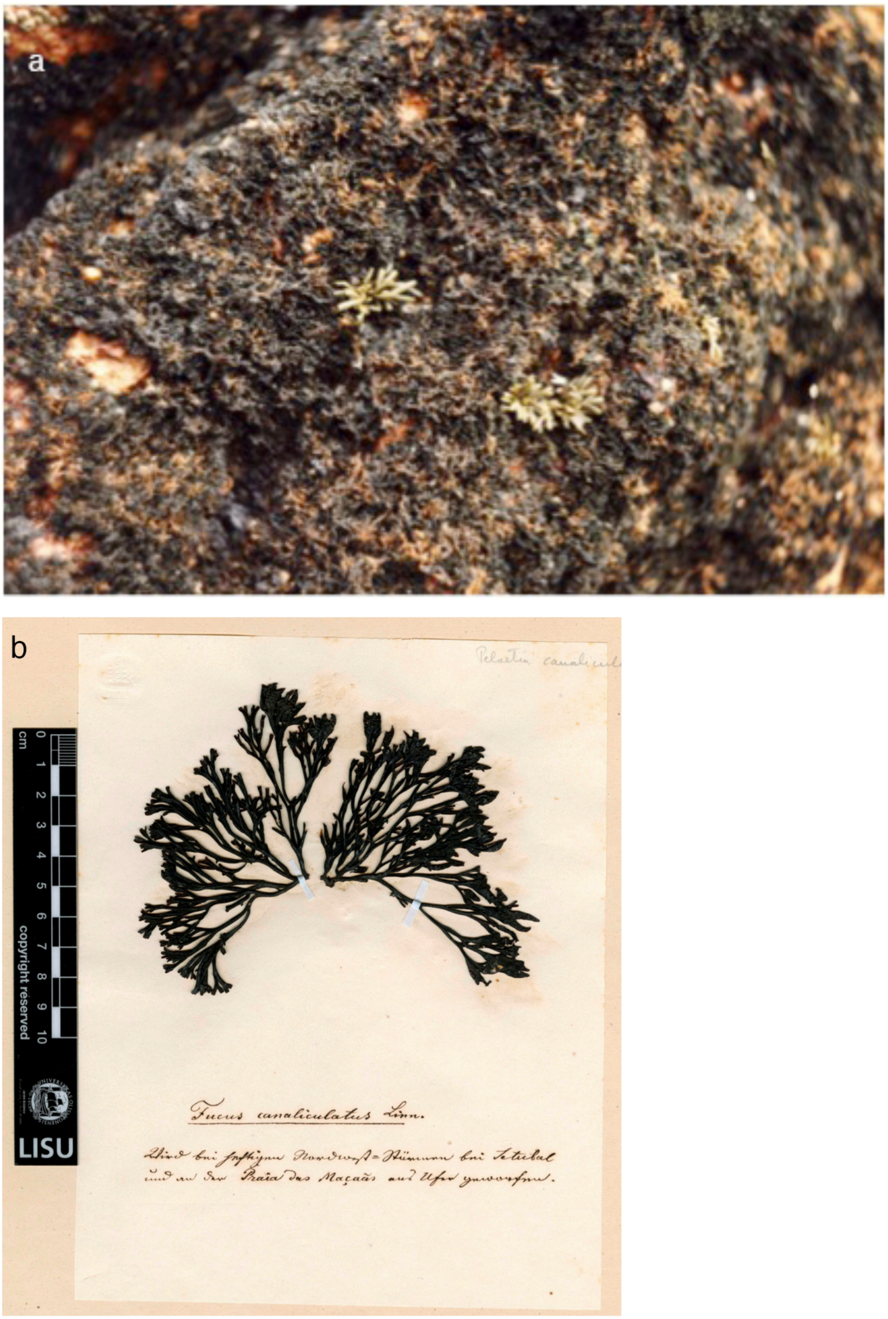
[3] Fan, Y. & van den Dool, H. (2008) A global monthly land surface air temperature analysis for 1948-present. *Journal of Geophysical Research-Atmospheres*, **113**,

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

[5] Egbert, G.D. & Erofeeva, S.Y. (2002) Efficient inverse modeling of barotropic ocean tides. *Journal of Atmospheric and Oceanic Technology*. **19**, 183-204.

[6] GEBCO (2010) General Bathymetric Chart of the Oceans. Liverpool, British Oceanographic Data Centre.

Appendix S2. (a) Photographic record of extinct *Pelvetia canaliculata* from Berlenga Island, off central Portuguese coast, taken in October 1992 (Photo credit: Ester Serrão). (b) Photographic record of an herbarium specimen of *Pelvetia canaliculata*, collected as drift near Lisbon and Setúbal by Friedrich Welwitsch after strong northwest storms (XIX century, University of Lisbon Herbarium). [Original legend: Wird bei heftigen Nordwest Sturmen bei Setubal und an der Praia das Maçãs ans Ufer geworfen]. Photo, collector identification and German translation were courtesy of Prof. Ana Isabel D. Correia (University of Lisbon Herbarium).



CHAPTER VI » CLIMATE CHANGES DRIVE RANGE DYNAMICS AND SHIFTING GENETIC BASELINES

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KEYWORDS » Climate change; niche conservatism; range shifts; genetic diversity; rear edge; Fucus vesiculosus.

ABSTRACT

The climate-driven dynamics of species ranges is a critical research question in evolutionary ecology. Here we ask whether present biodiversity is determined by the imprint of past climatic niches, an ongoing debate that is poorly understood at the intra-species genetic level, and requiring interdisciplinary examination of population genetic pools and persistence patterns across global ranges. We aim to describe and explain causes of geographical contrasts in genetic diversity and their consequences for the future baseline of the global genetic pool. We compared present global geographic distribution of genetic diversity and differentiation with predictive Species Distribution Modeling (SDM) during past extremes, present-time and future climate scenarios for a brown alga, *Fucus vesiculosus*, an ecosystem-structuring species occurring at the land-ocean interface (intertidal). SDM showed that both atmospheric and oceanic climatic forces shape the global distribution of intertidal species, revealing regions of persistence, extinction and expansion during glacial and postglacial periods. These explained the distribution and structure of present genetic diversity, consisting of differentiated genetic pools with maximal diversity in areas of long term persistence. Most of the species range comprises the postglacial expansion zone and derives from a single genetic pool. Besides unraveling the phylogeographic history and supporting the hypothesis of niche conservatism in this species, range shifts and loss of unique genetic pools at the rear edge were predicted for future climate scenarios. A species global genetic pool is determined by a mosaic of areas with long-term persistence adjacent to contraction / expansion zones. Contradicting expectations for rescue roles of refugia, range expansions involved only local fronts, leaving distinct genetic pools at range edges. The ongoing retraction trend and predicted future extinction of unique genetic lineages at the rear edges is impoverishing the global gene pool, strongly shifting the genetic baselines for the future.

INTRODUCTION

Under the niche conservatism hypothesis (Peterson et al., 1999), when environmental conditions fall outside physiological tolerances, species either shift their distribution or become extinct (reviewed by Parmesan, 2006). The glacial and interglacial cycles of the Quaternary (~2.6 MYA to present-time) were particularly important in shaping the distribution of species, which experienced expansions and contractions of ranges in response to the oscillating climate (Provan & Bennett, 2008). The Last Glacial Maximum (LGM: ~21 KYA BP) was one of the most extreme periods of the Quaternary, leading cold-temperate species to experience severe reductions of their northern ranges. It is frequently hypothesized that these species became restricted to small isolated regions of persistence or glacial refugia (reviewed by Maggs et al., 2008) although they might have maintained broad distributions if southern expansions were possible. As climate conditions ameliorated throughout the Holocene (~12 KYA to present-time), populations that persisted within glacial refugia or in extended southern ranges, gradually shifted to new suitable areas, recolonizing northwards (Provan & Bennett, 2008). By the mid-Holocene (MH: ~6 KYA BP) climate conditions were much similar to present but higher summer insolation resulted in seasonal higher air and sea surface temperatures (Mairesse et al., 2013), causing range edge contraction for many species (e.g., Smith & Betancourt, 2003). The Holocene has further potential for climate warming and range shifts in the immediate future.

Climate-driven range shifts can leave distinct footprints on the genetic and evolutionary traits of populations along biogeographic ranges. In regions where populations persisted for long periods of time, high genetic diversity and unique gene pools may be found, and differentiation may result from accumulation of distinct mutations in separated populations (Hewitt, 2000). The number, dimension, location and dispersal among such persistence areas may also play a fundamental role on the shape of genetic variation (Dechaine & Martin, 2004). In contrast, where range reduction occurs or niche peripherality prevails, leaving small and isolated marginal populations, drift and bottlenecks may reduce genetic diversity and increase genetic differentiation. The erosion of population genetic diversity may also occur during expansions due to founder effects at the ‘‘leading edge’’ of colonization, leaving fewer alleles and reduced or no differentiation in newly colonized areas (Neiva et al. 2012a). Such signatures retained in the current patterns of species’ genetic diversity and structure can be tested against independent species distribution models (SDM, see Rushton et al., 2004 for a review) based on past climate to further investigate phylogeographic questions (e.g., Waltari et al., 2007). These models use species distribution records and environmental data to predict the potential distribution of species (Rushton et al., 2004). Constrained by both atmospheric and oceanic climatic conditions, intertidal species represent a singular challenge to model and predict biogeographic distributions.

In the present study we ask whether a species genetic structure is determined by past climatic niches and predict their future implications. To do this, we combined predictive distribution models with microsatellite genetic variation for the intertidal seaweed *Fucus vesiculosus*. We aim to (1) identify the potential habitat during the LGM, MH and in present-time (1990s and 2000s), (2) test the hypothesis of niche conservatism by comparing patterns of genetic diversity and structure with the predictive distributions, (3) discriminate among hypotheses for its phylogeographic history, and (4) infer the consequences of future climate change for the global gene pool.

METHODS

STUDY AREA AND FOCAL SPECIES

The present study was conducted throughout the distribution of *F. vesiculosus*. This is a structural species in intertidal rocky shores and marshlands. Along the eastern Atlantic, it ranges from northern Norway south to western Morocco or more recently to southern Iberia (Nicastro et al. 2013), extending to the White Sea, the Baltic Sea, Faroe and Greenland. Along the Western Atlantic, it ranges from Canada to North Carolina. This distribution includes regions thought to be ancient refugia and where suitable habitat was extirpated in the past by the advance of ice sheets (Coyer et al., 2011). Fucoid algae can migrate across large distances when colonizing novel habitats, but gene flow remains extremely restricted among persistent nearby populations (Neiva et al., 2012b).

DATA ON SPECIES OCCURRENCE AND CLIMATE

Distribution maps of *F. vesiculosus* were constructed by developing a transferable model, trained with distribution records in relation to current climate conditions, and projected into different climate scenarios. Presence records, dated from 2000 to 2010, were collected from literature (dataset and references can be obtained upon request) and pseudo-absences were generated following the recommendations of Barbet-Massin et al. (2012). Distribution records were gridded (0.25º resolution cells), thus reducing the effects of spatial autocorrelation (e.g., Waltari et al., 2007), and divided in two sets. The first, for model training, was generated by randomly selecting 70% of the data. The second, for testing model results by cross-validation, was generated with the remaining 30%.

Environmental predictors were selected based on the biological relevance to *F. vesiculosus* and availability for both past and future climate simulations. These were driven by average remote sensing data from 2000 to 2010 (Appendix S1 in Supporting Information). Intertidal availability was determined by calculating the area above the hydrographic zero (GEBCO, 2010) within tidal amplitude (Egbert, 2004). All predictors were gridded using bilinear interpolation to the 0.25º resolution.

TRANSFERABLE DISTRIBUTION MODEL

Models were performed with the training data and all possible combinations of non-correlated predictors (Spearman's correlation $R < |0.7|$) by means of 3 methods known for their higher predictive performance: Boosted Regression Trees (BRT; De'ath 2007), Maximum Entropy (Maxent; Phillips et al., 2006) and Multivariate Adaptive Regression Splines (MARS; Leathwick et al., 2005). This iterative approach was performed 100 times, and in each, pseudo-absences were regenerated along with randomization of training and testing data. For each model, a predictive map was developed and reclassified into a binary presence-absence surface based on a threshold that maximized the sum of sensitivity and specificity. The discriminatory power of these maps and therefore of each subset of predictors was measured by cross-validation, using the Area Under the receiver-operated characteristic Curve (AUC). The importance of each single predictor was evaluated by the number of times it was selected for the best model (with the highest AUC).

PAST, PRESENT AND FUTURE DISTRIBUTION OF F. VESICULOSUS

Distribution maps were generated by merging with a median function the resulting surfaces of the most discriminatory subset of predictors per modeling method (i.e., ensemble modeling; Araújo & New, 2007). For the LGM and MH, ensemble maps were performed with data from two Atmospheric General Circulation Models (AGCM): the Community Climate System Model (CCSM4) and the Model for Interdisciplinary Research on Climate (MIROC5). Tidal amplitude simulations were also considered (see Egbert, 2004; Katsuto et al., 2006). More recent hindcasting was performed for 1990-2000 (before genetic sampling; see below) and 2000-2010, with remote sensing data (S1). CCSM4 and MIROC5 were also used to forecast the distribution to 2040-2050 and to 2090-2100, under 2 different scenarios: (1) RCP 2.6, a scenario where greenhouse gas emissions are reduced substantially over time; and (2) RCP 8.5, characterized by increasing greenhouse gas emissions over time (Moss et al., 2010).

Because ensemble modeling is also useful for uncertain datasets (Araújo & New, 2007), for those maps using AGCMs, in addition to multiple methods, predictions were performed by merging the resulting surfaces of both CCSM4 and MIROC5. The accuracy of the final predictions was evaluated by determining the sum of sensitivity and specificity (i.e., True Skill Statistic; TSS) of the ensembles made for the 2000s with data from remote sensing and from the two AGCMs for this particular period.

Distribution maps were reclassified into probability of occurrence (range 0 to 1) and for illustrative purpose, glacial ice for the LGM was introduced following the reconstructions of Peltier (1994). LGM coastline contour lines were simulated as the isobath of -120 m below current sea level (Peltier, 2002).

Regions of persistence and extinction were inferred for the pre-sampling prediction maps (LGM, MH and the 90s). A visual approach was chosen in detriment of others (e.g., Rebelo et al., 2012) since in the present study predicted cells differed in position through time due to changes in the coastline. The area of potential habitat was determined for the global distribution and for every region of persistence. All distribution models and related analysis were performed using the packages gbm, dismo, mda, gam and Biomod for R (R Development Core Team, 2013).

POPULATION GENETIC STRUCTURE AND DIVERSITY

Table I. List of samples of *F. vesiculosus* from the North Atlantic. Region name, site name, sampling year, latitude (Lat), longitude (Lon), number of sampled individuals (n), standardised allelic richness (A) and Expected heterozygosity (HE).

Region	Site	Year	Lat	Lon	n	A	Hs
USA	Maine Quoddy	2005	43,684	-69,857	24	3.579±0.196	0,515
USA	Maine Christmascove	2005	43,828	-69,487	23	2.992±0.441	0,372
Iceland	Reykjavik	2004	64,159	-22,053	24	5.5±0.234	0,645
Faroe	Sreymoy	2003	62,085	-7,047	24	5.81±0.211	0,681
Norway	Langesund	2004	58,991	9,772	24	6.444±0.269	0,701
Ireland	Porta Ferry	2004	53,858	-6,233	24	6.77±0.319	0,743
England	Bude	2002	50,828	-4,563	23	7.016±0.204	0,739
France	Pointe de la Crèche	2001	50,751	1,592	24	6.556±0.276	0,764
France	Brignognan	2001	48,672	-4,377	24	6.698±0.35	0,73
Spain	Ria del Eo	2004	43,539	-7,035	14	5.333±0	0,617
Spain	La Guardia	2001	41,902	-8,887	24	4.444±0.235	0,481
Portugal	Viana do Castelo	2001	41,693	-8,851	24	4.786±0.141	0,629
Portugal	Mindelo	2001	41,309	-8,742	24	3.738±0.161	0,457
Portugal	Figueira da Foz	2001	40,148	-8,855	24	4.413±0.236	0,526
Portugal	Alcochete	2001	38,762	-8,967	24	3.365±0.154	0,42
Portugal	Rio Mira	2001	37,721	-8,782	24	3.881±0.244	0,563
Portugal	Tavira	2001	37,124	-7,643	24	2.762±0.199	0,454
Morocco	Lixus	2004	35,198	-6,162	22	3.611±0.113	0,465

Eighteen sites throughout the distribution of *F. vesiculosus* were sampled (24 individuals per site) from 2001 to 2004 (Table I). DNA was extracted and genotyped using nine polymorphic microsatellite loci as described in Perrin et al. (2007).

The number of distinct genetic clusters (K) was estimated using the software Structure (Pritchard et al., 2000). The program ran with a burn-in time of 2x105 repetitions and 1x106 iterations exploring K from 1 to 10, with admixture allowed and without any a priori population assignments. The estimation of the likely number of clusters used the log probability of data Pr(X/K) (Pritchard et al., 2000) and the DK criteria of Evanno et al., (2005). Genetic structure was also analyzed by Factorial Correspondence Analysis (FCA) of population multiscores using GENETIX 4.05 (Belkhir et al., 2001).

Genetic diversity was estimated using allelic richness (A) and Nei's expected heterozygosity (HE) for each locus and site using StandArich and Adegenet for R. Allelic richness and number of unique alleles were also computed for each genetic cluster, and standardized to the smallest group size.

Levels of differentiation within genetic groups were determined by both mean pairwise FST and Jost's D. Hierarchical analysis of molecular variance (AMOVA) was computed using Genodive (Meirmans & Van Tienderen, 2004), based on allele frequency information under 4999 permutations. Variance components were extracted for two hierarchical levels: (1) among sites within groups and (2) between groups. These groups were partitioned following the outcomes of the Bayesian clustering and the FCA analysis.

RESULTS

PAST, PRESENT AND FUTURE DISTRIBUTION OF FUCUS VESICULOSUS

Considering all models performed (16124 x 100 iterations), the most important environmental predictors for the distribution of *F. vesiculosus* (predictors chosen > 10% of the times for best models) were MaxSSTS (99%), followed by MinSSTW (96%), IntertidalAv (65%), MaxAirTS (46%), MaxAirHumS (31%) and MinAirTW (29%). Tidal amplitude and ocean salinity were never chosen for best model.

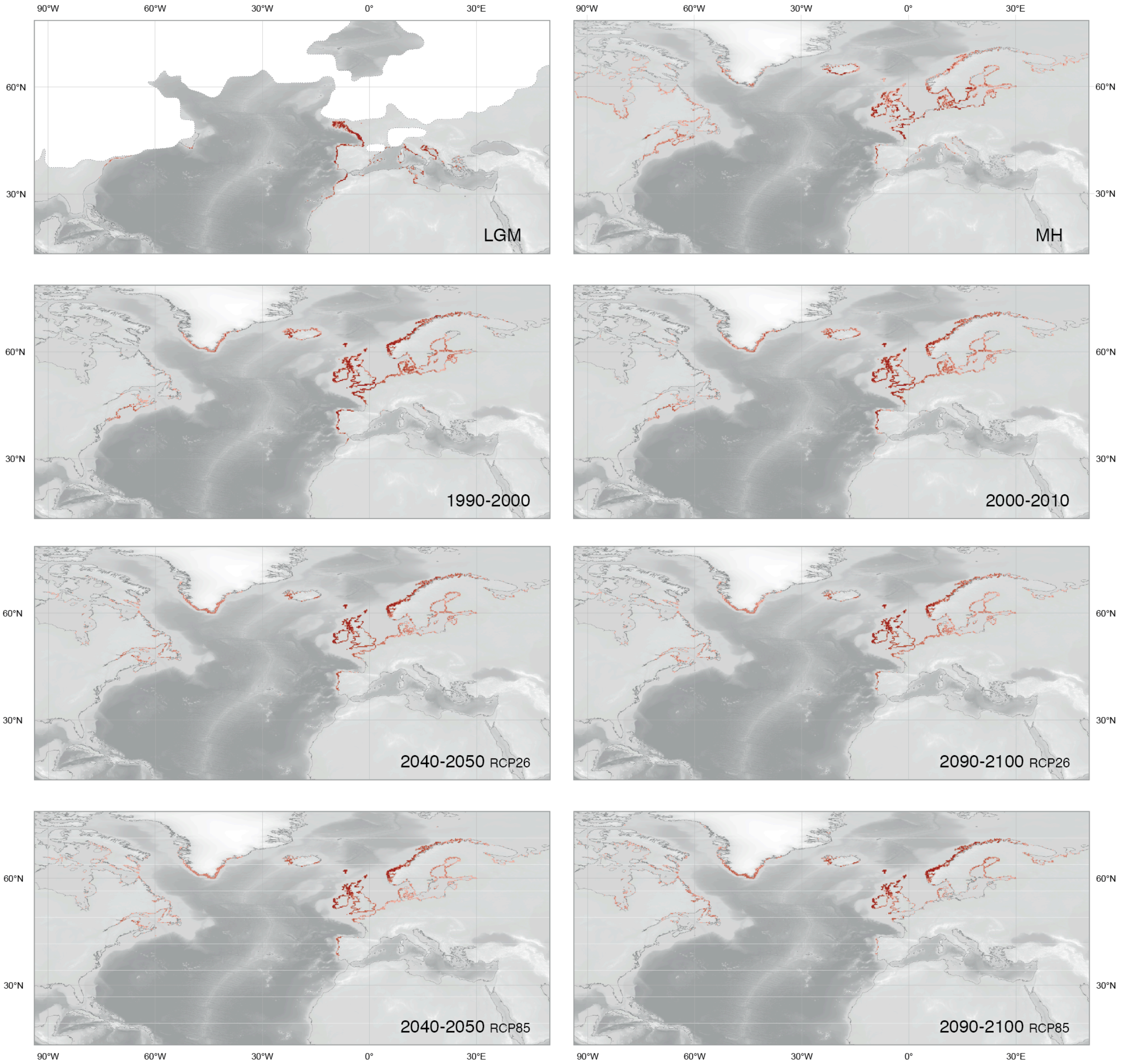

Fig. 1 Ensemble maps of distribution of *F. vesiculosus* for the Last Glacial Maximum (LGM), Mid-Holocene (MH), present-time (90s and 2000s) and future (2050s and 2100s) using remote sensing, direct observations and two Atmospheric General Circulation Models (CCSM4 and MIROC5) with different climate scenarios (RCP26 and RCP85).

The ensemble performed with data from the two AGCMs for the 2000s (Appendix S2 in Supporting Information) had very high discriminatory power (TSS: 0.946±0.009). Hindcasting to the LGM revealed a more southern and restricted distribution (Fig. 1). In the Western Atlantic, *F. vesiculosus* was predicted to have been confined to a narrow region south of the Laurentide ice sheet from Long Island south to the Connecticut coast, and northeast to the Grand Banks region (Newfoundland). On the Eastern Atlantic, models predicted a peri-glacial distribution along the southwest of Ireland and the western English Channel. The north and west coasts of the Iberian Peninsula (including Bay of Biscay) had highly suitable habitat. The Adriatic Sea, northwest Italy, southern France, Tunisia, Malta, eastern Iberia and Atlantic coast of Morocco also had high probability of occurrence (Fig. 1).

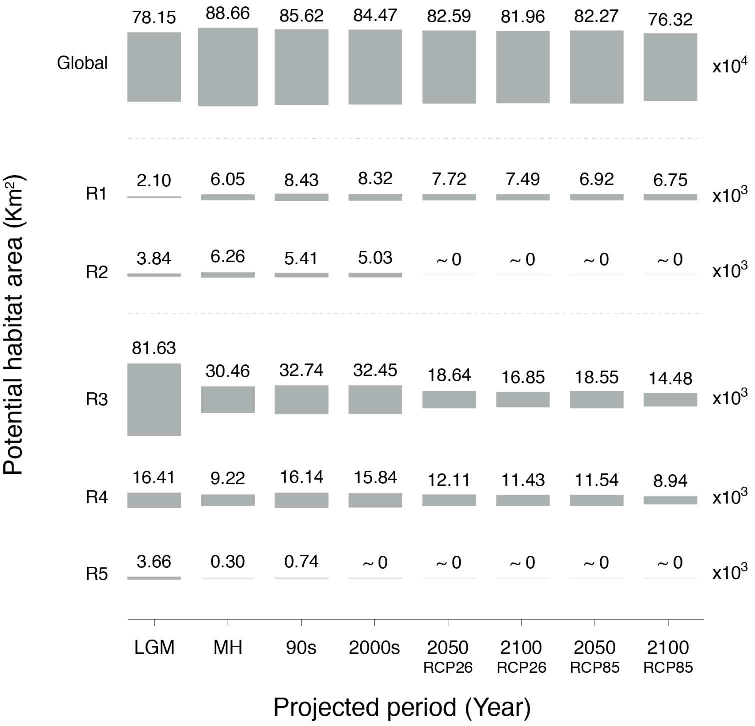

Fig. 2 Area of potential habitat of *F. vesiculosus* for each region of persistence and globally.

From the LGM to the MH a profound reshaping of the distribution was predicted, with a global northward expansion adding ~13.44% more potential habitat (Fig. 2), which left the distribution very similar to present-day's. Yet the distribution could have been more widespread in the Western Atlantic, specifically in Newfoundland, Quebec and throughout southern Hudson Bay, although with low probability of occurrence. Greenland's distribution was predicted to have been more restricted than currently. In the Eastern Atlantic, Norway's distribution was less continuous and northern Spain and southwest Portugal were generally unsuitable for *F. vesiculosus*, leaving the southern range reduced to few sites in southern Spain and northern Morocco (Fig. 1). The northern Adriatic Sea, northwest of Italy, southern France and eastern Iberia were also regions of occurrence but with lower probability than during the LGM (Fig. 1).

The predictions for present-time retrieved an accurate description of distribution (TSS: 0.954±0.011). These estimated a global contraction of distribution from the MH to the 90s (less ~3.55% habitat available; Fig. 2), with most incidence in northern territories like

Newfoundland and southern Hudson Bay in the Western Atlantic, and the Barents Sea in the Eastern Atlantic. This northern contraction was coupled with an expansion towards northern Iberia, southwest Portugal and northern Morocco.

These past projections together allowed to pinpoint 5 regions of long-term persistence (refugia, R) prior to our genetic sampling. These are, southeastern Grand Banks (R1) and south of the Laurentide Ice Sheet, from Long Island to Connecticut (R2) in the Western Atlantic, and southwest Ireland and the western English Channel (R3), northwest Iberia (R4), and a few sites in northern Morocco (R5) in the Eastern Atlantic. From the LGM to the 90s, refugia responded differently to climate. The Grand Banks refugium area was estimated to have expanded through time, while the refugium south of the Laurentide ice sheet expanded from the LGM to the MH and then contracted into the 90s (Fig. 2). In the Eastern Atlantic, all refugia experienced a maximum predicted area during the LGM, followed by a contraction during MH and expansion up to the 90s (Fig. 2).

A global decrease in distributional area was further predicted from the 90s to the 2000s (~1.36%), particularly at the southern range edge of the Eastern Atlantic distribution and at the northern Iberian Peninsula (specially in the Bay of Biscay). All refugia were predicted to decrease, especially at the southern ranges (losses: R1 ~1.43%, R2 ~7.54%, R3 ~0.89%, R4 ~1.86% and R5 ~35.24%). Future projections follow this recent trend, with range shifts and decreasing area (Fig. 2). Specifically, a northward shift is predicted in the Western Atlantic, expanding along Newfoundland and Hudson Bay, and contracting the southern limit to Nova Scotia. In the Eastern Atlantic, predictions include an expansion towards the Barents Sea and contraction of both southwest and northern populations of the Iberian Peninsula. The retreat of southern populations is intensified with RCP 8.5, which is predicted to impact populations from northwest Iberia and the western English Channel (Fig. 1). In both scenarios, historical refugium are expected to suffer a strong habitat reduction; of ~9.98-18.88% by 2100 in the Grand Banks, while the refugia south of the Laurentide Ice Sheet is predicted to be extinct in 2050, in any emissions scenario. Similarly, southwest Ireland and western English Channel are expected to lose ~49.13-57.22% and northwest Iberia ~18.4-46.5% (Fig. 1 & 2).

POPULATION GENETIC STRUCTURE AND DIVERSITY

A total of 163 alleles were observed in 418 unique multi-locus genotypes of *F. vesiculosus*. The 9 microsatellites had 8 to 30 alleles per locus (mean = 18.11, SD = 8.02).

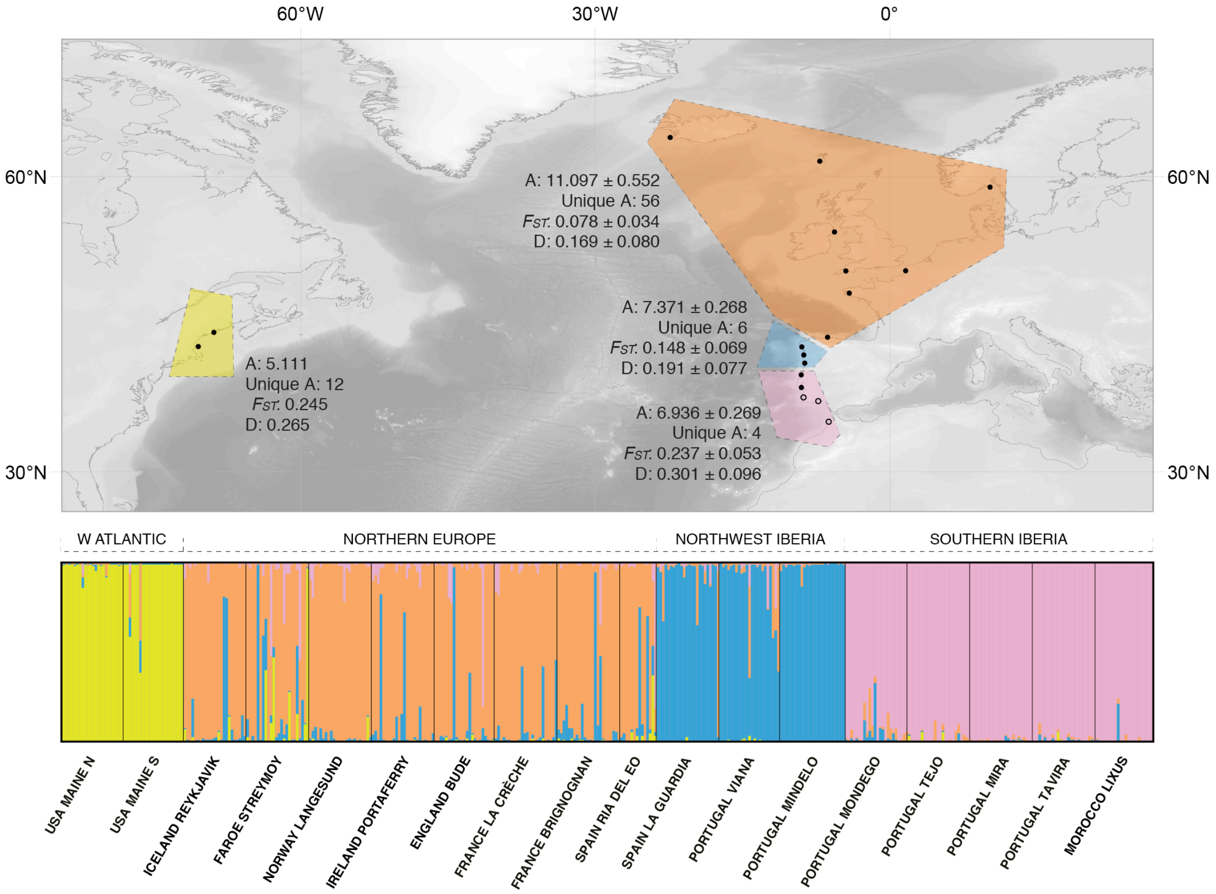

Fig. 3 Genetic subdivision of *F. vesiculosus* based on STRUCTURE. Standardised allelic richness (A), number of unique alleles (Unique A), mean FST and mean Jost's D levels of differentiation per genetic group. Circles indicate sampling sites (open circles currently extinct).

Structure revealed 3 main groups (K=3) using the Evanno criteria (Appendix S3 in Supporting Information): (1) western Atlantic, (2) northern Europe (from Norway and Iceland to northwest Iberia), and (3) western Iberia (from Figueira da Foz southwards) to Morocco. Using K = 4 (secondary level of subdivision revealed using the Pritchard criterion; S3), northwest Iberia became separated from northern Europe (Fig. 3).

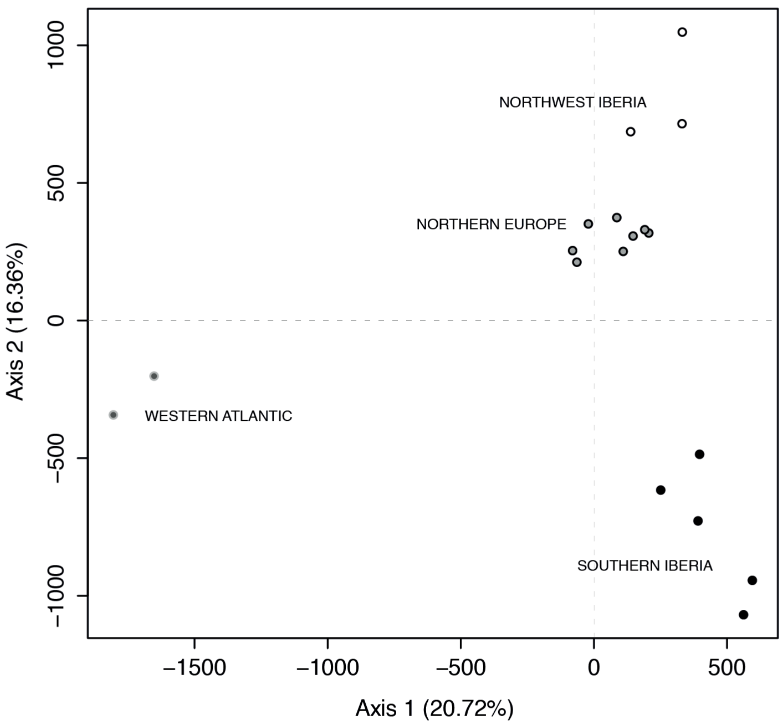

Fig. 4 Genetic differentiation of *F. vesiculosus* ilustrated by Factorial Correspondence Analysis of population multiscores. Inferred groups are divided by different circle patterns.

The FCA supported the same 4 clusters identified by Structure at K=4 (Fig. 4). Based on these results, some of the analyses below are conducted separately for these 4 populations, hereafter designated as Western Atlantic, Northern Europe, Northwest Iberia and Southern Iberia, composed of 2, 8, 3 and 5 sites, respectively (Fig. 3).

The allelic richness (A) per site varied from 2.762 ± 0.199 to 7.016 ± 0.204. Northern Europe had the highest values, on average ca. 1.5 fold higher than in Northwest Iberia, and ca. 2-fold higher than Western Atlantic and Southern Iberian sites (Table I). Gene diversity (HE) revealed a similar pattern, with higher levels predominantly in Northern Europe and Northwest Iberia and lower values in the Western Atlantic and Southern Iberian sites (Table I).

Within clusters, pairwise FST and Jost's D inter-population differentiation were higher in Western Atlantic (FST 0.245, D 0.265) and Southern Iberia (FST 0.237 ± 0.053, D 0.301 ± 0.096). In contrast, Northern Europe had the lowest differentiation among sites (FST 0.078 ± 0.034, D 0.199 ± 0.080), followed by Northwest Iberia (FST 0.148 ± 0.069, D 0.191 ± 0.077) (Fig 3; Appendix S4 in Supporting Information). All differentiation levels were significant among sites within genetic groups and among genetic groups (AMOVA; S4). The sites belonging to the Northern Europe group were less genetically distant than those within the 3 other groups (FCA analysis).

The allelic richness per cluster, standardized for a minimum common sample size of 47 individuals, was higher in Northern Europe (11.097 ± 0.552), followed by Northwest Iberia (7.371 ± 0.268), Southern Iberia (6.936 ± 0.269) and lowest in the Western Atlantic sites (5.111, Fig. 3). The number of unique alleles was also higher in Northern Europe (56 unique alleles) but this was followed by the Western Atlantic (12, very high given that this is the smallest sample size), and lowest in Northwest Iberia and Southern Iberia (6 and 4 unique alleles, respectively; Fig 3).

DISCUSSION

This study reports a perfect match between past range shifts and persistence refugia inferred by SDM, and an independent signature of range shifts, which is the species current genetic structure and diversity across the distributional range. In contrast with strictly marine or strictly terrestrial organisms, in this intertidal species range shifts were best explained by both air and sea temperatures and intertidal habitat area. Distribution models were also used to predict future distributional range shifts, indicating an expected significant range contraction involving further extinctions where unique genetic lineages occur.

TRANSFERABLE DISTRIBUTION MODEL

The performance of our models was generally high, and their integration in an ensemble proved to be a robust approach (as found also by Araújo & New, 2007), with the predicted distribution consistent with observed records.

The most relevant predictors of the geographic range of *F. vesiculosus* were extreme SST (minimum winter and maximum summer), together with intertidal availability. Maximum summer air temperatures and humidity were also identified as relevant predictors. These findings concur with experimental demonstration of the adverse effects of extreme values of those factors on the physiology of fucoids (Wahl et al., 2011; Davison & Pearson 1996, and references therein) and demonstrate the feasibility of combining both marine and terrestrial data to model intertidal species.

The model's transferability to AGCM data also produced accurate predictions, pointing to a good estimation of climate despite uncertainties of such simulations for hindcasting / forecasting (Ramstein et al., 2007). Here the ensemble may be particularly advantageous, since the weighting of different sources of data allows partial assessment of uncertainty (Araújo & New, 2007).

PERSISTENCE AND EXTINCTION OF *F. VESICULOSUS* THROUGH TIME

Hindcasting revealed expansions and contractions resulting in shifting distribution patterns, particularly in the LGM, relative to present time. The extreme environmental conditions of this period caused a substantial reduction of suitable habitat for *F. vesiculosus*, and shifted its distribution southwards, allowing a wide colonization of northern Africa and of the northern and eastern basins of the Mediterranean due to cooler SST conditions. However, it is recognized that the AGCM data used tend to underestimate the drying and cooling throughout southern Europe (Ramstein et al., 2007). Thus, our models might overestimate the Mediterranean distribution of *F. vesiculosus* during the LGM. Nevertheless, such an expansion towards the Mediterranean has been proposed for other Northern Atlantic marine species using different proxies of climate change (e.g., Kettle et al., 2011). Changes in coastal morphodynamics and intertidal habitat depletion for the LGM (Peltier, 1994) were evident in our predictions, namely in areas where ice sheets advanced over continental shelves and where sea level drop reduced the available intertidal area. In southwest Iberia, *F. vesiculosus* would have been absent due to habitat size limitation despite other favorable conditions, and at the southern Laurentide ice sheet, it could have persisted but highly restricted to a narrow stripe of intertidal coast.

The widest predicted distribution of *F. vesiculosus* took place during the MH when a northern shift was particularly boosted along the Barents Sea and southern Hudson Bay. At that time these regions where already ice free and warmed by ~2°C (Diffenbaugh & Sloan, 2002). Our models coupled this expansion with southern extinctions throughout the Mediterranean, northern Africa, southern and northern Iberia. Such a northern expansion-southern contraction is not unique for marine taxa (e.g., Maggs et al., 2008).

Hindcasting to ancient climate revealed five refugia where *F. vesiculosus* could have persisted during both the cold LGM and the warm MH climatic extremes. Similar refugia have been reported, each for distinct intertidal species. In the Western Atlantic, our two predicted refugia (southern Laurentide ice sheet and eastern Grand Banks) sustained several intertidal animal species (e.g., Ilves et al., 2010; Bigg et al., 2008). In the Eastern Atlantic, the region of southwest Ireland and western English Channel was partly ice free during the LGM and has been proposed as refugium for several species (reviewed in Maggs et al., 2008). Northwest Iberia and northern Africa (Morocco) have also been proposed to have been favourable habitats for several marine species, including fucoids (e.g., Neiva et al., 2012a; Coyer et al., 2011; Hoarau et al., 2007; Coyer et al., 2003).

PHYLOGEOGRAPHIC TRAITS OF *F. VESICULOSUS*

Genetic structure was congruent with expectations from the distribution models, as expected in such approaches. Four genetic groups were found, showing high differentiation among groups and private alleles, suggesting strong effects of genetic drift not offset by gene flow. Temporary barriers to connectivity created by climatic shifts are validated by our models. In the LGM, suitable habitat was predicted from southwest Ireland to southwest Iberia. Yet, along this coast, the MH warming shaped three isolated populations corresponding to the eastern Atlantic genetic groups found here: Northern Europe, Northwest Iberia and Southern Iberia. Such an agreement highlights the effect of climate in shaping intra-specific genetic diversity and is particularly remarkable for revealing a major role for the MH, which has received much less attention than the LGM, in this context.

If formerly panmictic populations became isolated by niche distribution changes (e.g., Maggs et al., 2008), admixture might have been expected to occur during subsequent expansion periods. Despite limited dispersive capacity of fucoid propagules, large scale spread driven by floating rafts certainly occurred during recolonization of distant newly available empty habitats (e.g., Neiva et al., 2010). Yet, the spread of new colonizers might be limited when encountering well established populations, maintaining genetic mosaics at scales of tens of km (e.g., Neiva et al., 2012b). Additionally, such species with limited dispersal, or dependent on rare dispersal opportunities, may remain absent from suitable habitats after historical range reduction despite the presence of suitable conditions, thus maintaining functional barriers to gene flow.

Our results show the Western Atlantic as a genetically distinct group, despite the few samples available from this region. The origin of *F. vesiculosus* on this coast has been hypothesized to be a recolonization from Europe following two possible events (see Muhlin & Brawley, 2009). A mitochondrial clock (Hoarau et al., 2007) suggested an ancient colonization from Europe, somewhere between the Sangamon interglacial (125–75 KYBP) and the Wisconsin glacial (35–65 KYBP). Conversely, the low haplotype variability in this region indicates a post-LGM colonization from Europe (Muhlin & Brawley, 2009). However Fucus organelle genomes do not reflect accurate phylogeographies due to extensive introgression at expansion fronts (Neiva et al., 2010). Our results show a considerable amount of private alleles and high levels of genetic differentiation between this region and the Eastern Atlantic groups. Together with our predictive modeling, we suggest a scenario of persistence rather than a post-LGM colonization. But whichever the origin of this differentiation, present day genetic structure demonstrates the occurrence of current barriers to gene flow.

The distribution models were consistent with the genetic diversity observed within groups. In the Northern Europe group, the high genetic diversity in Ireland, England and France, is supported by the distribution models that predicted these as a region of persistence (R3). This climatic niche was absent at more northern glaciated areas. During the post-glacial period, *F. vesiculosus* may have followed the melting ice, losing diversity in the course of colonization due to founder effects (as in other such expansions, e.g., Neiva et al., 2012a). This could explain the genetic differentiation and the lower levels of diversity of the northern sites Iceland, Faroe and Norway. This genetic group includes northern Iberia (Ria del Eo), most likely a more recent colonization from northern populations, since this was predicted as unsuitable for *F. vesiculosus* during the MH. Likewise, other species were extinct from northern Spain during the MH (e.g., L. littorea) and recently recolonized these shorelines (Clark, 1971).

Northwest Iberia was also characterized by relatively high genetic diversity. As a region of long term persistence, this was expected to retain higher diversity compared to the recently colonized northern areas. Yet, the size (area) of habitat within refugia may have limited the size of populations that persisted, and consequently their genetic diversity. The predicted habitat allowing persistence in Northwest Iberia was ca. 2-3 fold lower than in the Northern Europe refugium. Besides habitat size, the lower diversity in Northwest Iberia might also be a function of the geographic location of this refugium, less central than Northern Europe.

Genetic diversity tends to decrease towards the edges of species distributions (see Eckert et al., 2008 and references within), in line with the higher abundance and success of individuals in the centre of the range, where climatic conditions are optimal. This is also in agreement with the higher differentiation between the sites of this region, likely reflecting small population size (therefore high drift) and higher geographic isolation limiting gene flow (see Young et al., 1996).

The Southern Iberia and Western Europe groups had depauperate genetic diversity. Exposure to extreme climatic events and niche peripherality is likely to have resulted in a significant reduction of genetic diversity and increased differentiation through time. This hypothesis is consistent with the predictive models that placed both populations at the range edges of distribution during the MH and at present-time. A reduction of genetic diversity at the range edge has also been observed in the congeneric species *F. serratus* (Coyer et al., 2003).

NICHE CONSERVATISM AND FUTURE CLIMATE CHANGE

The congruence found between the predictive models and the patterns of genetic structure and diversity support the hypothesis of niche conservatism in *F. vesiculosus*, at least from the late Pleistocene to the Holocene (Waltari et al., 2007; Peterson et al., 1999). Absence of niche evolution is not unusual, as it has been demonstrated in a wide range of species (e.g., Peterson et al., 1999). This is particularly important since species that conserved their niche and experienced range shifts during the past are most likely to shift their distribution in future warming scenarios (Araújo et al., 2007).

Model projections predicted a future expansion to newer northern territories. Intertidal shores that will remain ice-free during the entire year are particularly good candidates to receive such shifting populations of *F. vesiculosus* (Adey & Hayek, 2005). Such shifts may well be an additional concerning outcome of future climate change. New settlements of this habitat-structuring species may have unpredictable effects on the recruitment, growth, and survival of native organisms of the cold northern Atlantic waters (Bertness et al., 1999).

Along the southern range edge on the eastern Atlantic, recent extinctions of *F. vesiculosus* have been documented and were particularly severe (Nicastro et al., 2013). Our models corroborate these findings by predicting a loss of suitable habitat from the 90s to the 2000s, at Iberia and northern Africa. *F. vesiculosus* is not a unique case of an intertidal species with distributional shifts associated to recent climate change; other species have recently shifted ranges along both sides of the North Atlantic (Helmuth et al., 2006). Our predictions for future climate change scenarios suggest increasingly stronger range shifts for *F. vesiculosus*, particularly for the long-term projection with increasing greenhouse gas emissions over time (RCP 8.5). Such shifts in range can cause genetic erosion of the remaining populations and compromise the evolutionary potential of *F. vesiculosus* as a whole (Pujol & Pannell, 2008). This is predicted to be more severe at the southern range edge of both sides of the Atlantic, where populations may vanish within the next 40 years, no matter the emission scenario. Such extinctions would result in the loss of entire genetic lineages, which cannot be preserved anywhere else over the entire species range. Because distinct genetic lineages are not evident morphologically, such major losses of entire genetic pools might occur at range edges while remaining undetected, as extant species ranges might be extensive elsewhere but with distinct genetic compositions; the process of shifting genetic baselines (Assis et al., 2013).

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REFERENCES

Adey, W.H. & Hayek, L.A.C. (2005) The biogeographic structure of the western North Atlantic rocky intertidal. Cryptogamie Algologie, 26, 35–66.

Araújo, M.B. & New, M. (2007) Ensemble forecasting of species distributions. Trends in ecology & evolution, 22, 42–7.

Assis, J., Castilho Coelho, N., Alberto, F., Valero, M., Raimondi, P., Reed, D. & Alvares Serrão, E. (2013) High and Distinct Range-Edge Genetic Diversity despite Local Bottlenecks. PLoS ONE, 8, e68646.

Barbet-Massin, M., Jiguet, F., Albert, C.H. & Thuiller, W. (2012) Selecting pseudo-absences for species distribution models: how, where and how many? Methods in Ecology and Evolution, 3, 327–338.

Belkhir, K., Borsa, P., Chikhi, L., Raufaste, N. & Bonhomme, F. (2004) GENETIX 4.05, Population genetics software for Windows TM.

Bertness, M.D., Leonard, G.H., Levine, J.M. & Bruno, J.F. (1999) Climate-driven interactions among rocky intertidal organisms caught between a rock and a hot place. Oecologia, 120, 446–450.

Bigg, G.R., Cunningham, C.W., Ottersen, G., Pogson, G.H., Wadley, M.R. & Williamson, P. (2008) Ice-age survival of Atlantic cod: agreement between palaeoecology models and genetics. Proceedings. Biological sciences / The Royal Society, 275, 163–72.

Clark, G. (1971) The Asturian of Cantabria: Subsistence Base and the Evidence for Post-Pleistocene Climatic Shifts1. American Anthropologist, 13, 1244–1257.

Coyer, J. a, Hoarau, G., Costa, J.F., Hogerdijk, B., Serrão, E. a, Billard, E., Valero, M., Pearson, G. a & Olsen, J.L. (2011) Evolution and diversification within the intertidal brown macroalgae Fucus spiralis/*F. vesiculosus* species complex in the North Atlantic. Molecular phylogenetics and evolution, 58, 283–96.

Coyer, J.A., Peters, A.F., Stam, W.T. & Olsen, J.L. (2003) Post-ice age recolonization and differentiation of Fucus serratus L. (Phaeophyceae; Fucaceae) populations in Northern Europe. Molecular Ecology, 12, 1817–1829.

Davison, I. & Pearson, G. (1996) Stress tolerance in intertidal seaweeds. Journal of Phycology, 32, 197–211.

De'ath, G. (2007) Boosted trees for ecological modeling and prediction. Ecology, 88, 243–251.

DeChaine, E.G., & Martini, A.P. (2004) Historic cycles of fragmentation and expansion in Parnassius smintheus (papilionidae) inferred using mitochondrial DNA. Evolution: International Journal of Organic Evolution, 58, 113–27.

Diffenbaugh, N.S. & Sloan, L.C. (2002) Global climate sensitivity to land surface change: The Mid Holocene revisited. Geophysical Research Letters, 29, 1998–2001.

Eckert, C.G., Samis, K.E. & Lougheed, S.C. (2008) Genetic variation across species' geographical ranges: the central-marginal hypothesis and beyond. Molecular ecology, 17, 1170–88.

Egbert, G.D. (2004) Numerical modeling of the global semidiurnal tide in the present day and in the last glacial maximum. Journal of Geophysical Research, 109, C03003.

Evanno, G., Regnaut, S. & Goudet, J. (2005) Detecting the number of clusters of individuals using the software STRUCTURE: a simulation study. Molecular ecology, 14, 2611–20.

GEBCO (2010) General Bathymetric Chart of the Oceans, Liverpool.

Helmuth, B., Mieszkowska, N., Moore, P. & Hawkins, S.J. (2006) Living on the edge of two changing worlds: Forecasting the responses of rocky intertidal ecosystems to climate change. Annual Review of Ecology Evolution and Systematics, 37, 373–404.

Hewitt, G. (2000) The genetic legacy of the Quaternary ice ages. Nature, 405, 907–913.

Hoarau, G., Coyer, J.A., Veldsink, J.H., Stam, W.T. & Olsen, J.L. (2007) Glacial refugia and recolonization pathways in the brown seaweed Fucus serratus. Molecular ecology, 16, 3606–16.

Ilves, K.L., Huang, W., Wares, J.P. & Hickerson, M.J. (2010) Colonization and/or mitochondrial selective sweeps across the North Atlantic intertidal assemblage revealed by multi-taxa approximate Bayesian computation. Molecular Ecology, 19, 4505–4519.

Kettle, a. J., Morales-Muñiz, a., Roselló-Izquierdo, E., Heinrich, D. & Vøllestad, L. a. (2011) Refugia of marine fish in the northeast Atlantic during the last glacial maximum: concordant assessment from archaeozoology and palaeotemperature reconstructions. Climate of the Past, 7, 181–201.

Leathwick, J.R., Rowe, D., Richardson, J., Elith, J. & Hastie, T. (2005) Using multivariate adaptive regression splines to predict the distributions of New Zealand's freshwater diadromous fish. Freshwater Biology, 50, 2034–2052.

Maggs, C. a, Castilho, R., Foltz, D., Henzler, C., Jolly, M.T., Kelly, J., Olsen, J., Perez, K.E., Stam, W., Väinölä, R., Viard, F. & Wares, J. (2008) Evaluating signatures of glacial refugia for North Atlantic benthic marine taxa. Ecology, 89, S108–22.

Mairesse, A., Goosse, H., Mathiot, P., Wanner, H. & Dubinkina, S. (2013) Investigating the consistency between proxies and between proxies and models using data assimilation: a mid-Holocene case study. Climate of the Past Discussions, 9, 3953–3991.

Meirmans, P.G. & Van Tienderen, P.H. (2004) Genotype and Genodive: Two Programs for the Analysis of Genetic Diversity of Asexual Organisms. Molecular Ecology Notes, 4, 792–794.

Moss, R.H., Edmonds, J. a, Hibbard, K. a, Manning, M.R., Rose, S.K., van Vuuren, D.P., Carter, T.R., Emori, S., Kainuma, M., Kram, T., Meehl, G. a, Mitchell, J.F.B., Nakicenovic, N., Riahi, K., Smith, S.J., Stouffer, R.J., Thomson, A.M., Weyant, J.P. & Wilbanks, T.J. (2010) The next generation of scenarios for climate change research and assessment. Nature, 463, 747–56.

Muhlin, J.F. & Brawley, S.H. (2009) Recent versus relic : discerning the genetic signature of *Fucus vesiculosus* (heterokontophyta ; phaeophyceae) in the Northwestern Atlantic. 837, 828–837.

Neiva, J., Pearson, G. a., Valero, M. & Serrão, E. a. (2012) Drifting fronds and drifting alleles: range dynamics, local dispersal and habitat isolation shape the population structure of the estuarine seaweed Fucus ceranoides. Journal of Biogeography, 39, 1167–1178.

Neiva, J., Pearson, G.A., Valero, M. & Serrão, E.A. (2012) Fine-scale genetic breaks driven by historical range dynamics and ongoing density-barrier effects in the estuarine seaweed Fucus ceranoides L. BMC Evolutionary Biology, 12, 78.

Neiva, J., Pearson, G.A., Valero, M. & Serrão, E.A. (2010) Surfing the wave on a borrowed board: range expansion and spread of introgressed organellar genomes in the seaweed Fucus ceranoides L. Molecular Ecology, 19, 4812–4822.

Nicastro, K.R., Zardi, G.I., Teixeira, S., Neiva, J., Serrão, E. a & Pearson, G. a (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.

Parmesan, C. (2006) Ecological and Evolutionary Responses to Recent Climate Change. Annual Review of Ecology, Evolution, and Systematics, 37, 637–669.

Peltier, W. (2002) On eustatic sea level history: Last Glacial Maximum to Holocene. Quaternary Science Reviews, 21, 377–396.

Peltier, W.R. (1994) Ice age paleotopography. Science, 265, 195–201.

Perrin, C., Daguin, C., Vliet, M. Van De, Engel, C.R., Pearson, G. a. & Serrão, E. a. (2007) Implications of mating system for genetic diversity of sister algal species: Fucus spiralis and *Fucus vesiculosus* (Heterokontophyta, Phaeophyceae). European Journal of Phycology, 42, 219–230.

Peterson, A.T. (1999) Conservatism of Ecological Niches in Evolutionary Time. Science, 285, 1265–1267.

Phillips, S., Anderson, R. & Schapire, R. (2006) Maximum entropy modeling of species geographic distributions. Ecological Modeling, 190, 231–259.

Pritchard, J.K., Stephens, M. & Donnelly, P. (2000) Inference of population structure using multilocus genotype data. Genetics, 155, 945–959.

Provan, J. & Bennett, K.D. (2008) Phylogeographic insights into cryptic glacial refugia. Trends in ecology & evolution, 23, 564–71.

Pujol, B. & Pannell, J.R. (2008) Reduced responses to selection after species range expansion. Science, 321, 96.

R Development Core Team (2013) R: A Language and Environment for Statistical Computing.

Ramstein, G., Kageyama, M., Guiot, J., Wu, H., Hély, C., Krinner, G. & Brewer, S. (2007) How cold was Europe at the Last Glacial Maximum? A synthesis of the progress achieved since the first PMIP model-data comparison. Climate Of The Past Discussions, 3, 197–220.

Rebelo, H., Froufe, E., Brito, J.C., Russo, D., Cistrone, L., Ferrand, N. & Jones, G. (2012) Postglacial colonization of Europe by the barbastelle bat: agreement between molecular data and past predictive modeling. Molecular ecology, 21, 2761–74.

Rushton, S.P., Merod, S.J.O.R. & Kerby, G. (2004) New paradigms for modeling species distributions. Journal of Applied Ecology 41, 193–200.

Uehara, K., Scourse, J.D., Horsburgh, K.J., Lambeck, K. & Purcell, A.P. (2006) Tidal evolution of the northwest European shelf seas from the Last Glacial Maximum to the present. Journal of Geophysical Research, 111, C09025.

Wahl, M., Jormalainen, V., Eriksson, B.K., Coyer, J. a, Molis, M., Schubert, H., Dethier, M., Karez, R., Kruse, I., Lenz, M., Pearson, G., Rohde, S., Wikström, S. a & Olsen, J.L. (2011) Stress ecology in fucus: abiotic, biotic and genetic interactions. Advances in marine biology, pp. 37–105.

Waltari, E., Hijmans, R.J., Peterson, a T., Nyári, A.S., Perkins, S.L. & Guralnick, R.P. (2007) Locating pleistocene refugia: comparing phylogeographic and ecological niche model predictions. PloS one, 2, e563.

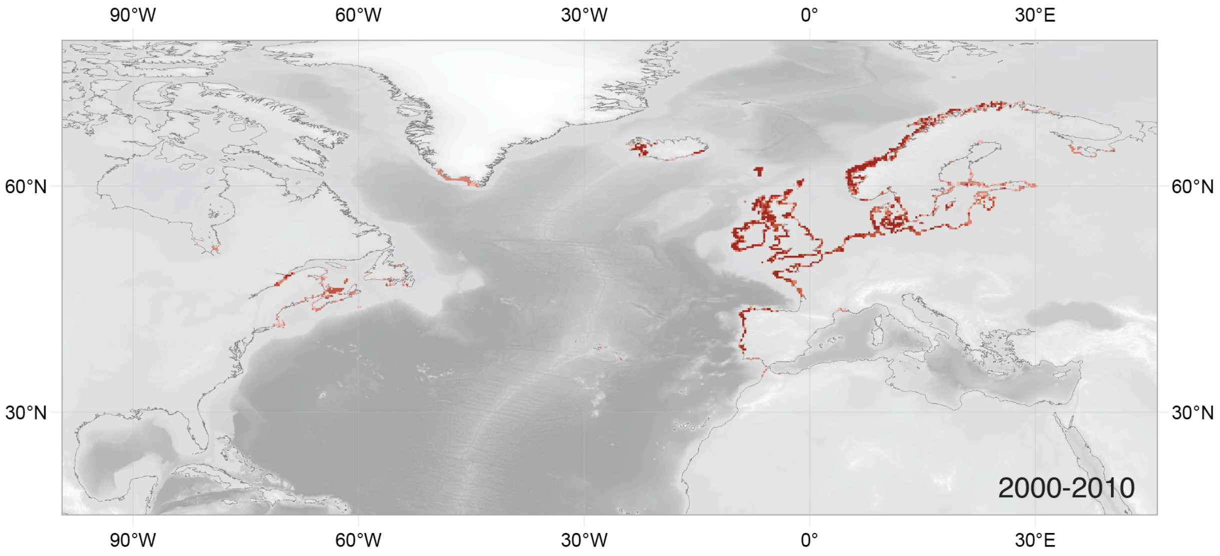
Young, A., Boyle, T. & Brown, T. (1996) The population genetic consequences of habitat fragmentation for plants. Trends in Ecology & Evolution, 11, 413–418.

SUPPLEMENTAL INFORMATION

Appendix S1. Environmental predictors used for modeling proposes (LT: Long term average). Derived metric by predictor (summer: AMJJAS; winter: ONDJFM), source of data, predictors' type (RS: Remote sensing, OM: Ocean model), predictors' units and spatial and temporal resolution. NCEP, OI SST, CPC and NCEP/NCAR data provided by the NOAA/OAR/ESRL PSD, Boulder, Colorado, USA, from www.esrl.noaa.gov/psd/

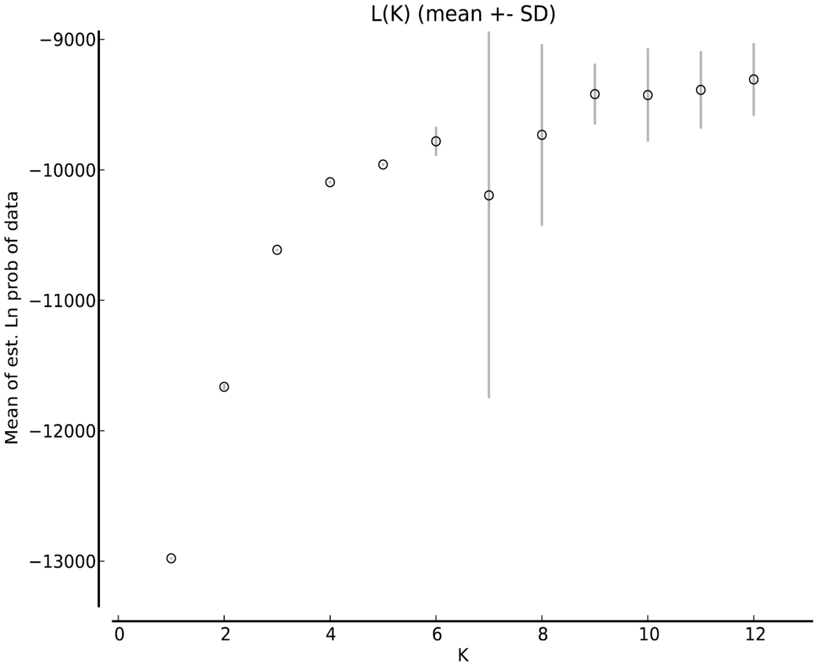
Predictor	**Abbreviation**	**Derived metric**	**Type**	**Units**	**Resolution**
Ocean Salinity	SalW	LTA of winter's salinity	RS	PPM	1º / 1980-2010
	SalS	LTA of summer's salinity			
	Source: NCEP Global Ocean Data Assimilation System (GODAS; Ji et al. 1995)				
Sea Surface Temperature	AverSSTW	LTA of winter's SST	RS	ºC	0.25º / 1981-2010
	AverSSTS	LTA of summer's SST			
	MaxSSTW	LTA SST of the hottest winter month			
	MinSSTW	LTA SST of the coldest SST winter month			
	MaxSSTS	LTA SST of the hottest SST summer month			
	MinSSTS	LTA SST of the coldest SST summer month			
	Source: OI SST V2 High Resolution Dataset (Reynolds et al. 2007)				
Air Temperature	AverAirTW	LTA of winter's air temperature	RS	ºC	0.5º / 1980-2010
	AverAirTS	LTA of summer's air temperature			
	MaxAirTW	LTA air temperature of the hottest winter month			
	MinAirTW	LTA air temperature of the coldest winter month			
	MaxAirTS	LTA air temperature of the hottest summer month			
	MinAirTS	LTA air temperature of the coldest summer month			
	Source: CPC Surface Air Temperature Data Set (Fan & Van den Dool, 2008)				
Relative Humidity	AverAirHW	LTA of winter's relative humidity	RS	%	1º / 1980-2010
	AverAirHS	LTA of summer's relative humidity			
	MaxAirHW	LTA relative humidity of the moisterest winter month			
	MinAirHW	LTA relative humidity of the moisterless winter month			
	MaxAirHS	LTA relative humidity of the moisterest summer month			
	MinAirHS	LTA relative humidity of the moisterless summer month			
	Source: ICOADS 1 Degree (Woodruff et al. 2011)				
Tidal amplitude	TideAmp	Global Tide range	OM	m	0.25º
	Source: Medium-resolution TPXO7.1 (Egbert & Erofeeva, 2002)				
Intertidal availability	IntertidalAv	A function of hydrographic zero + Tidal amplitude	OM	m^2	30''
	Source: Global General Bathymetric Chart of the Oceans (GEBCO, 2010)				

Appendix S2. Ensemble map of *F. vesiculosus* distribution for the 2000s, using two Atmospheric General Circulation Models (CCSM4 and MIROC5).

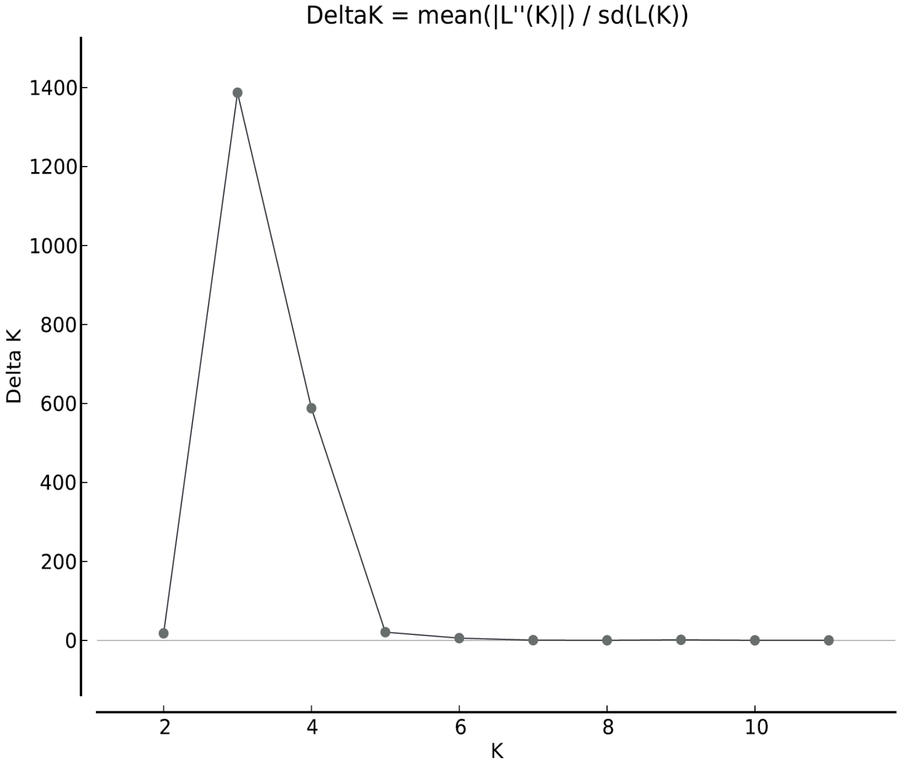


Appendix S3. Estimation of the most probable number of groups (K) based on Bayesian clustering for K = 1 to 12 and 25 runs each (STRUCTURE: Pritchard et al., 2000). (A) Mean log-likelihood of the data per K, i.e., standard output from Structure. (B) Mean absolute difference of the second order rate of change with respect to K (Evanno et al., 2005).

a



b



Appendix S4. Pairwise levels of differentiation between sites (FST and Jost's D) and Analysis of Molecular Variance, among sites within groups, and between groups.

Fst	Quoddy	Christmascove	Reykjavik	Sreymoy	Langesund	Porta Ferry	Bude	La Crèche	Brignognan	Ria del Eo	La Guardia	Viana do Castelo	Mindelo	Figueira da Foz	Alcochete	Rio Mira	Tavira	Lixus
Maine Quoddy	--	0.24599	0.280258	0.257668	0.249758	0.282091	0.285912	0.260051	0.262231	0.303796	0.43958	0.309901	0.458893	0.423543	0.449355	0.412385	0.417928	0.444292
Maine Christmascove	0.24599	--	0.352387	0.36282	0.376426	0.372709	0.382134	0.33817	0.342918	0.394317	0.535292	0.419446	0.531085	0.490339	0.548293	0.491981	0.501946	0.535013
Reykjavik	0.280258	0.352387	--	0.089956	0.067615	0.097626	0.077461	0.083584	0.048237	0.114236	0.199659	0.133953	0.280792	0.290549	0.332663	0.275495	0.300759	0.362425
Sreymoy	0.257668	0.36282	0.089956	--	0.073858	0.127596	0.10287	0.083297	0.069052	0.12618	0.193308	0.115743	0.256308	0.262014	0.317992	0.253952	0.257804	0.335953
Langesund	0.249758	0.376426	0.067615	0.073858	--	0.089282	0.05998	0.060456	0.057924	0.140849	0.206895	0.124958	0.297753	0.245281	0.281498	0.251356	0.264966	0.305231
Porta Ferry	0.282091	0.372709	0.097626	0.127596	0.089282	--	0.030753	0.024027	0.045593	0.101937	0.181999	0.114779	0.239156	0.262703	0.310927	0.218795	0.289197	0.309643
Bude	0.285912	0.382134	0.077461	0.10287	0.05998	0.030753	--	0.037256	0.021681	0.129797	0.181869	0.111044	0.261597	0.234661	0.28693	0.220234	0.276896	0.282847
Pointe de la Crèche	0.260051	0.33817	0.083584	0.083297	0.060456	0.024027	0.037256	--	0.030749	0.117447	0.158048	0.106248	0.222985	0.234488	0.258592	0.197421	0.231191	0.264816
Brignognan	0.262231	0.342918	0.048237	0.069052	0.057924	0.045593	0.021681	0.030749	--	0.086518	0.130918	0.067371	0.20489	0.237752	0.273626	0.223804	0.241415	0.288603
Ria del Eo	0.303796	0.394317	0.114236	0.12618	0.140849	0.101937	0.129797	0.117447	0.086518	--	0.2617	0.150826	0.319639	0.338312	0.343718	0.31259	0.323184	0.385041
La Guardia	0.43958	0.535292	0.199659	0.193308	0.206895	0.181999	0.181869	0.158048	0.130918	0.2617	--	0.075536	0.212911	0.38329	0.448864	0.370462	0.380979	0.463624
Viana do Castelo	0.309901	0.419446	0.133953	0.115743	0.124958	0.114779	0.111044	0.106248	0.067371	0.150826	0.075536	--	0.157831	0.308795	0.35758	0.301879	0.318643	0.364345
Mindelo	0.458893	0.531085	0.280792	0.256308	0.297753	0.239156	0.261597	0.222985	0.20489	0.319639	0.212911	0.157831	--	0.415083	0.480371	0.378534	0.444721	0.465175
Figueira da Foz	0.423543	0.490339	0.290549	0.262014	0.245281	0.262703	0.234661	0.234488	0.237752	0.338312	0.38329	0.308795	0.415083	--	0.230399	0.224527	0.175466	0.321598
Alcochete	0.449355	0.548293	0.332663	0.317992	0.281498	0.310927	0.28693	0.258592	0.273626	0.343718	0.448864	0.35758	0.480371	0.230399	--	0.234417	0.161685	0.232075
Rio Mira	0.412385	0.491981	0.275495	0.253952	0.251356	0.218795	0.220234	0.197421	0.223804	0.31259	0.370462	0.301879	0.378534	0.224527	0.234417	--	0.267978	0.204883
Tavira	0.417928	0.501946	0.300759	0.257804	0.264966	0.289197	0.276896	0.231191	0.241415	0.323184	0.380979	0.318643	0.444721	0.175466	0.161685	0.267978	--	0.321268
Lixus	0.444292	0.535013	0.362425	0.335953	0.305231	0.309643	0.282847	0.264816	0.288603	0.385041	0.463624	0.364345	0.465175	0.321598	0.232075	0.204883	0.321268	--

Jost' D	Quoddy	Christmascove	Reykjavik	Sreymoy	Langesund	Porta Ferry	Bude	La Crèche	Brignognan	Ria del Eo	La Guardia	Viana do Castelo	Mindelo	Figueira da Foz	Alcochete	Rio Mira	Tavira	Lixus
Maine Quoddy	--	0.265	0.539	0.511	0.516	0.657	0.664	0.629	0.588	0.541	0.791	0.604	0.828	0.805	0.72	0.825	0.682	0.779
Maine Christmascove	0.265	--	0.552	0.596	0.687	0.709	0.754	0.678	0.641	0.566	0.853	0.725	0.8	0.789	0.79	0.85	0.71	0.822
Reykjavik	0.539	0.552	--	0.197	0.152	0.251	0.191	0.22	0.113	0.224	0.321	0.274	0.486	0.575	0.561	0.581	0.523	0.707
Sreymoy	0.511	0.596	0.197	--	0.179	0.362	0.285	0.24	0.177	0.275	0.317	0.246	0.455	0.528	0.527	0.543	0.439	0.633
Langesund	0.516	0.687	0.152	0.179	--	0.256	0.164	0.177	0.154	0.322	0.374	0.282	0.593	0.511	0.486	0.571	0.486	0.603
Porta Ferry	0.657	0.709	0.251	0.362	0.256	--	0.094	0.076	0.133	0.249	0.336	0.279	0.47	0.604	0.584	0.513	0.586	0.643
Bude	0.664	0.754	0.191	0.285	0.164	0.094	--	0.116	0.06	0.325	0.342	0.268	0.53	0.519	0.539	0.521	0.555	0.588
Pointe de la Crèche	0.629	0.678	0.22	0.24	0.177	0.076	0.116	--	0.094	0.307	0.313	0.274	0.462	0.557	0.508	0.486	0.468	0.582
Brignognan	0.588	0.641	0.113	0.177	0.154	0.133	0.06	0.094	--	0.2	0.232	0.153	0.385	0.525	0.508	0.527	0.46	0.606
Ria del Eo	0.541	0.566	0.224	0.275	0.322	0.249	0.325	0.307	0.2	--	0.407	0.293	0.521	0.651	0.515	0.636	0.509	0.694
La Guardia	0.791	0.853	0.321	0.317	0.374	0.336	0.342	0.313	0.232	0.407	--	0.102	0.241	0.631	0.663	0.643	0.539	0.772
Viana do Castelo	0.604	0.725	0.274	0.246	0.282	0.279	0.268	0.274	0.153	0.293	0.102	--	0.23	0.611	0.607	0.636	0.55	0.69
Mindelo	0.828	0.8	0.486	0.455	0.593	0.47	0.53	0.462	0.385	0.521	0.241	0.23	--	0.699	0.723	0.643	0.67	0.752
Figueira da Foz	0.805	0.789	0.575	0.528	0.511	0.604	0.519	0.557	0.525	0.651	0.631	0.611	0.699	--	0.268	0.345	0.204	0.467
Alcochete	0.72	0.79	0.561	0.527	0.486	0.584	0.539	0.508	0.508	0.515	0.663	0.607	0.723	0.268	--	0.296	0.149	0.24
Rio Mira	0.825	0.85	0.581	0.543	0.571	0.513	0.521	0.486	0.527	0.636	0.643	0.636	0.643	0.345	0.296	--	0.377	0.273
Tavira	0.682	0.71	0.523	0.439	0.486	0.586	0.555	0.468	0.46	0.509	0.539	0.55	0.67	0.204	0.149	0.377	--	0.4
Lixus	0.779	0.822	0.707	0.633	0.603	0.643	0.588	0.582	0.606	0.694	0.772	0.69	0.752	0.467	0.24	0.273	0.4	--

Full AMOVA table

Source of Variation	Nested in	SSD	d.f.	MS	Var-comp	%Var	F-stat	F-value	P-value
Within Sites	--	1915.029	400	4.788	4.788	0.673	F_st	0.327	--
Among Sites	Group	357.758	14	25.554	0.898	0.126	F_sc	0.158	0.001
Among Groups	--	491.356	3	163.785	1.432	0.201	F_ct	0.201	0.001

CHAPTER VII » GENERAL DISCUSSION

FACTORS SHAPING THE SYNCHRONY AND OCCURRENCE OF MARINE FOUNDATION SPECIES

Using four foundation species as models, this thesis confirmed that environmental conditions alone play the primary role in shaping distributions. Predicted outcomes were in very good agreement with the field data of species ranges, despite biological interactions having not been taken into account (as verified by Pearson & Dawson, 2003). It was further verified that these conditions act on multiple spatial scales, varying from tens of meters to hundreds of kilometres.

Considering all environmental factors tested to explain species distributions, sea temperature was found to be particularly important, controlling the synchrony of populations' abundance and the occurrences at regional scales. This is not a novel finding since seaweeds are known to respond well to sea temperatures (Müller et al., 2009), but it is sometimes difficult to isolate the effect of this variable from other abiotic effects. For instance, along the coast of California, the abundance of *M. pyrifera* mirrored sea temperatures. However, as pointed in other studies (Dayton et al., 1999; Edwards, 2004; Reed et al., 2011), sea temperatures are correlated with the availability of nutrients, since high temperature water masses are typically nutrient depleted (Kamykowski & Zentara, 1986). Likewise, the effect of sea temperature on the occurrences of *S. polyschides* was in part linked to nutrient availability, but in this particular case, the relationship was due to seasonal upwelling conditions, which drive rich waters masses to coastal communities and are essential to the recruitment phase of this species.

Sea temperatures may directly limit the survival of species, particularly when extreme values overpass physiological tolerances. This explained the negative response of *S. polyschides* to extreme hot winter temperatures, a period when this species is reduced to microscopic stages known to tolerate nutrient depleted conditions (Dayton, 1985); this deduction was also made by Matson & Edwards (2007) for the southern ranges of the kelp *Pterygophora californica*. Extreme temperatures were also found to be important for the global distribution of the two fucoids studied (*F. vesiculosus* and *P. canaliculata*), limiting their southern and northern ranges. Furthermore, because these two species are intertidal, their distribution was also explained by extreme values of terrestrial climate (air temperature and humidity), an evidence concurring with several experimental demonstrations (Davison & Pearson, 1996 and references therein; Wahl et al., 2011), but rarely implemented in SDMs.

Ocean waves were also found important drivers for species distribution, particularly for kelps. In certain levels, this variable can stimulate biomass by moving nutrients through the canopy of species (Dayton, 1985; Leigh et al., 1987), but during storm events, physical damage may occur and populations can be wiped out. This may well be the case for the synchrony in abundance found for *M. pyrifera* populations, responding negatively to periods of high waves (also verified by Dayton et al., 1992; Reed et al., 2008). In the same way, at the southern distributions of *S. polyschides*, high waves were found to have a negative effect on the recruitment phase during spring. This may occur due to the presence of fine sediments, which have the potential to scour (Engledow & Bolton, 1994) and / or bury (Devinny & Volse, 1978; Norton, 1978) the young sporophytes.

The recruitment of seaweeds is a central stage for the success of populations, with long lasting effects on their cohorts' structure (Tegner et al., 1997; Dayton et al., 1999). This assumption was further highlighted by the synchrony of *M. pyrifera* distinct populations, which were primarily link to the success of recruits. Not surprisingly, sea urchins were also found to exert some degree of synchrony on the abundance of *M. pyrifera* populations, mainly at the scales of recruitment. Predation by sea urchins on giant kelp is a very well known ecological relationship (Harrold & Pearse, 1987) that may lead to severe reduction of abundances, mainly where trophic cascades are unbalanced (Nichols, 2009); other forms of grazing wield on California kelp forests (e.g., from fish or invertebrates) are generally less important (Foster & Schiel, 1985) and thus not considered on this thesis.

BRINGING REALISM TO SPECIES DISTRIBUTION MODELS

Although the general scope of this thesis did not intend to test how could models be improved by using state of the art explanatory variables, one should consider some of the novel approaches retrieving interesting insights about the biology and distribution of species. For instance, the multi-life cycle approach used for *S. polyschides*' models has rarely been implemented (Guisan & Thuiller, 2005), although this allowed understanding the factors controlling the seasonality of recruitment. Furthermore, this showed how the environment may act differently on each life stage and how these unique responses may be reflected (magnified or offset) on the upcoming stages (e.g., Ladah & Zertuche-González, 2007). These findings were further supported by environmental predictors based on high-resolution data, which allowed to use biologically meaningful predictors such as cumulative heat stress (as used by Carilli et al., 2012) and to capture specific coastal processes on a daily basis (as emphasized by Lima & Wethey, 2012), such as the triggering of seasonal upwelling.

The simulations of dispersal and arrested development were also an innovative approach that in our understanding has never been implemented. These reduce the bias on the reconstruction of species ranges and corroborated that kelp species are very limited in terms of dispersal capacity (as verified by Reed et al., 2006 and Alberto et al., 2010). However, no evidence was found for the long-term persistence of microscopic delayed stages. This is in line with the results from Barradas et al. (2011) but further work should be performed on this subject because if these stages are able to persist for longer than one generation, they would have the potential to buffer the negative effects of climate variability, particularly on short temporal scales.

In the same way, finding habitat area an important variable, whether in the form of available habitat area or tidal amplitude, was an interesting finding. In the case of *F. vesiculosus*, the importance of habitat area rather than tidal amplitude alone was linked to its mating success. This species reproduces through external unisexual outcrossing following broadcast spawning. This mating process is highly susceptible to failure by rapid gamete dilution (reviewed by Levitan & Petersen, 1995; Yund, 2000; Serrão & Havenhand, 2009). While these organisms have developed adaptations such as synchronized spawning under calm conditions (Serrão et al., 1996), their reproductive success is likely dependent on large population sizes, a function of available area rather than simple tidal amplitude. Conversely, since *P. canaliculata* is an hermaphrodite, occupying the higher intertidal shores, one can hypothesize that only those regions with very low tidal amplitude may not create the required amount of habitat, because having both sexes increases the fertilisation success of this species. This was in fact found for some regions of the contemporary Mediterranean that despite having a suitable climatic niche, don’t create the essential tidal conditions for *P. canaliculata* (data not shown).

The incorporation of the aforementioned processes seems to be central to the accurate reconstruction of species distributions and to capture species responses to the changing environment. As referred previously, ignoring these processes may lead to wrong estimations of the potential use of the available climatic space, particularly when inferring variability at local scales where changes occur beyond the large-scale isotherms or the regional patterns of exposure to ocean waves.

RANGE SHIFTS SHAPING THE GENETIC TRAITS OF FOUNDATION SPECIES

Transferring models to the LGM and MH revealed a set of expansions and contractions on species distributions. Particularly the extreme conditions of the LGM caused a severe reduction of ranges for both fucoids studied. These species' northern boundaries were restricted to the sharp temperature front that separated polar and temperate waters (approximately 50º N; Bigg et al., 2008) and their southern boundaries, although less obvious, most probably were set to a wide distribution throughout northern Africa and the northern and eastern basins of the Mediterranean. *F. vesiculosus* may have also persisted on a narrow stripe of coast southern Laurentide ice sheet and in the Grand Banks region in the Western Atlantic. The projections made for this period also confirmed severe changes in the coastal morphodynamics, namely in areas where the sea level dropped and the ice sheets advanced over continental shelves (as described by Peltier, 1994; Mitrovica, 2003).

By the MH, climate conditions were similar to present-days, but summer temperatures were in general higher (Bond et al., 1997; Cheddadi et al., 1997; Davis et al., 2003). This caused the extirpation of the southern range edge of both fucoids and the retreat of the Mediterranean distributions. At that time, these southern contractions were most likely coupled with expansions to northern territories, a pattern that is not unique for marine species (e.g., Graham et al., 2012; González-Wevar et al., 2012). This shifting left their distributions very close to present days', although currently their southern ranges are wider than in this past period. The integration of the MH is the projections revealed a major contribution of this period to species ranges, in opposition to most studies that only consider the influence of the LGM.

The past range shifts inferred from SDMs were a perfect match to the signatures left on the genetic diversity and structure across the sampled distributional ranges of both fucoids. This agreement was expected (e.g., Svenning et al., 2011) and allowed to better understand the phylogeography of these species and the processes (from the late Pleistocene to the Holocene) responsible for their contemporary distribution. Primarily, these results showed that the most important barriers to connectivity are in fact created by climate variability in the long-term. Unsuitable climatic niche may create regions that isolate populations, which will drift in time and increase their genetic differentiation due to poor gene flow. Even though admixture could occur during subsequent expansion periods, this thesis reinforces the idea that the spread of new colonizers is limited when encountering well-established populations. This may be responsible for the maintenance of mosaics of differentiated populations at scales of tens of km (Neiva et al., 2012).

According to expectations, it was further found that the genetic diversity of populations is a function of the long-term persistence in climatic refugia and that the exposure to range reduction results in a significant erosion of genetic diversity and increased differentiation of populations. Furthermore, this thesis found evidence of the importance of habitat size and peripherality of those persistent populations. Although some populations occur in regions of climatic refugia, their limited abundance due to reduced habitat area or available niche at the edge of distributions (see Eckert et al., 2008 and references within) may have lowered their levels of genetic diversity and increased differentiation (see Lawton, 1993; Young et al., 1996).

Contradicting previous assumptions of the rescue role of persisting refugia, range expansions seem to be accomplished by local fronts only, leaving distinct genetic pools at the rear edges. In the same way, the simplistic models relating contemporary abundance and genetic diversity were not corroborated. The results showed high and unique genetic diversity at a species range edge, despite evidence for decreased density, recent range contractions and increased fragmentation. However, since there is no baseline information about the genetic diversity of these populations, it was hypothesized that major losses of diversity may occur across multiple taxa and ranges while remaining undetected, a process that has been called shifting genetic baselines.

NICHE CONSERVATISM AND FUTURE RANGE CONTRACTIONS

The congruence found between the predictive models and the patterns of genetic structure and diversity, as well as the rapid range shits on recent times supported the hypothesis of niche conservatism for three of the four modelled species. This is not unusual, as it has been demonstrated in a wide range of species (e.g., Dépraz et al., 2008; Cordellier & Pfenninger, 2009; Peterson, 2011), although important consequences should be considered because species that conserved their niche and experienced range shifts in the past, will certainly due so in future climate change (Araújo & Whittaker, 2005).

In fact, this thesis demonstrated that climate change is already affecting the distribution of foundation species (as verified by others; e.g., Walther et al., 2002; Root et al., 2003; Parmesan, 2006; Moritz et al., 2008; Nicastro et al., 2013). These recent shifts were found to occur rapidly, once species tolerances are pushed beyond tipping points, and were particularly noticeable (i.e., local extinctions recorded) at the southern range edges during the last decade, following the 2000s. Such predictions were particular severe when the limited dispersal of these species was considering in the models, remaining absent from suitable habitats in the course of niche reduction (as shown by Pulliam, 2000; Araújo & Pearson, 2005; Guisan & Thuiller, 2005).

Although this thesis found no strong evidence for arrested development, it cannot be ruled out. Most of what is known about the longevity of small stages is derived from laboratory experiments, with some studies demonstrating that they may last for several years (e.g., Neushul, 1983). While the results obtained from the simulations performed on the distribution of S. polyschides were corroborated by field evidence from other authors, it seems clear that more studies are needed to better understand the factors controlling the delay of microscopic stages.

The predictions made for future climate change pointed to stronger range shifts at the range edges, especially for the long-term and considering increasing greenhouse gas emissions over time. This may cause the extinction of unique genetic lineages found at these southern regions, an effect that can be particularly important for species as a whole, because unique gene pools when lost cannot reappear latter on, no matter how suitable the habitat may be in the future. Such losses may compromise the evolvability and therefore the adaptive potential of populations to face further disturbances (Pujol & Pannell, 2008).

CHAPTER VIII » CONCLUSIONS AND FUTURE REMARKS

This thesis inferred the major forces shaping the synchrony and distribution of important foundation species and predicted significant range shifts on past and future scenarios of climate change. It further verified the importance of the LGM, MH and recent range shifts on the genetic diversity and structure of populations.

These results showed how the global genetic pool of a species is shaped by a mosaic of regions where populations persisted for long time, adjacent to others experiencing expansions and contractions. Contradicting expectations, during expansion periods, refugia seem to play a minor role than previously assumed. In the same way, populations holding higher genetic diversity do not rule out that they may have experienced strong genetic erosion because there is no information on past genetic baselines and sampling can only be done on extant populations.

Effective population sizes and dispersal capacities were found to be particularly important for the contemporary patterns of distribution and genetic diversity. However, some of the novel approaches such as the implementation of dispersal in the reconstruction of recent distributions or the hindcasting to paleoclimate were used separately. Thus, one should consider the use of a unified strategy, particularly attempting to infer past gene flow between populations, for instance, by using lagrangian dispersal models (see Siegel et al., 2003), which nowadays benefit from the data driven by state of the art AGCMs.

While the studied species are naturally resilient systems, it is clear that the ongoing warming of the oceans will further shift their distribution. This thesis stresses the possible extinction of unique genetic lineages at the rear edges, impoverishing the global gene pool and shifting genetic baselines for marine foundation species.

REFERENCES

Alberto, F., Raimondi, P.P.T., Reed, D.D.C., Coelho, N.C., Leblois, R., Whitmer, A. & Serrão, E.A. (2010) Habitat continuity and geographic distance predict population genetic differentiation in giant kelp. Ecology, 91, 49–56.

Araújo, M. & Whittaker, R. (2005) Reducing uncertainty in projections of extinction risk from climate change. Global Ecology and Biogeography, 14, 529–538.

Araújo, M.B., Pearson, R.G., Thuiller, W. & Erhard, M. (2005) Validation of species – climate impact models under climate change. Global Change Biology, 11, 1504–1513.

Barradas, A. & Alberto, F. (2011) Fast sporophyte replacement after removal suggests banks of latent microscopic stages of Laminaria ochroleuca (Phaeophyceae) in tide pools in northern Portugal. CBM-Cahiers de Biologie, 52, 435–439.

Bigg, G.R., Cunningham, C.W., Ottersen, G., Pogson, G.H., Wadley, M.R. & Williamson, P. (2008) Ice-age survival of Atlantic cod: agreement between palaeoecology models and genetics. Proceedings. Biological sciences / The Royal Society, 275, 163–72.

Bond, G. (1997) A Pervasive Millennial-Scale Cycle in North Atlantic Holocene and Glacial Climates. Science, 278, 1257–1266.

Carilli, J., Donner, S.D. & Hartmann, A.C. (2012) Historical temperature variability affects coral response to heat stress. PloS one, 7, e34418.

Cheddadi, R., Yu, G., Guiot, J., Harrison, S.P. & Prentice, I.C. (1996) The climate of Europe 6000 years ago. Climate Dynamics, 13, 1–9.

Cordellier, M. & Pfenninger, M. (2009) inferring the past to predict the future: climate modeling predictions and phylogeography for the freshwater gastropod Radix balthica (Pulmonata, Basommatophora). Molecular Ecology, 18, 534–544.

Davis, B. a. S., Brewer, S., Stevenson, a. C. & Guiot, J. (2003) The temperature of Europe during the Holocene reconstructed from pollen data. Quaternary Science Reviews, 22, 1701–1716.

Davison, I. & Pearson, G. (1996) Stress tolerance in intertidal seaweeds. Journal of Phycology, 32, 197–211.

Dayton, P. (1985) Ecology of kelp communities. Annual Review of Ecology and Systematics, 16, 215-245.

Dayton, P., Tegner, M.J., Edwards, P.B. & Riser, K.L. (1999) Temporal and spatial scales of kelp demography: the role of oceanographic climate. Ecological Monographs, 69, 219–250.

Dayton, P.K., Tegner, M.J., Parnell, P.E. & Edwards, P.B. (1992) Temporal and spatial patterns of disturbance and recovery in a kelp forest community. Ecological Monographs, 62, 421–445.

Dépraz, A., Cordellier, M., Hausser, J. & Pfenninger, M. (2008) Postglacial recolonization at a snail's pace (Trochulus villosus): confronting competing refugia hypotheses using model selection. Molecular Ecology, 17, 2449–2462.

Devinny, J.S. & Volse, L.A. (1978) Effects of Sediments on the Development of Macrocystis pyrifera Gametophytes. Marine Biology, 348, 343–348.

Eckert, C.G., Samis, K.E. & Lougheed, S.C. (2008) Genetic variation across species' geographical ranges: the central-marginal hypothesis and beyond. Molecular ecology, 17, 1170–88.

Edwards, M.S. (2004) Estimating scale-dependency in disturbance impacts: El Ni¤os and giant kelp forests in the northeast Pacific. Oecologia, 138, 436–447.

Engledow, H.R. & Bolton, J.J. (1994) Seaweed Alpha-Diversity within the Lower Eulittoral Zone in Namibia - the Effects of Wave Action, Sand Inundation, Mussels and Limpets. Botanica Marina, 37, 267–276.

Foster, M. & Schiel, D. (1985) The ecology of giant kelp forests in California: A community profile. Biological report: United States Fish and WIldlife Service, 85.

Gaylord, B., Reed, D.C., Raimondi, P.T. & Washburn, L. (2006) Macroalgal spore dispersal in coastal environments: mechanistic insights revealed by theory and experiment. Ecological Monographs, 76, 481–502.

González-Wevar, C.A., Hüne, M., Cañete, J.I., Mansilla, A., Nakano, T. & Poulin, E. (2012) Towards a model of postglacial biogeography in shallow marine species along the Patagonian Province: lessons from the limpet Nacella magellanica (Gmelin, 1791). BMC evolutionary biology, 12, 139.

Graham, N.E., Ammann, C.M., Fleitmann, D., Cobb, K.M. & Luterbacher, J. (2010) Support for global climate reorganization during the "Medieval Climate Anomaly. Climate Dynamics, 37, 1217–1245.

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

Harrold, C. & Pearse, J.S. (1987) Echinoderm studies. (ed. by E. M. Jangoux and J. M. Lawrence), pp. 137–233. Rotterdam, the Netherlands.

Kamykowski, D. & Zentara, S.-J. (1986) Predicting plant nutrient concentrations from temperature and sigma-t in the upper kilometer of the world ocean. Deep Sea Research Part A. Oceanographic Research Papers, 33, 89–105.

Ladah, L. & Zertuche-González, J. (2007) Survival of microscopic stages of a perennial kelp (Macrocystis pyrifera) from the center and the southern extreme of its range in the Northern Hemisphere after exposure to simulated El Niño stress. Marine Biology, 152, 677–686.

Lawton, J.H. (1993) Range, population abundance and conservation. Trends in ecology & evolution, 8, 409–13.

Leigh, E.G., Paine, R.T., Quinn, J.F. & Suchanek, T.H. (1987) Wave energy and intertidal productivity. Proceedings of the National Academy of Sciences of the United States of America, 84, 1314–1318.

Levitan, D.R. & Petersen, C. (1995) Sperm limitation in the sea. Trends in Ecology & Evolution, 10, 228–231.

Lima, F.P. & Wethey, D.S. (2012) Three decades of high-resolution coastal sea surface temperatures reveal more than warming. Nature communications, 3, 704.

Matson, P.G. & Edwards, M.S. (2007) Effects of ocean temperature on the southern range limits of two understory kelps, Pterygophora californica and Eisenia arborea, at multiple life-stages. Marine Biology, 151, 1941–1949.

Mitrovica, J.X. (2003) Recent controversies in predicting post-glacial sea-level change. Quaternary Science Reviews, 22, 127–133.

Moritz, C., Patton, J.L., Conroy, C.J., Parra, J.L., White, G.C. & Beissinger, S.R. (2008) Impact of a century of climate change on small-mammal communities in Yosemite National Park, USA. Science, 322, 261–264.

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

Neiva, J., Pearson, G. a., Valero, M. & Serrão, E. a. (2012) Drifting fronds and drifting alleles: range dynamics, local dispersal and habitat isolation shape the population structure of the estuarine seaweed Fucus ceranoides. Journal of Biogeography, 39, 1167–1178.

Neushul, M. (1983) An overview of basic research on kelp and the kelp forest ecosystem. W Bascom. The Effects of Waste Disposal on Kelp Communities (ed. by Univ Calif Inst Mar Res), pp. 282–300. San Diego.

Nicastro, K.R., Zardi, G.I., Teixeira, S., Neiva, J., Serrão, E. a & Pearson, G. a (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.

Nichols, K.D. (2009) The Effects of Predators and Habitat on Sea Urchin Density and Behavior in Southern California Kelp Forests. Research Theses and Dissertations. University of San Diego.

Norton, T.A. (1978) The factors influencing the distribution of Saccorhiza polyschides in the region of Lough Ine. Journal of the Marine Biological Association of the United Kingdom, 58, 527–536.

Parmesan, C. (2006) Ecological and Evolutionary Responses to Recent Climate Change. Annual Review of Ecology, Evolution, and Systematics, 37, 637–669.

Pearson, R.G. & Dawson, T.P. (2003) Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? Global Ecology and Biogeography, 12, 361–371.

Peltier, W.R. (1994) Ice age paleotopography. Science, 265, 195–201.

Peterson, a. T. (2011) Ecological niche conservatism: a time-structured review of evidence. Journal of Biogeography, 38, 817–827.

Pujol, B. & Pannell, J.R. (2008) Reduced responses to selection after species range expansion. Science, 321, 96.

Pulliam, H.R. (2000) On the relationship between niche and distribution. Ecology Letters, 3, 349–361.

Reed, D.C., Rassweiler, A. & Arkema, K.K. (2008) Biomass rather than growth rate determines variation in net primary production by giant kelp. Ecology, 89, 2493–505.

Reed, D.C., Rassweiler, A., Carr, M.H., Cavanaugh, K.C., Malone, D.P. & Siegel, D. a (2011) Wave disturbance overwhelms top-down and bottom-up control of primary production in California kelp forests. Ecology, 92, 2108–16.

Root, T.L., Price, J.T., Hall, K.R., Schneider, S.H., Rosenzweig, C. & Pounds, J.A. (2003) Fingerprints of global warming on wild animals and plants. Nature, 421, 57–60.

Serrão, E., Kautsky, L. & Brawley, S. (1996) Distributional success of the marine seaweed Fucus vesiculosus L. in the brackish Baltic Sea correlates with osmotic capabilities of Baltic gametes. Oecologia, 107, 1-12.

Serrão, E.E.A. & Havenhand, J. (2009) Fertilization strategies. in: Wahl M (ed.) Marine Hard Bottom Communities. Ecological Studies 206, Springer Verlag.

Siegel, D., Kinlan, B., Gaylord, B. & Gaines, S. (2003) Lagrangian descriptions of marine larval dispersion. Marine Ecology Progress Series, 260, 83–96.

Svenning, J.-C., Fløjgaard, C., Marske, K. a., Nógues-Bravo, D. & Normand, S. (2011) Applications of species distribution modeling to paleobiology. Quaternary Science Reviews, 30, 2930–2947.

Tegner, M.J., Dayton, P.K., Edwards, P.B. & Riser, K.L. (1997) Large-scale, low-frequency oceanographic effects on kelp forest succession:a tale of two cohorts. Marine Ecology Progress Series, 146, 117–134.

Wahl, M., Jormalainen, V., Eriksson, B.K., Coyer, J. a, Molis, M., Schubert, H., Dethier, M., Karez, R., Kruse, I., Lenz, M., Pearson, G., Rohde, S., Wikström, S.A. & Olsen, J.L. (2011) Stress ecology in fucus: abiotic, biotic and genetic interactions. Advances in Marine Biology, 59, 37-105.

Walther, G.-R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T.J.C., Fromentin, J.-M., Hoegh-Guldberg, O. & Bairlein, F. (2002) Ecological responses to recent climate change. Nature, 416, 389–395.

Young, A., Boyle, T. & Brown, T. (1996) The population genetic consequences of habitat fragmentation for plants. Trends in Ecology & Evolution, 11, 413–418.

Yund, P.P.O. (2000) How severe is sperm limitation in natural populations of marine free-spawners? Trends in ecology & evolution, 15, 10–13.